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# How increasing levels of private land enrollment in conservation agreements affect the population viability of grassland birds

**Alison B. Seigel · Julie L. Lockwood**

**Abstract**  There is a growing recognition that to effectively conserve biodiversity efforts have to extend into the realm of engaging private landowners. Agricultural lands have been particularly attractive targets for integrating conservation and production goals. Changes in hayfield management associated with agricultural intensification, including earlier and more frequent harvests, have a severe impact on grassland birds. Government-administered conservation incentive programs benefit grassland birds by delaying harvest dates on enrolled land to allow nesting pairs to successfully fledge at least one brood during the breeding season. In contrast, hayfields that are mowed during the breeding season support sink populations and may function as ecological traps. We examined the effect of increasing levels of hayfield enrollment on grasshopper sparrow population viability using a spatially-explicit, stage-structured, stochastic model of a grasshopper sparrow meta-population in an urbanizing region of New Jersey. The probability of metapopulation extinction (POE) decreased as the proportion of enrolled hayfields increased and fell below 10% when about half of all available agricultural land was enrolled. POE also decreased with increasing numbers of enrolled hayfields most likely because hayfield enrollment removes a sink population from the landscape in addition to creating a source population. Our results are encouraging as they demonstrate that extinction risk for this grassland-dependent imperiled species can be reduced without having to protect or manage all remaining grassland habitat in the landscape.

**Keywords**  *Ammodramus savannarum* · Conservation incentive programs · Grasshopper sparrow · Grassland birds · Grassland management · Metapopulation · Population viability analysis

A. B. Seigel · J. L. Lockwood (✉)
Department of Ecology, Evolution and Natural Resources, Rutgers University,
14 College Farm Road, New Brunswick, NJ 08901, USA
e-mail: lockwood@aesop.rutgers.edu

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## Introduction

The need to consider the conservation of biodiversity through the lens of private land ownership is critical because private lands house a large number of imperiled species (Knight 1999; Robles et al. 2008) and dominate land uses in many countries (Mattison and Norris 2005). Agricultural lands have been particularly attractive targets for integrating conservation and production goals (Pejchar and Press 2006; Mattison and Norris 2005; Van Buskirk and Willi 2004). The loss of agricultural landscapes via residential and industrial development can be rapid and thus citizens see these lands as opportunities to preserve open space (Ernst and Wallace 2008). In addition, governments and conservation organizations have found a receptive audience in farmers that would like to de-intensify their production practices and instead adopt biodiversity friendly management in exchange for payments (Kabii and Horwitz 2006). The effectiveness of these land enrollment programs has recently been evaluated in terms of their ability to support a diverse set of species (e.g., Van Buskirk and Willi 2004). However, there are far fewer studies that view effectiveness through the lens of metapopulation ecology, thereby recognizing that each enrolled farm may serve as a subpopulation for a threatened or endangered species (Perlut et al. 2008a). From this perspective, effectiveness is a product of the number of farms enrolled in a region, the proximity of these farms relative to one another, and the biological impact of the farms that are not enrolled. Here we explore these issues within the context of the conservation of North American grassland birds, however the methods we develop and the conclusions we draw should be applicable to any private land set-aside program.

For several decades North American grassland birds have been experiencing continental-scale population declines so consistent that they constitute a conservation crisis (Peterjohn and Sauer 1999; Brennan and Kuvlesky 2005; Sauer et al. 2008). A variety of factors have contributed to these declines including habitat loss and fragmentation, brood parasitism, and reforestation (Peterjohn and Sauer 1999; Norment 2002). Because most native grassland habitat in North America has been converted to farmland, many grassland bird species have become highly dependent upon agricultural grasslands (hayfields) for breeding habitat throughout their ranges. Consequently, changes in hayfield management associated with agricultural intensification have a particularly severe impact on these grassland birds (Bollinger et al. 1990; Murphy 2003; Perlut et al. 2006; Askins et al. 2007). Farmers are harvesting hay earlier and more frequently during the breeding cycle of grassland birds causing a reduction in productivity and survival (Bollinger et al. 1990; Troy et al. 2005; Perlut et al. 2006, 2008b). Hayfields undergoing such intensified management function as ecological traps for grassland birds because they appear to be suitable, high quality nesting habitat at the onset of the breeding season despite acting as population sinks during the breeding season (Gates and Gysel 1978; Kershner and Bollinger 1996; Perlut et al. 2006).

