MAXIMIZING THE EFFECTIVENESS OF GRASSLAND MANAGEMENT FOR A GRASSHOPPER SPARROW (*AMMODRAMUS SAVANNARUM*) METAPOPULATION

By

ALISON B. SEIGEL

A Dissertation submitted to the

Graduate School-New Brunswick

Rutgers, The State University of New Jersey

in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

Graduate Program in Ecology and Evolution

written under the direction of

Dr. Julie L. Lockwood

and approved by

____

____

____

____

New Brunswick, New Jersey

May 2009

ABSTRACT OF THE DISSERTATION

Maximizing the effectiveness of grassland management for a grasshopper sparrow (*Ammodramus savannarum*) metapopulation

by ALISON B. SEIGEL

Dissertation Director: Dr. Julie L. Lockwood

Grassland bird population declines have been attributed to habitat loss and fragmentation and the intensification of agricultural practices. Hayfields are being cut earlier and more frequently during the breeding season resulting in low reproductive success. Grassland bird conservation efforts generally focus on enrolling farmland into landowner incentive programs that require mowing to be delayed until after July 15. Delayed mowing improves grassland bird reproductive success by enabling breeding pairs to fledge at least one brood during the breeding season. This dissertation examines the effect of hayfield management on population viability of a grasshopper sparrow metapopulation in a fragmented landscape in New Jersey and uses statistical power analysis to assess the cost-effectiveness of grasshopper sparrow metapopulation monitoring programs.

I built a spatially-explicit, stage-structured, stochastic model of a grasshopper sparrow metapopulation to determine how probability of extinction (POE) is affected by: (1) total hayfield area enrolled, (2) size of enrolled hayfields, (3) number of hayfield patches enrolled, and (4) isolation of enrolled hayfields. I found that POE decreased quickly with increasing amounts of enrolled hayfield area. After 31 to 48% of hayfield area in the landscape was enrolled, POE decreased minimally with further enrollment. The number of grassland parcels enrolled was also negatively related to POE. When I incorporated a patch size effect (fecundity was directly related to hayfield size) into the model, POE increased within each enrollment category but still decreased with increasing amounts of enrolled grassland (Chapter 2). POE was directly related to the degree of isolation of enrolled hayfields.

Of the monitoring programs we evaluated, the most cost-effective program to detect a 7% population decline included 18 hayfields surveyed six times annually over five years. Additional survey effort would be necessary to detect a smaller population decline and to overcome observer variability in density estimates due to sampling error.

Hayfield management for grassland birds will be most effective when there is not only a focus on the amount of managed habitat, but also on local and landscape scale variables such as patch size and configuration. Cost-effective population monitoring is critical to evaluating the success of management decisions.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my advisor, Julie Lockwood, for being so incredibly helpful and involved throughout this journey. Her support and constant encouragement has had a profound influence on my experience as a graduate student. I cannot thank her enough. I would also like to thank my committee members, David Drake, Rebecca Jordan, and Rick Lathrop for their advice, time, and expertise since I began my graduate career many years ago. This has been a truly positive experience because of the interactions I have shared with my committee members.

Thank you to Tabby Fenn, Ryan Sklar, Thom Almendinger, and Brian Clough for their participation in field data collection. A very special thanks goes to Matt Sileo not only for his excellent work conducting bird surveys and searching for nests, but also for his companionship in the field. Troy Ettel provided extremely helpful insights into grassland bird conservation and grassland management. Financial support came from the Duke Farms Foundation and The Rutgers School of Environmental and Biological Sciences.

I am grateful for the constant and immeasurable support and love from my family and friends. I feel very lucky to have them by my side now and always. And finally, thank you to my best friend and fiancé, Saul, for always being there for me.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 3

LIST OF FIGURES

CHAPTER 3

INTRODUCTION

North American grassland birds are habitat specialists, breeding exclusively in native grassland habitats such as short and tallgrass prairie or agricultural grasslands such as hayfields and pasture. In recent decades, populations of most grassland bird species have declined significantly (Askins 1993, Peterjohn and Sauer 1999, Murphy 2003). For example, between 1966 and 1996, the grasshopper sparrow experienced a range-wide, annual population decline of 3.6% and several grassland bird species are currently listed as threatened or endangered in multiple states. Population declines have been attributed to habitat loss and fragmentation and the intensification of agricultural practices (Bollinger et al. 1990, Herkert 1994, Murphy 2003). In regions such as the northeastern United States where grassland birds breed almost entirely in agricultural grasslands, changes in agricultural practices may be particularly influential on population dynamics (Bollinger et al. 1990). Hayfields are cut earlier and more frequently during the breeding season leading to a reduction in annual fecundity of birds nesting in these fields (Kershner and Bollinger 1996). Mowing hayfields during the breeding season has been shown to reduce nest success by 96% in bobolinks and 61% in savannah sparrows (Bollinger et al. 1990, Perlut et al. 2006).

One form of hayfield management for grassland bird conservation focuses on improving reproductive success by delaying the first harvest date until after July 15. This allows breeding grassland birds to successfully fledge at least one brood during the breeding season. To minimize monetary losses incurred by forgoing a harvest in May or June, farmers can enroll their land in government-administered conservation incentive programs such as the Wildlife Habitat Incentive Program (WHIP) and the Conservation Reserve Program (CRP). These programs offer financial compensation to landowners who manage their hayfields to support grassland birds.

Many studies have demonstrated the conservation value of grasslands enrolled in incentive programs. CRP grasslands generally have higher grassland bird densities than other types of agricultural land (Johnson and Schwartz 1993, Johnson and Igl 1995) and function as source habitat (McCoy et al. 1999). Most studies of grassland bird response to grassland management thus far have focused on correlations between local-scale habitat characteristics and one or two grassland bird response variables (e.g. density, reproductive success). For example, Ribic et al. (2009) found that patch vegetation type (e.g. CRP land, row crop) was highly correlated with grassland bird density in that patch. However, in fragmented agricultural landscapes, grassland birds frequently exist as metapopulations; suitable breeding habitat (i.e. managed hayfields) is scattered within a diverse matrix of row crop agriculture, residential development, and other land uses (Balent and Norment 2003). Therefore, in addition to focusing on local-scale factors that affect grassland bird populations, an effective conservation plan must also consider landscape-scale variables (e.g. hayfield configuration) and how they affect metapopulation dynamics. My research examines hayfield management for a grassland bird metapopulation in a fragmented agricultural landscape in New Jersey. I explore multiple factors at both the local and landscape scale, which contribute to the effectiveness of hayfield management.

I chose to use the grasshopper sparrow as a model grassland bird species in my research. Between 1966 and 2007 this species declined at an annual rate of 3.6% range-wide and 5.6% in the eastern United States (Sauer et al. 2008). The grasshopper sparrow's geographic range extends across much of temperate North America but it is frequently locally distributed and even uncommon in parts of its range (Vickery 1996). Females build well-hidden nests at the base of tufts of grass and prefer breeding in grasslands with patchy, bare ground (Whitmore 1981, Dieni and Jones 2003). In the northeast, grasshopper sparrows depend on agricultural grasslands (e.g. hayfields) for breeding as other types of grasslands are limited in availability (Askins 2007). As a result, grasshopper sparrow populations are vulnerable to habitat loss and agricultural intensification that continue to occur in the region (Askins 1999, Murphy 2003). Because of its reliance on fragmented agricultural grasslands in the northeast and status as a declining grassland bird species, the grasshopper sparrow is an ideal species for use in exploring hayfield management within a landscape context.

I used a metapopulation model to conduct a population viability analysis (PVA) for the grasshopper sparrow under multiple hayfield management scenarios. PVA predicts the probability of population extinction during a particular time period based on user-defined vital rates and ecological conditions and enables a comparison of the effectiveness of different management scenarios (Boyce 1992). It is a valuable tool for conservation as it can provide data to support management recommendations for threatened and endangered species and it is a rigorous analysis method that can be replicated by different researchers

(Akcakaya and Sjogren-Gulve 2000). PVA can incorporate multiple data types such as GIS and it can incorporate uncertainty due to factors such as environmental stochasticity. Population viability analysis has been criticized for its single-species focus; however, because the grasshopper sparrow functions as an indicator species for many other declining grassland birds, I contend my use of PVA to evaluate hayfield management options is of significant value to conservation (Akcakaya and Sjogren-Gulve 2000). A second criticism lies in the predictive accuracy of population viability analyses, which require large amounts of data, some of which may not be available (e.g. juvenile survival rates). However, the main goal of my PVA was to evaluate the relative effectiveness of multiple hayfield management scenarios rather than to make predictions regarding absolute numbers of sparrows many years into the future. Moreover, PVA predictions were shown to be surprisingly accurate when validated retrospectively (Brook et al. 2000).

Models can provide a way to obtain valuable data relatively quickly; however, to fully understand how well they are performing they must be validated. In the context of my research, this meant conducting annual surveys of the grasshopper sparrow metapopulation to determine if it is increasing or decreasing as predicted by my model. Adaptive management can be achieved by incorporating data gained through model validation back into the model, running the model again, and then using the output to improve on-the-ground management (i.e. hayfield enrollment). This type of back and forth interaction between model and reality is a powerful tool that can be used to improve the effectiveness of grassland bird management.