The United States Department of Agriculture (USDA) administers several voluntary private land enrollment programs that offer financial incentives to convert environmentally sensitive cropland to hayfield. Enrollment conditions typically call for delayed mowing of the hayfields such that grassland birds can successfully fledge their first, or sometimes their only, broods for the year. Thus, these enrollment programs provide conservation benefits while also providing the farmer with a commercially viable product. The Conservation Reserve Program (CRP) is the largest of the private lands conservation programs in the United States with over 11 million ha enrolled in various types of grassland in 2007 (Barbarika 2007). Landowners typically enroll for 10–15 years and receive annual rental

payments based on the value of the land and cost-share assistance to establish approved conservation practices. The Wildlife Habitat Incentive Program (WHIP) promotes the creation of high quality wildlife habitat by offering technical assistance and up to 75% cost-share to landowners to establish and improve wildlife habitat during a 5–10 year contract.

In New Jersey, landowner incentive programs play a vital role in the grassland bird conservation effort. New Jersey is one of the most rapidly urbanizing states in the country. Over 6,000 ha of open space were converted to urban development annually between 1995 and 2002, increasing the total proportion of urbanized land in the state to 30% by the end of this period. During that time, agricultural land experienced greater losses than any other land use (22,000 ha), and more specifically, grasslands/hayfields were impacted most severely with an almost 5% reduction in total area (Hasse and Lathrop 2008). This trend has made the remaining parcels essential to the future success of grassland bird conservation in the state.

The Central Piedmont Plains (CP Plains), a sub-section of the 20–30 mile belt of piedmont plains running through the center of New Jersey, contains some of the most extensive agricultural complexes left in the state. There are 36,000 ha of agricultural land, including hayfields, in this region providing critical breeding habitat for the state's threatened and endangered grassland birds. Management of the remaining grasslands however, may be equally as important as their presence. Hayfields that persist in the landscape, but where early mowing still takes place, may be detrimental to the persistence of grassland bird populations if they are functioning as ecological traps. In this case, it is necessary to document the effectiveness of conservation incentive programs within a metapopulation context because all hayfields are not created equal in terms of their benefit to grassland bird population persistence.

Using the population viability analysis software, RAMAS GIS, we developed a spatially-explicit, stage-structured, stochastic model of the grasshopper sparrow (*Ammodramus savannarum*) metapopulation in the Central Piedmont Plains of New Jersey. We used the grasshopper sparrow as a model species because it is a ground-nesting, grassland obligate that breeds from 20 May through 30 July (Vickery 1996). Between 1966 and 2007 the grasshopper sparrow experienced a range-wide population decline of 3.54% per year (Sauer et al. 2008). A considerably higher rate of decline, 15.8%, occurred within the state of New Jersey where it is listed as threatened. Thus, the persistence of the grasshopper sparrow is a good indicator of how successful New Jersey and similarly urbanizing landscapes are in utilizing private land incentive programs in sustaining threatened species.

## Methods

### Metapopulation spatial structure

To build our metapopulation, we imported the New Jersey Landscape Project grassland layer into the Spatial Data program of RAMAS GIS. This remotely sensed dataset contained 11,700 ha of agricultural 'grasslands' within our study area representing 126 patches ranging in size from 11 to 2,209 ha (Fig. 1). Some of these 126 patches lie very close to one another and thus could be considered the same subpopulation within the full
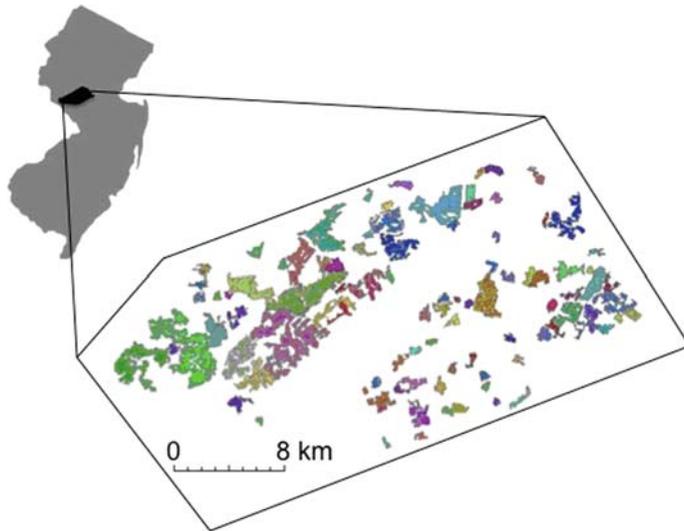
**Fig. 1** Map of New Jersey Central Piedmont Plains grasshopper metapopulation. Metapopulation patches were delineated using New Jersey Landscape Project grassland habitat maps, designation of habitat suitability thresholds, and a 40 m neighborhood distance. There are 96 patches totaling 4,694 ha of suitable hayfield habitat

grasshopper sparrow metapopulation. Thus we used the Spatial Data program to clump close patches into one subpopulation. This program merges two or more patches if they are separated by a distance less than or equal to a user-specified neighborhood distance. We chose a neighborhood distance of 40 m based on our knowledge of grasshopper sparrow site fidelity and on-the-ground surveys of hayfields. We found that marked sparrows (see below for details on mark-recapture efforts) were unlikely to move across roads and other unsuitable habitat (e.g., forest) once they established breeding territories, thus perceiving those habitats as patch boundaries. After exploring a range of neighborhood distances and the resulting patch configuration, we determined that 40 m best approximated the patch configuration as would be perceived by the sparrows. After the Spatial Data program identified the patch structure of the metapopulation, we removed any resultant patches smaller than 10 ha. Minimum area requirements for grasshopper sparrows vary substantially by region (Herkert 1994; Vickery et al. 1994; Johnson and Igl 2001) and we found this value to be a conservative minimum based on our observations of hayfields in the CP plains. Our final estimate of total metapopulation extent was 4,694 ha, which included 96 subpopulations (hayfield patches). Mean grassland area per patch was 66.1 ha (SE = 17) and mean distance between patches was 11.3 km (SE = 0.1).

From on-the-ground surveys of these patches, we found that they frequently contained a mosaic of cropland, pasture, and hayfield. Grasshopper sparrows do not breed in cropland or horse pasture. We visited each of the 96 patches in the fall of 2007, and visually estimated the proportion of each that were currently suitable for sparrow breeding (i.e. hayfields). We reduced the carrying capacity of each patch based on the observed proportion of each patch that was determined to be hayfield.

Model input

*Stage matrix*

We modeled grasshopper sparrow population dynamics within each patch using a stage-structured, stochastic (Leslie) matrix model with juvenile and adult stages. We considered birds to be juveniles from the time they fledged through the end of their first breeding season. The matrix was built under the following assumptions: (1) all reproduction occurred in a relatively short breeding season ("birth-pulse"), (2) the population was censused directly after each breeding season, (3) there was no mortality between the onset of breeding and the census, (4) the maternity rate (number of offspring per breeder) is the same for returning juveniles and adults, (5) vital rates are the same for all adults regardless of age. Thus, our general stage matrix took the following form,

$$
\begin{array}{cc}
S_j \cdot M & S_a \cdot M \\
S_j & S_a
\end{array}
$$

where $S_j$ is the survival rate of juveniles; $S_a$ is the survival rate of adults; and $M$ is maternity or the number of total offspring per breeder. In the top row, $S_j \cdot M$ is the returning juvenile fecundity and $S_a \cdot M$ is adult fecundity. We built two stage matrices to simulate population dynamics within hayfield patches that were mowed mid-breeding season (Mow stage matrix) and patches that were mowed after the breeding season had concluded (No Mow stage matrix) (Table 1). We estimated survival and maternity rates based on data we collected within a 70 ha field in the CP Plains study area (Skeet Shoot Field) that was not mowed until after the breeding season, and from published sources (McCoy et al. 1999; Jones 2000; Gill et al. 2006).

The maternity estimate in the No Mow stage matrix was derived by averaging the maternity estimate from our field observation at Skeet Shoot Field with three published values of grasshopper sparrow maternity taken within fields that were not mowed during the breeding season (McCoy et al. 1999; Jones 2000). Using the Mayfield Method for determining nest success, we calculated 84% overall nest success based on our observations from Skeet Shoot Field ($n = 16$, SE = 0.16; Mayfield 1975; White and Burnham

**Table 1** Mean and standard deviation of stage matrix parameters used to model the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation

| Matrix | $M$ | $S_a$ | $S_j$ | $F_a$ | $F_j$ |
|---|---|---|---|---|---|
| No Mow | | | | | |
| Mean | 2.41 | 0.64 | 0.32 | 1.54 | 0.77 |
| SD | 0.44 | 0.12 | 0.06 | 0.88 | 0.39 |
| Mow | | | | | |
| Mean | 0.92 | 0.50 | 0.25 | 0.46 | 0.23 |
| SD | 0.17 | 0.094 | 0.047 | 0.12 | 0.05 |

Matrix elements were derived from a combination of direct observations in New Jersey and published values. See text for details. Maternity ($M$), adult survival ($S_a$), juvenile survival ($S_j$), adult fecundity ($F_a = M \cdot S_a$), and juvenile fecundity ($F_j = M \cdot S_j$)