In the first chapter of my dissertation, "How increasing levels of private land enrollment in conservation agreements affect the population viability of grassland birds," I use a spatially-explicit, stage-structured, stochastic metapopulation model to determine how delayed mowing of hayfields affects grasshopper sparrow metapopulation persistence in an agricultural landscape in New Jersey. I build on that model in the second chapter, "The Effects of Patch Size and Configuration on Persistence of a Grasshopper Sparrow Metapopulation." Here I take a landscape scale perspective to hayfield management by evaluating the effect of hayfield isolation and patch size on metapopulation persistence. In the third chapter, "Finding an efficient monitoring scheme to determine the response of a grassland bird metapopulation to conservation actions," I use power analysis to explore the trade-offs between survey cost and statistical power when monitoring the grasshopper sparrow metapopulation.

Each of the main chapters of my dissertation was written as a stand-alone manuscript, formatted according to a target journal. I wrote the manuscripts with my dissertation advisor, Julie L. Lockwood; they are therefore narrated in the first-person plural. The target journals are as follows: Chapter 1 – Ecological Applications, Chapter 2 – Biodiversity and Conservation, and Chapter 3 – Journal of Field Ornithology.

LITERATURE CITED

Akcakaya, H. R. and P. Sjogren-Gulve. 2000. Population viability analysis in conservation planning: an overview. Ecological Bulletins 48: 9-21

Askins, R. A. 1993. Population trends of grassland, shrubland, and forest birds in eastern North America. Current Ornithology 11: 1-34

Askins, R. A. 1999. History of grassland birds in eastern North America. Studies in Avian Biology 19: 60-71

Askins, R. A., F. Chavez-Ramirez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs 64: 1-46

Balent, K. L. and C. J. Norment. 2003. Demographic characteristics of a grasshopper sparrow population in a highly fragmented landscape of western New York state. Journal of Field Ornithology 74: 341-348

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of the bobolink. Wildlife Society Bulletin 18: 142-150

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecological Systematics 23: 481-506

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akcakaya, and R. Frankham. 2000. Nature 23: 385-387

Dieni, J. S. and S. L. Jones. 2003. Grassland songbird nest site selection patterns in northcentral Montana. Wilson Bulletin 115: 388-396

Herkert, J.R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461-471

Johnson, D. H. and L. D. Igl. 1995. Contributions of the Conservation Reserve Program to populations of breeding birds in North Dakota. Wilson Bulletin 107: 709-718

Johnson, D. H. and M. D. Schwartz. 1993. The Conservation Reserve Program and grassland birds. Conservation Biology 7: 934-937

Kershner, E. L. and E. K. Bollinger. 1996. Reproductive success of grassland birds at east-central Illinois airports. American Midland Naturalist 136: 358-366

McCoy, T. D., M. R. Ryan, E. W. Kurzejeski, and L. W. Burger, Jr. 1999. Conservation Reserve Program: Source or sink habitat for grassland birds in Missouri? Journal of Wildlife Management 63: 530-538

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk 120: 20-34

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications **16**:2235-2247

Peterjohn, B. G. and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966-1996. Studies in Avian Biology 19: 27-44

Ribic, C. A., M. J. Guzy, and D. W. Sample. 2009. Grassland bird use of remnant prairie and Conservation Reserve Program fields in an agricultural landscape in Wisconsin. American Midland Naturalist 161: 110-122

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. Version 5.15.2008. *USGS Patuxent Wildlife Research Center*, Laurel, MD

Vickery, P. D. 1996. Grasshopper Sparrow (Ammodramus savannarum). In The Birds of North America, No. 239 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

Whitmore, R. C. 1981. Structural characteristics of grasshopper sparrow habitat. Journal of Wildlife Management 45: 811-814

CHAPTER 1

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

ALISON B. SEIGEL* AND JULIE L. LOCKWOOD

Ecology, Evolution and Natural Resources

14 College Farm Road

Rutgers University

New Brunswick, NJ 08901

*Corresponding author e-mail Alison.Seigel@gmail.com

Abstract.

Changes in hayfield management associated with agricultural intensification, including earlier and more frequent harvests, have a particularly 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 even 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 metapopulation in an urbanizing region of New Jersey. The probability of metapopulation extinction (POE) decreased quickly with increasing proportion of enrolled hayfields. We identified a threshold at 31 to 48% enrollment after which POE decreased minimally with an increase in enrollment. 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. This effect diminished with increasing enrollment. Our results are encouraging as they demonstrate that extinction risk can be reduced without having to protect or manage all remaining grassland habitat in the landscape.

Key words: Ammodramus savannarum; *conservation incentive programs; grasshopper sparrow; grassland birds; grassland management; metapopulation; population viability analysis*

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 is 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 will serve as a subpopulation for a threatened or endangered species. 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, grassland birds 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 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, Perlut et al. 2008). 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 to 15 years and receive annual rental payments based on the value of the land and cost-share assistance to establish approved conservation practices. While CRP grasslands have been primarily concentrated in the central United States, the Wildlife Habitat Incentives Program (WHIP) allocates a large portion of its funding to the New England states and New Jersey (Natural Resources Conservation Service 2008). WHIP promotes the creation of high quality wildlife habitat by offering technical assistance and up to 75 percent cost-share to landowners to establish and improve wildlife habitat during a five to ten 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 five percent 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 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 success of grassland bird conservation in New Jersey and similarly urbanizing landscapes depends heavily on the success of 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 hectares of agricultural ‘grasslands’ within our study area representing 126 patches ranging in size from 11 to 2,209 ha (Figure 1). Some of these 126 patches lie very close to one another and thus could be considered the same subpopulation within the full 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 40m based on our knowledge of grasshopper sparrow behavior and on-the-ground surveys of hayfield locations. 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 (patches).

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, and thus, based on our ground survey, we estimated the proportion of each of the 96 patches 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,

$$\boxed{\begin{matrix} \boldsymbol{S_j \cdot M} & \boldsymbol{S_a \cdot M} \\ \boldsymbol{S_j} & \boldsymbol{S_a} \end{matrix}}$$

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) and patches that were mowed after the breeding season had concluded (No Mow) (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 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 and 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 1999, Rotella et al. 2004). This value is high relative to other published estimates, which range from 0.41 (SE = 0.09) (McCoy et al. 1999) to 0.62 (Jones 2000). We observed an average of 2 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). Thus, when we averaged published estimates of maternity with our estimate we calculated an average maternity estimate of 2.41 (Table 1).

We calculated the survival rate of grasshopper sparrows in the No Mow matrix using both our field observations from Skeet Shoot Field and from published literature (Jones 2000 and 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 three 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), and thus our average estimate for adult survival 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 matrix, we decreased the grasshopper sparrow adult and juvenile maternity estimates used in our No Mow 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 (Wheelwright et al. 1992, Vickery 1996). Because the savannah sparrow’s breeding season extends two 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 in the mid- to late-season is a conservative estimate of the negative impact mowing has on their fecundity. We did not reduce adult or juvenile survivorship in the Mow matrix, thus assuming no significant effect of mid- to late-season mowing on survival rate of savannah or grasshopper sparrows. Again, this assumption is conservative as assuming a reduction in survival would increase the rate at which subpopulations subjected to mid-season mowing would decline through time.

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 published variance estimates 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 metapopulation is inversely related to the distance between them (LaHaye et al. 1994). RAMAS 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 38km, 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). In general, grasshopper sparrows appear to be highly breeding-site fidelic (Jones 2000), however 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 the value of the variables in the dispersal function by 25%. Our results did not differ between simulations across the full range of dispersal functions we explored, 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 four hayfield enrollment percentages: (1) 7 to 12% of all hayfield in our study area enrolled in no-mow management, (2) 19 to 24%, (3) 31 to 36%, and (4) 43 to 48%. Within each enrollment category, we ran ten 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 matrix to each of the enrolled patches and the Mow matrix to the remaining patches. While total area of hayfield enrolled remained constant within each enrollment category, the number of hayfield patches enrolled varied. 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 (λ) and elasticities for each stage matrix.

Modeling ecological trap removal scenarios

To determine the effect of the non-enrolled (mowed) hayfield patches on grasshopper sparrow metapopulation persistence, we randomly selected one simulation out of the ten from each enrollment category and re-ran it with 10, 25, and 40% of mowed hayfield area removed. Prior to running each simulation, we randomly deleted hayfield patches that were not enrolled in no-mow management until the amount of area removed reached the desired proportion (10, 25, or 40%). All other parameters in each simulation remained the same.

To isolate the effects of increasing enrollment and trap removal on metapopulation persistence, 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.

RESULTS

The finite rate of increase (λ) for the Mow matrix was 0.9334, thus indicating a steadily declining metapopulation. Elasticity analysis indicated that survival rate of adults made the largest contribution to λ (Table 2). Lambda for the No Mow 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 quickly with increasing proportion of hayfield enrolled in no-mow management (Figure 2). However, there was a threshold at 31 to 48% enrollment after which POE decreased minimally with an increase in hayfield area enrolled (Figure 2).