1999; Rotella et al. 2004). This value was higher than other published estimates, which ranged from 41% (McCoy et al. 1999) to 62% (Jones 2000). We observed an average of two broods per season, which is in agreement with other published observations (Vickery 1996). Finally, we observed an average of 3.71 young per successful clutch (SE = 0.7), with published estimates ranging from 3.78 (SE = 0.09) (McCoy et al. 1999) to 4.37 (SE = 0.13) (Wray et al. 1982). Following the method used in Donovan et al. (1995) and McCoy et al. (1999), we combined the average number of broods per season, nest survival rates, and average number of young per successful clutch to produce a maternity value of 3.35 (SE = 0.55). Published estimates of grasshopper sparrow maternity within no-mow fields using the same, or very similar methods, ranged from 1.66 (SE = 0.08) (Jones 2000) to 2.61 (SE = 0.36) (McCoy et al. 1999). In our model, we used a maternity value of 2.41, which we derived by averaging three published estimates of maternity with our maternity estimate from Skeet Field (McCoy et al. 1999; Jones 2000) (Table 1).

We calculated the survival rate of grasshopper sparrows in the No Mow stage matrix using both our field observations from Skeet Shoot Field and from published literature (Jones 2000; Gill et al. 2006). During two breeding seasons (2005–2006) we captured adult male sparrows in mist nets using song playbacks in known territories. We fitted each individual with a unique combination of color bands and an aluminum band issued by the US Fish and Wildlife Service. In 2006 and 2007 we re-sighted any banded individuals that returned to Skeet Shoot Field. Based on 3 years of banding-resight data, we calculated male adult survivorship as 0.58 (SE = 0.14) using standard Cormack–Jolly–Seber models within program MARK (White and Burnham 1999). Published survival estimates for grasshopper sparrows produced using similar methodologies range from 0.56 (SE = 0.09) (Gill et al. 2006) to 0.77 (SE = 0.07) (Jones 2000). After combining our field-derived estimate with these published estimates, our average estimate for adult survival in the model is 0.64 (Table 1). We could not calculate juvenile survival using our field data because too few juveniles were banded and re-sighted. The difficulty in directly estimating juvenile survival within passerines is well known, and thus our review of published literature resulted in no other estimates of juvenile survival of grasshopper sparrows. We thus set juvenile survival as half that of adults (Table 1; Donovan et al. 1995; McCoy et al. 1999).

To construct our Mow stage matrix, we decreased the grasshopper sparrow adult and juvenile maternity estimates used in our No Mow stage matrix by 62% to simulate the effects of mid-breeding season mowing (Table 1). Perlut et al. (2006) found that in Vermont hayfields that were mowed early in the breeding season (between 27 May and 11 June), and then mowed a second time in early to mid-July, savannah sparrow (*Passerculus sandwichensis*) fecundity was 62% lower than within fields mowed only once in the late-breeding season. We could not find similar information for grasshopper sparrows, however, both savannah and grasshopper sparrows typically produce two broods of similar clutch sizes during a breeding season and share other life history traits (Wheelwright et al. 1992; Wheelwright and Rising 1993; Vickery 1996). Because the savannah sparrow's breeding season extends 2 weeks later into August than the grasshopper sparrow's breeding season, savannah sparrows likely have a better chance for successful re-nesting after mowing. Consequently, we believe a reduction of 62% in grasshopper sparrow maternity due to mowing during the breeding season is a conservative estimate of the negative impact mowing has on their fecundity.

Using the same study system as their previous publication, Perlut et al. (2008b) found that hayfield mowing regimes also influenced survival rates of adult savannah sparrows. Survival rates of breeding adults were 22% lower in hayfields mowed once early in the breeding season and once mid-breeding season than in hayfields mowed late in the

breeding season. Based on the findings of this study, we reduced adult grasshopper sparrow survival in our Mow stage matrix by 22%.

## Density dependence

We assigned the ceiling-type density dependence to all subpopulations with the carrying capacity serving as the ceiling. Thus, populations fluctuate according to the stage matrix and its variation. If the population rises above the ceiling then it is brought down to the carrying capacity within the next time step.

## Carrying capacity

We based carrying capacity on the area (ha) of hayfield present in each patch. We used 2 ha as a reasonable and conservative estimate of grasshopper sparrow territory size, making carrying capacity equal to the number of 2 ha territories that could be packed into the hayfield in each patch (Vickery 1996).

## Environmental and demographic stochasticity

For each of the two stage matrices, we built a standard deviation matrix based on the average interannual variation in fecundities and survival rates caused by environmental changes (Table 2). We obtained standard deviation estimates for each matrix element by combining our observed variance estimates of maternity and survival generated from program MARK with the variance estimates derived within chosen published sources (see above) using the delta method (Akcakaya and Raphael 1998). To model the effects of interannual environmental variation on the vital rates for each population, we sampled fecundity and survival rates from random, lognormal distributions of the means in the stage matrix and the standard deviations in a standard deviation matrix. We also incorporated demographic stochasticity into the model by drawing the number of survivors at each time step from a binomial distribution and the number of offspring from a Poisson distribution (Akcakaya 1991).

## Correlation-distance function

The correlation of environmental variation experienced by populations within a meta-population is inversely related to the distance between them (LaHaye et al. 1994). RAMAS

**Table 2** Elasticity analysis results for the Mow and No Mow stage matrices associated with our grasshopper sparrow metapopulation

|  | Mow stage matrix | No Mow stage matrix |
|---|---|---|
| Juvenile fecundity | 0.0993 | 0.2982 |
| Adult fecundity | 0.2158 | 0.2479 |
| Juvenile survival | 0.2158 | 0.2479 |
| Adult survival | 0.4691 | 0.2060 |

Elasticities are relative measures of the contribution that each matrix element makes toward $\lambda$, the finite rate of population increase

GIS allowed us to specify correlations among growth rates of populations through a correlation-distance function, $C = \exp(-D/b)$, where $C$ is the coefficient of correlation between the vital rates of two populations, $D$ is the distance between the two populations, and $b$ describes the rate at which correlation declines with increasing distance between populations. In our study area, the maximum distance between two populations was 38 km, which is a relatively short distance in terms of the spatial autocorrelation of environmental conditions. We detected high spatial autocorrelation of historical monthly rainfall amounts for June (National Weather Service 2008). Consequently, we used a high value of $b$ (100) to simulate relatively high correlation of environmental variation among patches (LaHaye et al. 1994; Akcakaya and Atwood 1997). We ran metapopulation simulations with lower values of $b$ to determine how sensitive the model was to the correlation-distance function. Lower values of $b$ had little effect on simulation outcomes so we report only on simulations with $b = 100$.

*Dispersal*

Dispersal refers to individuals moving from one population to breed within another and tends to occur at a higher rate between populations that are geographically close (Wolfenbarger 1949; Hill et al. 1996). We used a dispersal-distance function that defined dispersal rates as a function of the distance between populations with the maximum dispersal distance being greater than the maximum distance between patches in our study area. Dispersal rate of grasshopper sparrows was also a function of age. Adults exhibit high site fidelity among years while almost all juveniles disperse, thus we defined adult dispersal rate as only 10% of the juvenile dispersal rate (Jones 2000). Although grasshopper sparrows appear to be highly breeding-site fidelic (Jones 2000), birds can move great distances between or within breeding seasons. To determine the sensitivity of probability of metapopulation extinction to the dispersal-distance function, we ran simulations in which we increased and decreased dispersal rates by 10%. These changes in dispersal rates did not lead to a significant change in POE and thus all results are presented using our original dispersal function, $y = 0.2 \cdot \exp(-x/10)$.

Modeling hayfield enrollment scenarios

To determine how increasing the amount of hayfield enrolled in no-mow management affects sparrow metapopulation viability, we simulated the CP Plains grasshopper sparrow metapopulation under five hayfield enrollment percentages. We labeled these as enrollment categories 1–5 where 1 = 7–12% of all hayfield in our study area enrolled in no-mow management, 2 = 19–24%, 3 = 31–36%, 4 = 43–48%, and 5 = 55–60%. Within each enrollment category, we ran 10 simulations. For each simulation, we randomly chose patches in the study area to be enrolled in no-mow management until we reached the desired proportion of enrolled hayfield. We assigned the No Mow stage matrix to each of the enrolled patches and the Mow stage matrix to the remaining patches. While total area of hayfield enrolled remained constant within each enrollment category, the number of hayfield patches enrolled varied. We set the total initial abundance of sparrows in the metapopulation at one-half carrying capacity (2,704 individuals). However, we spread these individuals between patches in a random fashion so that initial abundance of sparrows in each patch fell somewhere between 50 and 100% of that patch's carrying capacity.

These starting conditions did not vary across simulations. Each simulation projected metapopulation abundance and extinction risk at yearly increments for 50 years and was replicated 1,000 times. We used a quasi-extinction threshold of 100 individuals. We calculated the finite rate of increase ($\lambda$) and elasticities for each stage matrix.

We ran model simulations under the following assumptions: (1) habitat quality was equal among enrolled hayfields and equal among non-enrolled hayfields, (2) the enrollment status (enrolled or non-enrolled) of a hayfield did not change at any time during the 50 year simulation period, (3) the composition of the surrounding matrix did not change during the 50 year simulation period, and (4) the matrix consisted of only one habitat type and that habitat was unsuitable for grasshopper sparrow breeding.