Probability of metapopulation extinction also decreased with increasing numbers of patches enrolled in no-mow management (Figure 3). As the amount of land in each enrollment category increased, the average number of enrolled patches per simulation within each category increased as well and thus the trends shown in Figures 2 and 3 are naturally very similar to each other. Despite this relationship, the number of patches enrolled in no-mow management had a distinct effect on POE. To illustrate this we ran three additional simulations. In the first simulation, to simulate many small patches, we included as many hayfield patches as possible in no-mow management while keeping the percent enrollment at the lowest level (7 to 12%). The POE associated with this 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 (Figure 3). In the second and third simulations we produced the opposite effect by including the fewest patches possible in no-mow management while keeping the percent enrollment high (31 to 36% or 43 to 48%). The POE associated with these simulations were high despite their being within the higher enrollment categories (Figure 2), and indeed were near the high POE simulations that resulted from having low percentage enrollment.

Ecological trap removal

Within each enrollment category, probability of extinction of the CP Plains grasshopper sparrow metapopulation decreased as more ecological trap habitat (mowed hayfield) was removed from the metapopulation (Figure 4). The effect of removing trap habitat was highest in the lowest percentage enrollment categories, with decreasing influence as enrollment percentages increased. At the highest enrollment levels (43 to 48%), the removal of trap habitat essentially had no effect on POE because the initial POE was very low.

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 88% with an increase in enrollment of 10 to 15%, beyond which, additional enrollment would yield only a minimal decrease in extinction risk. 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 reduced without having to protect or manage all 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 is a result of the non-enrolled hayfields acting as “equal-preference” ecological traps (Robertson and Hutto 2006). Sparrow population growth (λ) 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. Hayfield enrollment does not only create a source population, it also removes a sink population from the metapopulation. Thus, it is not surprising that removing non-enrolled hayfields (ecological traps) increases grasshopper sparrow persistence. Of greater import is our observation that this effect diminished with increasing enrollment. In addition, we found that the threshold of persistence was reduced by 10% when 40% of the traps were removed. These trends suggest that metapopulation persistence can be achieved at a lower level of enrollment if non-enrolled 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 functioning as ecological traps.

One way in which a trap hayfield can be removed 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 such land conversions. Our model did not account for edge effects, which may vary according to the land use of adjacent patches (Johnson and Temple 1990). 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 hayfields experiencing edge effects. 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 develop 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 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.

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. (2008) 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 subpopulation 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.

ACKNOWLEDGMENTS

We thank Brian Clough, Matthew Sileo, Tabby Fenn, Thom Almendinger, and Ryan Sklar for their participation in field data collection. We thank Troy Ettel for input on the logistics of farm enrollment and other insights into management. Partial funding for this work was provided by the Duke Farms Foundation and Rutgers University to JLL.

LITERATURE CITED

Akcakaya, H. R. 1991. A method for simulating demographic stochasticity. Ecological Modelling **54**:133-136

Akcakaya, H. R. and J. L. Atwood. 1997. A habitat-based metapopulation model of the California gnatcatcher. Conservation Biology **11**:422-434

Akcakaya, H. R. and M. G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. Biodiversity and Conservation **7**:875-894

Askins, R. A., F. Chavez-Ramirez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs **64**:1-46

Barbarika, A. 2007. Conservation Reserve Program Summary and Enrollment Statistics, Fiscal Year 2007. http://www.fsa.usda.gov/Internet/FSA_File/annual_consv_2007.pdf

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of the bobolink. Wildlife Society Bulletin **18**:142-150

Brennan, L. A. and W. P. Kuvlesky. 2005. North American grassland birds: An unfolding conservation crisis? Journal of Wildlife Management **69**:1-13

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology **9**:1380-1395

Ernst, T. and G. N. Wallace. 2008. Characteristics, motivations, and management actions of landowners engaged in private land conservation in Larimer County Colorado. Natural Areas Journal **28**: 109-120

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology **59**:871-883

Gill, D. E., P. Blank, J. Parks, J. B. Guerard, B. Lohr, E. Schwartzman, J. G. Gruber, G. Dodge, C. A. Rewa, and H. F. Sears. 2006. Plants and breeding bird response on a managed Conservation Reserve Program grassland in Maryland. Wildlife Society Bulletin **34**:944-956

Hasse, J. and R. G. Lathrop. 2008. Tracking New Jersey's dynamic landscape: Urban growth and open space loss 1986-1995-2002. Center for Remote Sensing and

Spatial Analysis, Rutgers University, New Brunswick, NJ. http://www.crssa.rutgers.edu/projects/lc/urbangrowth/
Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications **4**:461-471
Hill, J., C. Thomas, and O. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: Implications for metapopulation structure. Journal of Animal Ecology **65**:725-735
Johnson, D. H. and L. D. Igl. 2001. Area requirements of grassland birds: a regional perspective. Auk **118**:24-34
Johnson, R. G. and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management. 54: 106-111
Jones, A. 2000. Grasshopper sparrow (*Ammodramus savannarum*) metapopulation dynamics and conservation strategies in Massachusetts. Masters Thesis. University of Massachusetts, Amherst, MA
Kabii, T. and P. Horwitz. 2006. A review of landholder motivations and determinants for participation in conservation covenanting programmes. Environmental Conservation **33**:11-20
Kershner, E. L. and E. K. Bollinger. 1996. Reproductive success of grassland birds at East-Central Illinois airports. American Midland Naturalist **136**:358-366
Knight, R.L. 1999. Private lands: the neglected geograph. Conservation Biology **13**:223-224
LaHaye, W. S., R. J. Gutierrez, and H. R. Akcakaya. 1994. Spotted owl metapopulation dynamics in southern California. Journal of Animal Ecology **63**:775-785
Mattison, E. H. A.and K. Norris. 2005. Bridging the gaps between agricultural policy, land-use and biodiversity. Trends in Ecology and Evolution **20**:610-616
Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin **87**:456-466
McCoy, T. D., M. R. Ryan, E. W. Kurzejeski, and L. W. Burger. 1999. Conservation Reserve Program: Source or sink habitat for grassland birds in Missouri? Journal of Wildlife Management **63**:530-538
Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk **120**:20-34
National Weather Service (NWS) Cooperative Observer Program precipitation data. Obtained from the Office of the New Jersey State Climatologist, Rutgers University on September 19, 2008 http://climate.rutgers.edu/stateclim_v1/monthlydata/index.html
Norment, C. 2002. On grassland bird conservation in the Northeast. Auk **119**:271-279
Pejchar, L. and D. M. Press. 2006. Achieving conservation objectives through production forestry: The case of the Acacia koa on Hawaii Island. Environmental Science and Policy **9**:439-447
Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications **16**:2235-2247
Peterjohn, B. G. and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966-1996. Studies in Avian Biology: **19**:27-44

Robertson, G. A. and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology **87**:1075-1085

Robles, M. D., C. H. Flather, S. M. Stein, M. D. Nelson, and A. Cutko 2008. The geography of private forests that support at-risk species in the conterminous United States. Frontiers in Ecology and the Environment **6**: 301-307

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation **27**:187-205

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, MD

Troy, A. R., A. M. Strong, S. C. Bosworth, T. M. Donovan, N. J. Buckley, and M. L. Wilson. 2005. Attitudes of Vermont dairy farmers regarding adoption of management practices for grassland songbirds. Wildlife Society Bulletin **33**:528-538

Natural Resources Conservation Service (NRCS), United States Department of Agriculture,. 2007. FY 2007 WHIP allocations to states. http://www.nrcs.usda.gov/programs/2007_allocations/07WHIPAlloc.pdf

Van Buskirk, J. and Y. Willi. 2004. Enhancement of Farmland Biodiversity within Set-Aside Land. Conservation Biology **18**:987-994

Vickery, P. D. 1996. Grasshopper sparrow (*Ammodramus savannarum*). *In* A. Poole and F. Gill, editors. The Birds of North America, No. 175. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Vickery, P. D., M. L. Hunter, Jr., and S. M. Melvin. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology **8**:1087-1097

Wheelwright, N. T., C. B. Schultz, and P. J. Hodum. 1992. Polygyny and male parental care in Savannah Sparrows: effects on female fitness. Behavioral Ecology and Sociobiology **31:279-289**

White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study **46:** Supplement 120-138

Wolfenbarger, D. O. 1949. Dispersion of small organisms. American Midland Naturalist **35**:1-152

Wray, II, T. K. A. Strait, and R. C. Whitmore. 1982. Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. Auk **99**:157-164

TABLES

TABLE 1. Mean and standard deviation of stage matrix parameters. Maternity (*M*), adult survival (S_a), juvenile survival (S_j), adult fecundity ($F_a = M \cdot S_a$), and juvenile fecundity ($F_j = M \cdot S_j$).

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	0.64	0.32	0.59	0.29
	SD	0.17	0.12	0.06	0.17	0.07

TABLE 2. Elasticity analysis results for the Mow and No Mow stage matrices. Elasticities are measures of the contribution that each matrix element makes toward lambda.

	Mow stage matrix	No Mow stage matrix
Juvenile fecundity	0.0973	0.2982
Adult fecundity	0.2159	0.2479
Juvenile survival	0.2159	0.2479
Adult survival	0.4709	0.2060

FIGURE LEGEND

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 40m neighborhood distance. There are 96 patches totaling 4,694ha of suitable hayfield habitat.