Modeling ecological sink removal scenarios

In our simulations above, even at high percentages of hayfield enrollment, mowed fields persist in the landscape. We wanted to determine the effect of the continued presence of these sink populations on grasshopper sparrow metapopulation persistence. Thus, we randomly selected 1 simulation out of the 10 from each enrollment category above and re-ran it with 10, 25, and 40% of the unenrolled mowed hayfield area removed from the landscape. Prior to running each simulation, we randomly deleted sink (i.e. mowed hayfield patches) from the landscape until the amount of area deleted reached the desired proportion (10, 25, or 40%). Deleting these unenrolled patches effectively removed sink habitat from the landscape while leaving the amount of enrolled source habitat intact. All other parameters in each simulation remained the same.

## Results

The finite rate of increase ($\lambda$) for the Mow stage matrix was 0.73, thus indicating a steadily declining metapopulation. Elasticity analysis indicated that survival rate of adults made the largest contribution to $\lambda$ (Table 2). Lambda for the No Mow stage matrix was 1.41 indicating a rapidly expanding metapopulation, with returning juvenile fecundity having the largest elasticity (Table 2).

Using these values as the basis for evaluating the effects of enrolling larger percentages of land in grassland conservation programs, we evaluated the effect of increasing enrollment on probability of metapopulation extinction. The probability of extinction (POE) decreased with increasing proportion of hayfield enrolled in no-mow management (Fig. 2). However, there was an apparent threshold at enrollment category 4 (i.e. 43–48% of all lands enrolled) after which POE decreased considerably (Fig. 2).

Probability of metapopulation extinction also decreased with increasing numbers of patches enrolled in no-mow management (Fig. 3). This relationship was not solely due to the fact that, within enrollment categories, simulations with a larger proportion of enrolled hayfield area also generally had a larger number of enrolled patches. Rather, number of enrolled patches had an independent effect on probability of extinction. To illustrate this point we ran three additional simulations. In the first simulation, we kept the total area of enrolled hayfield low (falling within category 1), but we enrolled as many hayfield patches as possible in no-mow management. This effort effectively removed the positive relationship between number of enrolled patches and total area enrolled. The POE for this

Fig. 2 Probability of extinction of the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation under five hayfield enrollment scenarios: 1 7–12% of total hayfield area enrolled, 2 19–24% enrolled, 3 31–36% enrolled, 4 43–48% enrolled, and 5 55–60% enrolled
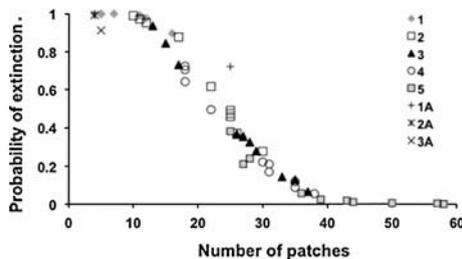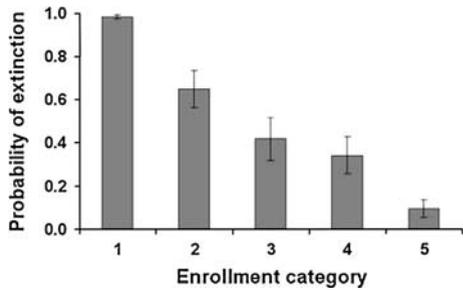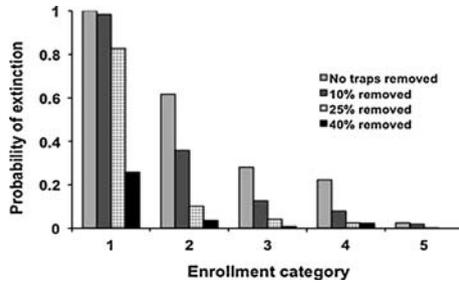


Fig. 3 Probability of extinction as a function of number of hayfield patches enrolled in no-mow management for a total of 53 simulations of the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation. Ten simulations were run in each of five hayfield enrollment categories 1–5. The simulation where we minimized the number of grassland patches (subpopulations) enrolled within enrollment category 1 is represented by 1A. Simulations where we maximized the number of grassland patches (subpopulations) enrolled within categories 3 and 4 are represented by 2A and 3A, respectively

simulation was low relative to the other simulations in this category, and was only slightly higher than the POE for simulations with the same number of patches but in higher enrollment categories (Fig. 3). In the second and third simulations we produced the opposite effect by enrolling the fewest patches possible in no-mow management while keeping the percent enrollment relatively higher (falling within enrollment categories 3 and 4). The probabilities of extinction associated with these simulations were high despite their being within the higher enrollment categories (Fig. 3), and indeed were similar to those of simulations in the lower enrollment categories. These additional simulations illustrated the distinct and inverse relationship between number of patches enrolled in delayed mowing management and probability of extinction.