FIG. 2. Probability of extinction of the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation under four hayfield enrollment scenarios: 7 to 12 % of total hayfield area enrolled, 19 to 24% enrolled, 31 to 36% enrolled, and 43 to 48% enrolled.

FIG. 3. Probability of extinction and number of patches for a total of 43 simulations of the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation. Ten simulations were run in each of 4 hayfield enrollment categories. Three simulations (the larger data labels) show the effect of low percentage enrollment combined with large number of patches and high enrollment combined with small number of patches.

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.

FIGURES

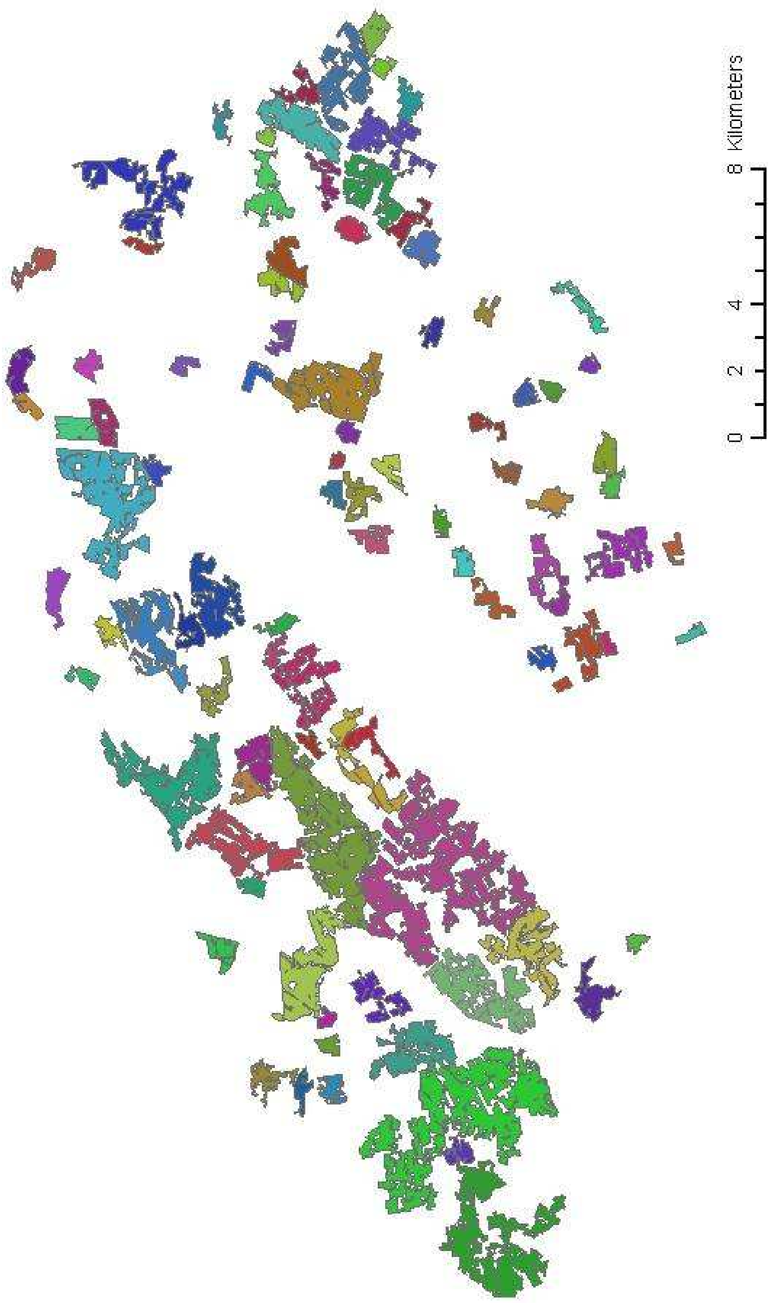


Figure 1.

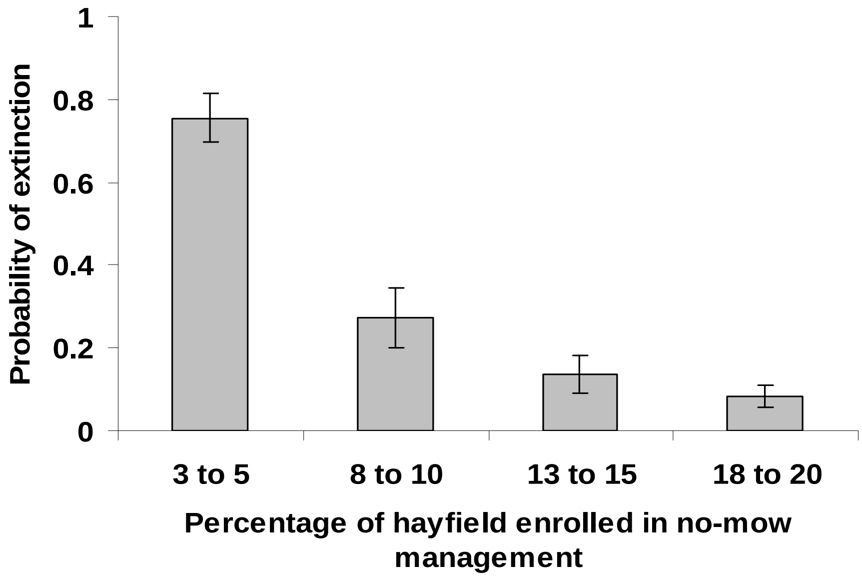

1
0.8
0.6
0.4
0.2
0
Probability of extinction
3 to 5
8 to 10
13 to 15
18 to 20
Percentage of hayfield enrolled in no-mow management

Figure 2.

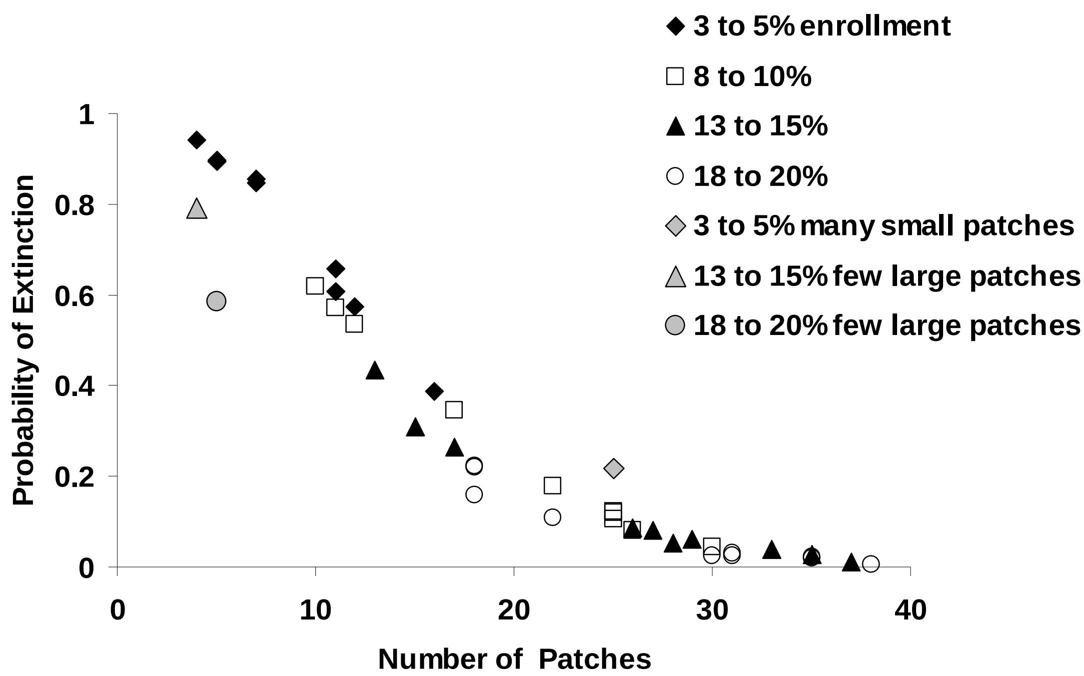

3 to 5% enrollment
8 to 10%
13 to 15%
18 to 20%
3 to 5% many small patches
13 to 15% few large patches
18 to 20% few large patches
Probability of Extinction
1
0.8
0.6
0.4
0.2
0
0
10
20
30
40
Number of Patches

Figure 3.

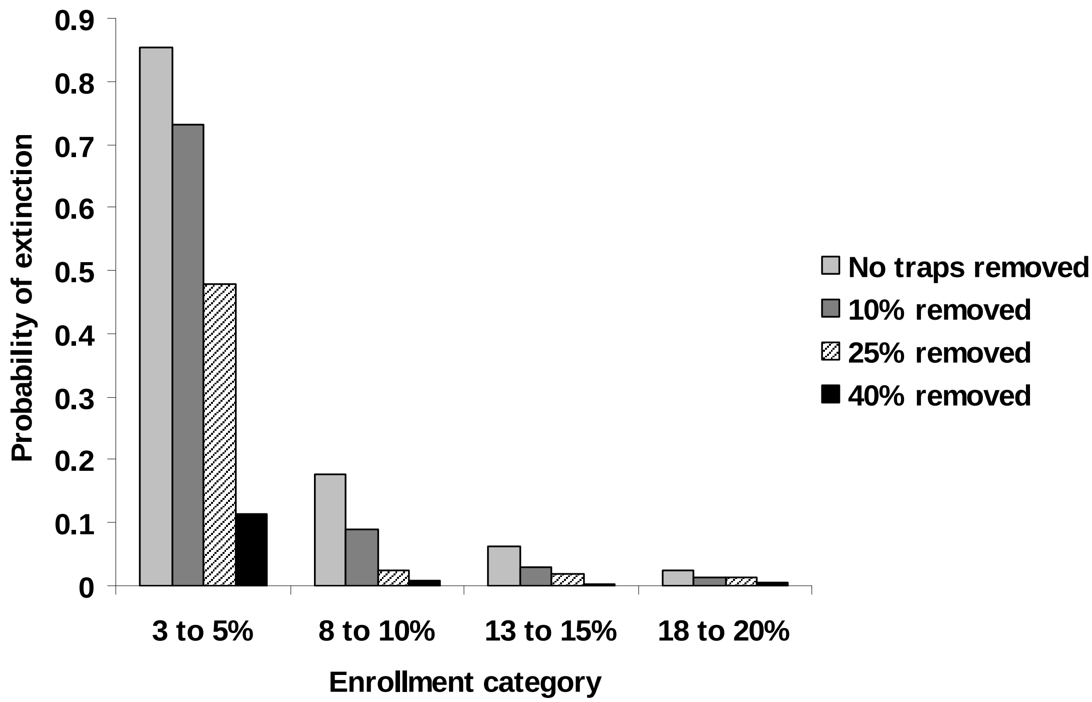

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Probability of extinction
3 to 5%
8 to 10%
13 to 15%
18 to 20%
Enrollment category
No traps removed
10% removed
25% removed
40% removed

Figure 4.

CHAPTER 2

The Effects of Patch Size and Configuration on Persistence of a Grasshopper Sparrow Metapopulation

Alison B. Seigel and Julie L. Lockwood

Ecology, Evolution and Natural Resources

14 College Farm Road

Rutgers University

New Brunswick, NJ 08901

Alison.Seigel@gmail.com

Abstract Grassland bird declines have been attributed in part to the intensification of agricultural practices in hayfields. Grassland bird nesting success is drastically reduced as hayfields are cut earlier and more frequently during the breeding season. Grassland bird conservation efforts have focused on enrolling agricultural hayfields in landowner incentive programs that improve reproductive success by requiring mowing to be delayed during the breeding season. Our objective was to determine how size and landscape configuration of enrolled hayfields affected risk of extinction. When we incorporated a direct relationship between hayfield size and grasshopper sparrow fecundity into the model, POE decreased with increasing proportion of enrolled land. However, within each enrollment category, POE was higher than when no patch size effect was included. Because a patch size effect has the potential to increase the risk of extinction of a grassland bird metapopulation, it is critical to understand and consider how grassland bird fecundity is related to patch size in the geographic region being targeted for management. We also found that POE was higher when enrolled hayfields were isolated than when they were spatially clumped. Hayfield management for grassland birds will be most effective when there is not only a focus on the amount of managed habitat, but also on local and landscape scale variables such as patch size and configuration.

Keywords Ammodramus savannarum; *conservation incentive programs; grasshopper sparrow; grassland birds; grassland management; metapopulation; patch isolation; patch size, population viability analysis*

Introduction

It is critical for conservation planners to make informed decisions when setting aside and managing land in order to aid the recovery of imperiled species (Noss et al. 1997). Effective conservation is achieved through an in-depth understanding of the target species' habitat requirements, and how the spatial configuration of suitable habitat drives population dynamics (Noss et al. 1997). These requirements are then overlain on the realities associated with land acquisition, or with engaging private landowners in managing their property for the benefit of the target species. Grassland bird conservation programs are a good example of the need to balance these forces. Conservation programs like the Wildlife Habitat Incentives Program frequently utilize monetary incentives to encourage landowners to delay mowing their agricultural hayfields such that target species can produce at least one successful clutch during the breeding season. This approach satisfies the first component of effective conservation planning because it explicitly ties the target species to the management of its habitat. However, it does not consider how conservation organizations should determine the spatial configuration of the entire suite of enrolled private lands. We used population viability modeling to explore how landscape-scale spatial attributes of farmland enrolled in conservation schemes affect the persistence of a grasshopper sparrow (*Ammodramus savannarum*) metapopulation.

North American grassland birds are experiencing consistent and widespread population declines throughout their ranges (Samson and Knopf 1994, Peterjohn and Sauer 1999), and grasshopper sparrows are no exception. In the northeastern United States, grassland birds rely almost exclusively on agricultural grasslands for breeding habitat (Askins et al. 2007). Population declines in this region have been linked to the loss of farmland and the intensification of use within agricultural hayfields (Bollinger et al. 1990, Perlut et al. 2006, Murphy 2003, Askins et al 2007). Hayfields are cut earlier and more frequently during the growing season, which serves to substantially reduce breeding habitat quality for grassland birds as it effectively destroys all active nests and prevents re-nesting until the grasses have regrown (Bollinger and Gavin 1992, Troy et al. 2005). To ameliorate this effect, conservation incentive programs have been implemented within the United States Department of Agriculture and US state wildlife agencies to encourage farmers to manage for the benefit of imperiled grassland species. These programs require that mowing be delayed until at least July 15 to allow grassland birds to successfully fledge at least one brood per year, improving their reproductive success.

These programs have seen considerable success in terms of convincing landowners to participate (Barbarika 2007). This success brings with it the problem of deciding which lands to enroll of those owned by individuals that have applied to the program because of limited funding. Decades of research on avian metapopulation biology have shown that population dynamics are as reliant on the size and spatial proximity of the habitat patches as on the quality of each patch itself (e.g. Verboom et al. 1991, Wilson et al. 2009). From this perspective, it is important to prioritize parcels of agricultural grassland for enrollment based on landscape-scale attributes such as grassland parcel size and distance to nearest other enrolled land. Indeed, the failure to consider these factors may lead to large inefficiencies whereby money is spent to enroll large amounts of land, but the spatial configuration of these lands is not optimal for maximizing grassland bird metapopulation growth rates. Do large enrolled grasslands make a greater contribution to metapopulation persistence than small grasslands? Should enrolled grasslands be dispersed across the landscape or clumped into one local area? To maximize the effectiveness of grassland bird conservation programs, it is critical for planners and managers to know the answers to these questions for the landscape they are working within.

We build on our previous results (Seigel and Lockwood 2009) that showed an effect of farmland enrollment in delayed mowing management on grasshopper sparrow extinction risk. We developed a spatially-explicit, stage-structured, stochastic model of the grasshopper sparrow metapopulation in the Central Piedmont (CP) Plains of New Jersey (USA) using the population viability analysis software RAMAS GIS. Seigel and Lockwood (2009) found that the extinction risk for this metapopulation decreased quickly with the increasing percentage of available hayfield enrolled in no-mow management within the region. We also showed that, after a threshold percentage enrollment, extinction risk reached a plateau. In this paper, we explore the effect of patch size and spatial configuration of enrolled hayfields on probability of extinction of this same grasshopper sparrow metapopulation using a simple extension of our previous model (Seigel and Lockwood 2009).

Methods

Metapopulation Spatial Structure

We modeled the CP Plains grasshopper sparrow metapopulation, which consisted of 96 sparrow subpopulations (i.e. patches) inhabiting a total of 4,694 ha of agricultural hayfield. We limited the patches included in our metapopulation to only hayfields ≥ 10ha. This area is considered the minimum area requirement for grasshopper sparrows, although there is considerable geographic variability in this value (e.g., Herkert 1994, Vickery et al. 1994, Johnson and Igl 2001). We set carrying capacity of each subpopulation to match the proportion of each patch that consisted of hayfield as opposed to other habitat types such as row crops. For a full explanation of how we arrived at the metapopulation spatial structure, see Seigel and Lockwood (2009).

Model Input

Stage matrix. We modeled grasshopper sparrow population dynamics within each hayfield patch using a stage-structured, stochastic, (Leslie) matrix model with juvenile and adult stages. Our general stage matrix took the following form,

$$\boxed{\begin{matrix} S_j \cdot M & S_a \cdot M \\ S_j & S_a \end{matrix}}$$

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. Our model assumed that population censuses occurred immediately after each breeding season, no mortality occurred between the onset of breeding and the census, adults and returning juveniles had the same maternity rate, and adult vital rates were the same regardless of age class (Seigel and Lockwood 2009).

We constructed two stage matrices; a No Mow and a Mow. The “No Mow” matrix represented hayfields enrolled in a delayed (after July 15) mowing program, and the “Mow” matrix represented hayfields that were mowed during the breeding season (Table 1). We derived the maternity and adult survival estimates in the No Mow matrix by averaging published values (McCoy et al. 1999, Jones 2000, Gill et al. 2006) with our estimates obtained from data collection at a 70 ha hayfield in the CP Plains study area (Seigel and Lockwood 2009). We could not obtain estimates for juvenile survival through our field data or from the literature, thus we set juvenile survival as half that of adults (Table 1; Donovan et al. 1995, McCoy et al. 1999). In the Mow matrix, we simulated the effects of mowing during the grasshopper sparrow breeding season by decreasing the grasshopper sparrow adult and juvenile maternity estimates used in the No Mow matrix by 62%. We believe this is a conservative estimate based on a study of the effects of mid-breeding season mowing on savannah sparrows (Perlut et al. 2006).