Ecological sink removal

Finally, we were interested in the effect on probability of metapopulation extinction of the mowed hayfields that persist in the landscape after the enrollment percentage was met. Within each enrollment category, probability of extinction of the CP Plains grasshopper sparrow metapopulation decreased as more ecological sink habitat (mowed hayfield) was deleted from the landscape (Fig. 4). The effect of deleting sink habitat was highest in the lowest percentage enrollment categories, with decreasing influence as enrollment percentages increased. At the category 5 enrollment (55–60%), the deletion of sink habitat essentially had no effect on POE.

**Fig. 4** Probability of extinction of the grasshopper sparrow metapopulation in response to three scenarios of ecological trap habitat removal: 10% of trap area removed, 25% removed, and 40% removed (original simulations from Fig. 3). Trap removal scenarios were simulated separately within each enrollment category

## Conclusion

Our results clearly indicate a positive effect on grasshopper sparrow metapopulation persistence achieved by enrolling grassland in a delayed mowing management program. Probability of extinction decreased 58% when moderate levels of farmland enrollment are achieved (category 3, 31–36%) and was reduced to less than 10% at our highest enrollment (category 5, 55–60%). Where conservation funds are limited and landowners are not always willing to participate in set-aside programs, this relationship is encouraging as it demonstrates that extinction risk can be substantially reduced without having to protect or manage all or even most remaining grassland habitat in the landscape.

Grasshopper sparrow metapopulation persistence was not strictly a function of the total amount of land enrolled as we also found an inverse relationship between the number of patches enrolled and probability of extinction. This relationship became particularly evident when we ran an additional simulation within enrollment category 4 (43–48% of hayfield enrolled) that contained the lowest possible number of enrolled patches. Reducing the number of patches enrolled from an average of 28 down to 5, lead to a marked increase in POE from 8 to 91%. This relationship is a result of the non-enrolled hayfields acting as "equal-preference" ecological traps (Robertson and Hutto 2006). Sparrow population growth ($\lambda$) for non-enrolled hayfields is less than one (therefore functioning as a sink) and our model assumes that all hayfields (enrolled or non-enrolled) appear equally suitable to grasshopper sparrows when they are selecting breeding sites. Thus, sparrows are choosing to nest in hayfields that are sinks. Hayfield enrollment not only creates a source population, but it also simultaneously removes a sink population from the metapopulation resulting in an increase in population persistence.

However, we found that an increase in enrolled hayfield area is not always necessary to increase grasshopper sparrow persistence. Un-enrolled hayfields that persists in the landscape after a target percentage of overall enrollment is met tends to suppress the positive response of the entire metapopulation to conversion of some patches into sources. This result stems from sink habitat functioning as traps, and thus as we removed more sink/trap patches from the landscape, the probability of extinction decreased. This effect diminished with increasing enrollment, as POE remained consistently low in the higher enrollment categories even when relatively large numbers of sink/trap patches were removed. In addition, we found that the threshold of persistence was reduced by 36% when a third or more of the traps were removed. These trends suggest that metapopulation persistence can be achieved at a lower level of enrollment if non-enrolled, trap hayfields are removed from

the landscape. Put another way, our results suggest that conservationists can get more 'biological bang for their buck' by enrolling a smaller percentage of the total hayfield in a landscape while also removing non-enrolled hayfields, which function as ecological traps.

One explanation for this result is related to juvenile dispersal. Juveniles disperse to both source and sink patches, as both types of patches are equally attractive at the onset of the breeding season. The greater the proportion of sink/trap habitat in the landscape, the greater the probability that a dispersing juvenile will select a sink/trap opposed to a source. By definition, individuals in sink/trap habitat do not contribute to future population abundance. However, as sink habitat is removed from the landscape, there is a greater probability that a dispersing juvenile will select a source patch. These individuals, if they establish a territory, make a greater reproductive contribution to the population than individuals in sink patches. In addition, even if they do not establish a territory and reproduce, they will have a higher probability of survival in the enrolled patch and thus may live to breed in a subsequent year. This effect is particularly pronounced under conditions where source patches are below their carrying capacity, as evinced by the higher effect of removing sink habitat within our simulations with low overall hayfield enrollment.

One way in which a sink/trap hayfield can be removed from the landscape is to convert it to a non-hayfield land use, such as cropland or housing. It would be premature, however, to construe these results as justification for widespread land conversions of non-enrolled hayfields. Our model did not account for edge effects, which may vary according to the land use of adjacent patches and species composition of the predator community in the area (Johnson and Temple 1990; Ribic et al. 2009). If edge effects do exist in our study area, then our model underestimated the amount of enrolled hayfield necessary to achieve grasshopper sparrow metapopulation persistence as maternity and/or survival rates may be lower in smaller hayfields. Further, in a dynamic landscape such as the agricultural-urban one we modeled, it is essential to have a 'hayfield reserve' from which fields can be enrolled in the event that additional grassland bird habitat is necessary to maintain a metapopulation.

Our results demonstrate the importance to grassland bird population persistence of removing or minimizing ecological trap habitat and the need to create a means of doing so that does not involve development. Perlut et al. (2006) found that early-hayed (mid-June) fields were functioning as ecological traps in a savannah sparrow metapopulation as first-time breeders and immigrants disproportionately selected these fields over late-hayed fields as breeding habitat. The authors suggested that early-hayed fields have a unique physical appearance in the spring due to fall mowing and novice breeders may perceive this appearance as indicative of high quality habitat. If this holds true for grasshopper sparrows as well, perhaps individuals would be discouraged from selecting trap habitat for breeding if there were a "pre-season" mow in mid to late April before the traditional first harvest that usually occurs in late May and early June. Changing the physical structure of hayfields through mowing just prior to the arrival of grasshopper sparrows may affect their breeding site selection. Arrival and first egg dates of other grassland bird species in the region should be considered when planning a pre-season mowing date. We do not know if this type of management would discourage birds from nesting in hayfields which function as ecological traps, however, research exploring this and other potential ways to minimize the attractiveness of hayfields acting as population sinks will prove very beneficial to grassland bird conservation.

Of course all conclusions from models are dependent on the assumptions made. Our model is relatively insensitive to dispersal distances and degree of environmental

stochasticity, but this is likely a consequence of modeling a relatively small spatial extent. Thus our results may not hold when considering metapopulations that function over a larger spatial scale. Our model is, however, very sensitive to adult survival (mowed fields) and returning juvenile maternity (un-mowed fields) rates. This result emphasizes the need to collect data on survival and maternity rates for grasshopper sparrow populations that exist in mowed hayfields to increase the predictive accuracy of our metapopulation model. This point is particularly relevant since we had to rely on information from a surrogate species to estimate the effects of early-season mowing on grasshopper sparrow survival and fecundity. It is unknown to what extent the effects of early-mowing on grassland bird survival and fecundity are species- or region-specific and thus it is difficult to estimate the extent to which our results are biased. However, there is no doubt that models such as ours would benefit greatly from the direct study of how grasshopper sparrows respond to different hayfield mowing regimes.

The vital rates used in a population model will inevitably affect the outcome. In our case, higher survival and fecundity would lead to a lower risk of extinction. Our field work-based estimate of nest success was higher than the range of estimates we found in the literature. However, we found very little evidence of nest predation in a follow up study of nest success that used artificial nests within our study area. We believe this relatively high rate of nest success is due to the degraded condition of adjacent forest patches supporting few predators.

Finally, we modeled the New Jersey Central Piedmont Plains as a static landscape in terms of management; enrolled patches remained so throughout the 50-year time interval of our projections, and non-enrolled hayfields consistently functioned as ecological traps. In reality, however, agricultural landscapes are quite dynamic and thus the manner in which hayfields are managed very likely changes through time (Perlut et al. 2006). For example, we have noticed that several non-enrolled hayfields are not mowed until late June or July because of other on-farm logistics that take priority over mowing. As a result, those non-enrolled hayfields likely function as source habitat in some years and traps in other years. Incorporating this temporal variability in hayfield quality into a model such as ours would be a worthwhile next step. It may also be interesting to incorporate the preference of first-time breeders and immigrants for early-hayed fields as was documented for savannah sparrows by Perlut et al. (2008b) as it is closely tied to the temporal variability in hayfield quality.

Private landowner incentive programs are a key component in the conservation of grassland birds in North America and our model provides a practical and adaptable way to assess the relative effects of management scenarios on grassland bird metapopulation persistence. We were able to determine which parameters were most influential on sub-population dynamics and therefore warrant more study in the field. We also found our model to be extremely useful in generating new hypotheses to be tested in the field or in another model. Our next goal is to consider explicitly the spatial configuration of the enrolled hayfields on metapopulation persistence.

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