Density dependence. Population dynamics for all subpopulations fluctuated under ceiling-type density dependence. The ceiling for each hayfield was equal to the carrying capacity of that hayfield.

Carrying capacity. Carrying capacity was equal to the number of grasshopper sparrow territories that could fit within the hayfield area in each patch. We used a territory size of 2 ha (Vickery 1996).

Demographic and environmental stochasticity. To incorporate demographic stochasticity into the model, we drew the number of surviving grasshopper sparrows at each time step from a binomial distribution and we drew the number of offspring from a Poisson distribution (Akcakaya 1991). Environmental stochasticity was incorporated by sampling fecundity and survival rates at each time step from a lognormal distribution with mean from the stage matrix and standard deviation from a standard deviation (SD) matrix. We built the SD matrix for each of the two stage matrices (Mow and No Mow) by combining our observed variance in maternity and survival rates from our on-site research (Seigel and Lockwood 2009) with published variance estimates using the Delta Method (Akcakaya and Raphael 1998).

Correlation-distance function. The maximum distance between two hayfields in our study area was 38 km, a distance over which spatial autocorrelation of environmental conditions is relatively high (National Weather Service 2008). We simulated these conditions using the correlation-distance function, $C = \exp(-D/100)$, 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.

Dispersal. We used the dispersal-distance function, $y = 0.2 \cdot exp(-x/10)$, to simulate 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. We also specified the relative dispersal rates of adult and juvenile grasshopper sparrows. Adults tend to be highly breeding site-fidelic, while juveniles typically move to other breeding grounds during natal dispersal (Jones 2000). Thus we defined the adult dispersal rate as 10% of the juvenile dispersal rate (Jones 2000).

Modeling the Effect of Patch Size on Probability of Extinction

We assigned stage matrices to hayfields based on three patch sizes: small < 30 ha, medium 30 – 70 ha, and large > 70 ha. We reduced fecundity by 30% in small hayfields and 15% in medium hayfields and did not reduce fecundity in large hayfields. These values lie within the range of values published by authors that directly measured reductions in nesting success due to grassland area (e.g., Winter and Faaborg 1999, Balent and Norment 2003, Herkert et al. 2003, Skagen et al. 2005). This assignment created six stage matrices; three in which mowing occurred and three in which mowing did not occur. The three matrices within each mowing category represented fecundity values associated with small, medium and large hayfields. We calculated the deterministic growth rate (λ) for each matrix in order to evaluate whether each represents an increasing or decreasing population.

To determine how the size of hayfields affected grasshopper sparrow metapopulation viability relative to delayed mowing programs, we ran ten simulations in each of three enrollment categories (low, medium, and high) where fecundity was scaled to patch size. Small hayfields were more common than medium or large hayfields in all three enrollment categories (Fig. 1). We ran each simulation for 50 years and determined the probability of extinction (POE) as the probability that metapopulation abundance will fall below 100 individuals at least once during that time period. We kept all other parameters as they were in Seigel and Lockwood (2009) so that our calculations of POE here are directly comparable to those previously reported. We used MANOVA to evaluate whether percentage of land enrolled had an effect on mean POE once the patch size effect is accounted for, and whether this effect was the same as when no patch size effect was incorporated. The latter values were taken from Seigel and Lockwood (2009).

Finally, we recorded the number of patches enrolled across the 10 simulations within each enrollment category and related this number to the associated POE where patch size effects were included. We used ANCOVA to test for an overall effect of patch number on POE, and to determine if the effect size (i.e. the slope of the relationship between patch number and POE) changed according to enrollment category. We were interested in examining if, once patch size effects are included, incorporating more hayfield patches within any one enrollment category decreases POE as is the case when patch size effects are not included (Seigel and Lockwood 2009).

Modeling the Effect of Landscape Configuration on Probability of Extinction

To determine if the degree of isolation of enrolled hayfields affected grasshopper sparrow metapopulation persistence, we ran ten simulations in which enrolled hayfields were highly clumped in the landscape and ten simulations in which enrolled hayfields were highly dispersed. In all simulations, we held the number of hayfields enrolled constant at seven and we held the mean total enrolled hayfield area constant at 388 ha (SD=4.7 ha). We calculated the degree of isolation of enrolled hayfields in each simulation by summing the total pairwise distances (TPD) in km between all enrolled hayfields. Small values of TPD directly equate to a low degree of isolation, and vice versa. We compared the mean POE for each dispersion category (i.e. clumped or dispersed) using a t-test. We report here only the results for the low enrollment category. Preliminary analyses indicated that the effect of spatial configuration diminishes with increasing enrollment, and thus spatial configuration had the largest effect in this enrollment category.

To isolate the effects of patch size and landscape configuration on metapopulation persistence, we ran model simulations under the following assumptions: 1) the enrollment status (enrolled or non-enrolled) of a hayfield did not change at any time during the 50 year simulation period, 2) the composition of the surrounding matrix did not change during the 50 year simulation period, and 3) the matrix consisted of only one habitat type and that habitat was unsuitable for grasshopper sparrow breeding.

Results

The three No Mow matrices had $\lambda > 1$, indicating positive population growth rates, whereas the three Mow matrices had $\lambda < 1$, indicating declining populations (Table 2). Thus, the reduction in grasshopper sparrow fecundity associated with even the smallest hayfields does not outweigh the negative effect of mowing on fecundity.

Probability of extinction (POE) declined at a lower rate when patch size effects were incorporated (Fig. 2; $F=69.7$, $p<0.0001$). In addition, POE significantly increased in all enrollment categories when we incorporated a patch size effect ($F=104.4$, $p<0.0001$). Within each enrollment category and with patch size effect incorporated, we found that the number of patches enrolled in delayed mowing management significantly negatively influenced POE (low: $R^2=0.81$, $p<0.0004$, $n=10$; medium: $R^2=0.97$, $p<0.0001$, $n=10$; $R^2=0.97$, $p<0.0001$, $n=10$) (Fig. 3). However, the three slopes relating patch number to POE were significantly different ($F=25.5$, $p<0.0001$). The slopes for POE in medium and high enrollment categories (0.026 and 0.031) were notably higher than the slope for POE in the low enrollment category (0.006).

In the low enrollment category, mean total pairwise distances of enrolled hayfields was 48.5 km (SD = 3.5, n=10) in simulations where hayfields were clumped and 288.6 km (SD = 5.5, n=10) in simulations where hayfields were isolated. The POE for the populations that were clumped was significantly lower than the POE for populations where dispersed ($t = -9.5$, $p<0.0001$).

Discussion

As in Seigel and Lockwood (2009), we found that enrolling hayfields in delayed mowing management increases the probability of grasshopper sparrow metapopulation persistence. Within each enrollment category, however, POE increased as a result of the reduction in fecundity (and hence λ) for grasshopper sparrows breeding in small and medium sized hayfields. This reduction had a significant effect on POE because small and medium sized hayfields accounted for an average of 75% (SE=3) of the hayfields enrolled in delayed mowing management in the low, medium, and high enrollment categories. Small hayfields are likely to be relatively common in other highly fragmented agricultural landscapes. Thus, it is important to determine the relationship between patch size and fecundity in the targeted geographic region prior to making management decisions regarding the amount of land necessary to sustain a grasshopper sparrow metapopulation.

Because fecundity is one of the drivers of population growth, the relationship between patch size and fecundity is an important consideration in both modeling grassland bird population dynamics and also in landscape-scale grassland bird conservation planning. The effect of patch size on fecundity, however, is not well understood; patch size had no effect on grassland bird fecundity in some studies (Winter

2006) while in other studies the effect was pronounced (Johnson and Temple 1990, Herkert et al. 2003). This variation may be a result of the differences in landscape composition and nest predator community composition in different geographic regions. In prairie fragments in five states in the Midwest, Herkert et al. (2003) found that nest success of four grassland bird species increased with increasing fragment size as a result of higher nest predation rates in smaller fragments. Winter et al. (2000) found proximity to woody habitat (and not agricultural fields) explained more variation in nest success than did grassland size. These authors suggested that edge habitat type rather than patch size may be more important in determining fecundity because predator communities varied according to edge type. Because the relationship between patch size and fecundity is not well understood and varies geographically, and we show that patch size has a relatively large role to play in determining population persistence, it would be of great benefit to conservation planning to study grassland bird fecundity in a wide range of patch sizes in the region being targeted.

Within each hayfield enrollment category, the number of hayfield parcels enrolled in delayed mowing management had a notable influence on probability of extinction for our grasshopper sparrow metapopulation. Extinction risk decreased as number of patches increased. The effect was strongest, however, in the medium and high enrollment categories, while number of hayfields enrolled only had a marginal effect on probability of extinction in the low enrollment category. This result stemmed from the fact that low hayfield enrollment outweighed the effect of number of patches in terms of their effects on extinction risk. Thus, under the simulated conditions we specified, when a relatively low proportion of hayfield in a landscape is enrolled in delayed mowing management, the key to improving grasshopper sparrow metapopulation persistence is to make further enrollment of land a priority, regardless of whether it is added as one large patch or many smaller patches. However, once at least 8% of the total area of grassland in the landscape is enrolled in delayed mowing management, further enrollment should be spread across as many grassland parcels as possible. For example, enrolling 300 ha of grassland in the form of three parcels of land would produce a greater reduction in the risk of extinction than enrolling one large, 300 ha grassland parcel.

The metapopulation model in Seigel and Lockwood (2009) did not include an effect of patch size on fecundity. As a result, we were able to examine how incorporating a patch size effect altered the relationship between percentage of land enrolled and extinction risk. We found that higher enrollment decreased extinction risk just as is the case when patch size effects are not included. However, the rate of decrease was substantially lower when the patch size effect was included. Finally, by including the patch size effect on fecundity, the number of enrolled hayfield parcels became less important in determining probability of extinction in the low enrollment category (i.e. extinction risk remained high regardless of number of patches included in the low enrollment scenario). In the medium enrollment category, although extinction risk was consistently higher when we included the effect of hayfield size on fecundity, the effect of number of enrolled hayfields on extinction probability remained the same. In the high enrollment category, the number of hayfields enrolled became more important in determining extinction risk when we added the hayfield size effect. However, as number of enrolled hayfields approached its maximum (37), the difference in probability of extinction with and without the patch size effect diminished, indicating that hayfield size became less important when a large portion of hayfield (divided into many parcels) was enrolled in delayed mowing management.

When we arranged enrolled hayfields in a clumped spatial configuration, grasshopper sparrow metapopulation extinction risk was almost 10% lower than when enrolled hayfields were dispersed throughout the study area. In our metapopulation model, we used a dispersal function that specified an indirect relationship between probability of moving between hayfields and the distance between the hayfields. Although little is known about natal dispersal distances in grassland birds, other migratory songbirds have been found to disperse relatively short distances from their natal habitat (e.g. indigo bunting ~1km) (Payne 1991, Paradis et al. 1998, Winkler et al. 2005). Consequently, when enrolled hayfields were spatially clumped, juveniles had a greater chance of dispersing to another enrolled hayfield with positive population (source) growth than to a non-enrolled hayfield with a negative growth rate (sink). We believe this mechanism of increasing abundance in population sources most likely enabled the metapopulation abundance to grow at a faster rate than if juveniles had a greater chance of dispersing to a population sink. We are aware that in some cases, when habitat patches are spatially clumped, individuals in a metapopulation may be vulnerable to local environmental catastrophes. However, because of the relatively small scale of our study (max distance between two hayfields = 38 km), environmental conditions are highly correlated across all grasslands. Based on these results, when enrolling grassland parcels in grassland bird friendly management programs, emphasis should be put on the spatial relationship among these hayfields, in particular enrolling grasslands in close proximity to each other.

Conclusions

Managing grasslands for the benefit of grassland birds requires both a local and landscape-scale perspective. The most effective conservation plan should focus not only on the amount of habitat managed for breeding grassland birds, but also on the local scale patch characteristics and landscape scale spatial configuration of managed grasslands. It is important to determine whether there is a patch size effect on fecundity and then determine the amount of hayfield that needs to be enrolled to overcome that effect. Managers should focus on acquiring grasslands in close proximity to each other to maximize metapopulation persistence.

Acknowledgements

We thank the Duke Farms Foundation for funding a portion of this research. We also thank Matt Sileo and Brian Clough for their efforts in the field.

References

Akcakaya, H. R. 1991. A method for simulating demographic stochasticity. Ecological Modelling 54:133-136

Akcakaya, H. R. and M. G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. Biodiversity and Conservation 7:875-894

Askins, R. A., F. Chavez-Ramirez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs 64: 1-46

Balent, K. L. and C. J. Norment. 2003. Demographic characteristics of a grasshopper sparrow population on a highly fragmented landscape of western New York state. Journal of Field Ornithology 74: 341-348

Barbarika, A. 2007. Conservation Reserve Program Summary and Enrollment Statistics, Fiscal Year 2007. http://www.fsa.usda.gov/Internet/FSA_File/annual_consv_2007.pdf

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of the bobolink. Wildlife Society Bulletin 18: 142-150

Bollinger, E. K. and T. A. Gavin. 1992. Eastern Bobolink populations: Ecology and conservation in an agricultural landscape. Pages 497–508 *in* J. M. Hagan III and D. M. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380-1395

Gill, D. E., P. Blank, J. Parks, J. B. Guerard, B. Lohr, E. Schwartzman, J. G. Gruber, G. Dodge, C. A. Rewa, and H. F. Sears. 2006. Plants and breeding bird response on a managed Conservation Reserve Program grassland in Maryland. Wildlife Society Bulletin 34:944-956

Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461-471

Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson. 2003. Effects of Prairie Fragmentation on the Nest Success of Breeding Birds in the Midcontinental United States. Conservation Biology 17: 587-594

Johnson, D. H. and L. D. Igl. 2001. Area requirements of grassland birds: a regional perspective. Auk 118:24-34

Johnson, R. G. and S. A. Temple. 1990. Nest Predation and Brood Parasitism of Tallgrass Prairie Birds. Journal of Wildlife Management 54: 106-111

Jones, A. 2000. Grasshopper sparrow (*Ammodramus savannarum*) metapopulation dynamics and conservation strategies in Massachusetts. Masters Thesis. University of Massachusetts, Amherst, MA

McCoy, T. D., M. R. Ryan, E. W. Kurzejeski, and L. W. Burger. 1999. Conservation Reserve Program: Source or sink habitat for grassland birds in Missouri? Journal of Wildlife Management 63:530-538

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk 120:20-34

National Weather Service (NWS) Cooperative Observer Program precipitation data. Obtained from the Office of the New Jersey State Climatologist, Rutgers University on September 19, 2008 http://climate.rutgers.edu/stateclim_v1/monthlydata/index.html

Noss, R.F., M.A. O'Connell, and D.D. Murphy. 1997. The science of conservation planning. Island Press, Washington DC.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67: 518-536

Payne, R. 1991. Natal dispersal and population structure in a migratory songbird, the indigo bunting. Evolution 45: 49-62

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications 16:2235-2247

Peterjohn, B. G. and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966-1996. Studies in Avian Biology: **19**:27-44

Samson, F. B., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44: 418-421

Seigel, A. B. and J. L. Lockwood. 2009 How increasing levels of private land enrollment in conservation agreements affect the population viability of grassland birds. Ecological Applications *In review*.

Skagen, S. K., A. A Yackel Adams, and R. D. Adams. 2005. Nest survival relative to patch size in a highly fragmented shortgrass prairie landscape. Wilson Bulletin 117: 23-34

Troy, A. R., A. M. Strong, S. C. Bosworth, T. M. Donovan, N. J. Buckley, and M. L. Wilson. 2005. Attitudes of Vermont dairy farmers regarding adoption of management practices for grassland songbirds. Wildlife Society Bulletin 33:528-538

Verboom, J., A. Schotman, P. Opdam, J. A. J. Metz. 1991. European nuthatch metapopulations in fragmented agricultural landscape. Oikos 61: 149-156

Vickery, P. D. 1996. Grasshopper sparrow (*Ammodramus savannarum*). *In* A. Poole and F. Gill, editors. The Birds of North America, No. 175. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Vickery, P. D., M. L. Hunter, Jr., and S. M. Melvin. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology 8:1087-1097

Wilson, T. L., E. J. Johnson, and J. A. Bissonette. 2009. Relative importance of habitat area and isolation for bird occurrence patterns in a naturally patchy landscape. Landscape Ecology 24: 351-360

Winter, M. and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. Conservation Biology 13: 1424-1436

Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102: 256-266

Winter, M., D. H. Johnson, J. A. Shaffer, T. M. Donovan, and W. D. Svedarsky. 2006. Patch Size and Landscape Effects on Density and Nesting Success of Grassland Birds. Journal of Wildlife Management 70: 158-172

Winkler, D. W., P. H. Wrege, P. E. Allen, T. L. Kast, P. Senesac, M. F. Wasson, and P. J. Sullivan. 2005. The natal dispersal of tree swallows in a continuous mainland environment. Journal of Animal Ecology 74: 1080-1090

Tables

Table 1. Mean and standard deviation of stage matrix parameters. Maternity (*M*), adult survival (S_a), juvenile survival (S_j), adult fecundity ($F_a = M \cdot S_a$), and juvenile fecundity ($F_j = M \cdot S_j$).

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	0.64	0.32	0.59	0.29
	SD	0.17	0.12	0.06	0.17	0.07

Table 2. Lambda (λ)values for the six stage matrices, where λ > 1 indicates an increasing population and λ < 1 indicates a declining population Matrices are divided between those where a no-mow management regime is in place and those where mowing happens early in the grasshopper sparrow breeding season. In addition, matrices were divided based on whether they included only small hayfields (< 30 ha), medium hayfields (30 – 70 ha), and large hayfields (>70 ha). Fecundity was reduced according to hayfield size category (see text for details).

Matrix	Lambda
No Mow Small	1.18
No Mow Medium	1.3
No Mow Large	1.41
Mow Small	0.845
Mow Medium	0.89
Mow Large	0.93

Figure legend

Fig. 1. Mean (±SE) relative proportions of small, medium, and large hayfields enrolled in no-mow management in low (7 to 12%), medium (19 to 24%), and high (31 to 36%) enrollment categories.

Fig. 2. Probability of extinction of the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation under three hayfield enrollment scenarios: low (7 to 12 %), medium (19 to 24%), and high (31 to 36%), without and with the effect of patch size on fecundity.

Fig. 3. Probability of extinction of the New Jersey Central Piedmont Plains grasshopper sparrow metapopulation plotted as a function of number of patches included in within three hayfield enrollment categories, where enrollment means no-mow management is in place: low (7 to 12 %), medium (19 to 24%), and high (31 to 36%). These results reflect a reduction in fecundity based on patch size.

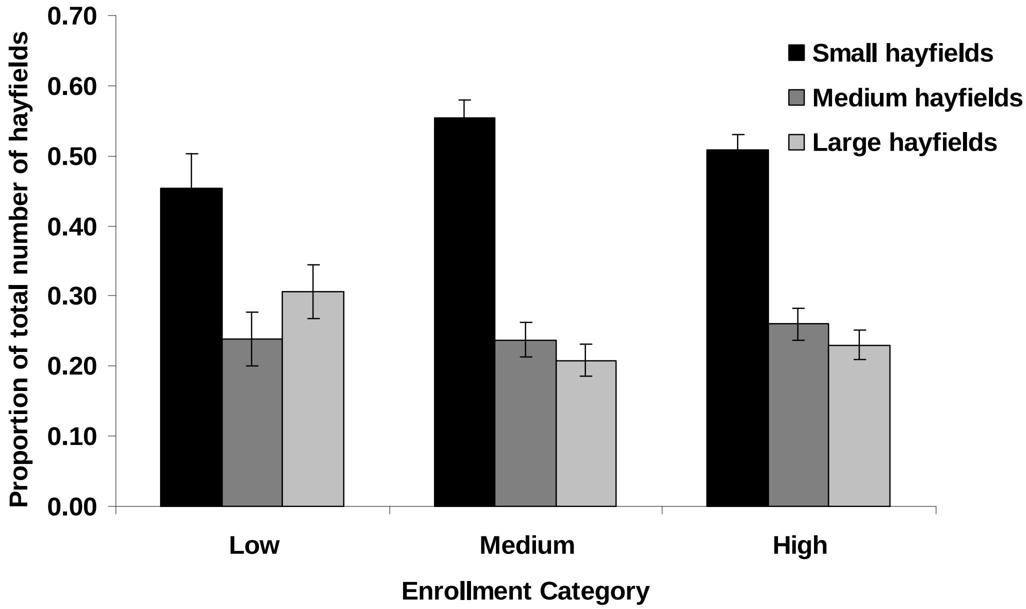

0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Proportion of total number of hayfields
Small hayfields
Medium hayfields
Large hayfields
Low
Medium
High
Enrollment Category

Figure 1

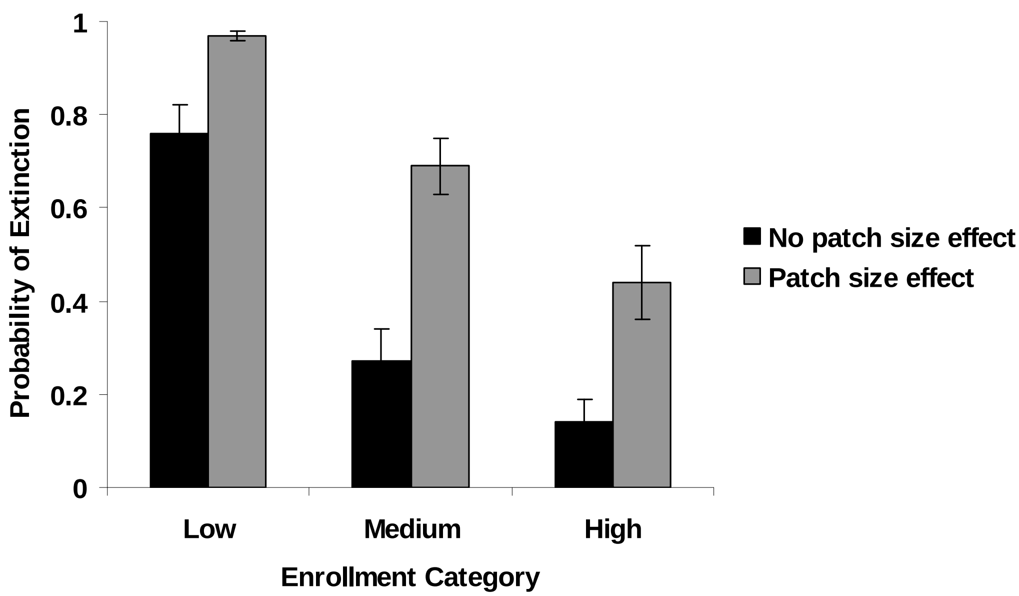
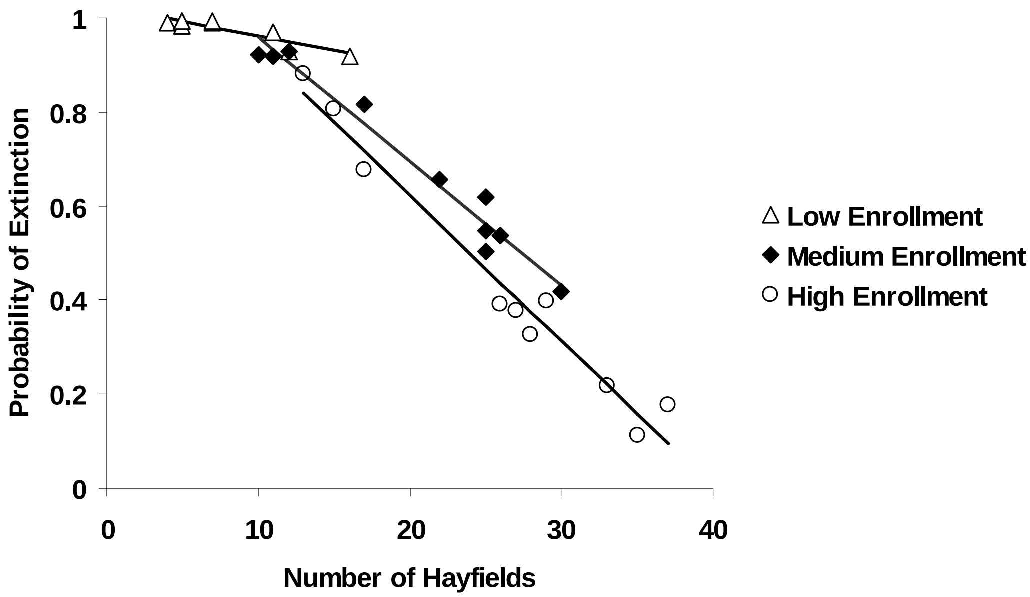

1
0.8
0.6
0.4
0.2
0
Probability of Extinction
Low
Medium
High
Enrollment Category
No patch size effect
Patch size effect

Figure 2



1
0.8
0.6
0.4
0.2
0
0
10
20
30
40
Probability of Extinction
Number of Hayfields
Low Enrollment
Medium Enrollment
High Enrollment

Figure 3

CHAPTER 3

Finding an efficient monitoring scheme to determine the response of a grassland bird metapopulation to conservation actions.

Alison B. Seigel* and Julie L. Lockwood

Ecology, Evolution and Natural Resources

14 College Farm Road

Rutgers, The State University of New Jersey

New Brunswick, NJ 08901

*Corresponding author

ABSTRACT.

Intensification of agricultural practices has led to grassland bird population declines. To address these population declines, hayfields may be enrolled in land owner incentive programs that require grassland bird friendly mowing regimes. Long-term population monitoring is necessary to assess the effectiveness of these avian conservation management actions. Funding for conservation is frequently limited, thus it is critical to design monitoring programs that maximize statistical power to detect population trends while minimizing monetary costs. We explored the trade-offs between survey cost and statistical power when monitoring the response of a simulated grasshopper sparrow metapopulation to enrollment of hayfields in delayed mowing programs. Of three potential monitoring programs, we found that the program most cost-effective in detecting a 7% population decline included 18 hayfields surveyed six times annually over five years. The program most cost-effective in detecting a 2% population decline consisted of 34 hayfields surveyed 8 times annually over seven years. Based on surveys of grasshopper sparrows in a hayfield in our study area conducted independently by three observers we found a high degree of inter-observer variability in density estimates. When we included that variability in our power analysis an additional year of surveying was required to reach the same power level.

Key words: Ammodramus savannarum; *grasshopper sparrow; grassland birds; grassland management; monitoring; observer variability; power analysis; statistical power*

A substantial amount of effort and funding have been expended on monitoring bird populations, especially those that are vulnerable to extinction (e.g. Johnson et al. 2006), resulting in the successful creation of management guidelines and conservation plans. The effectiveness of these efforts, however, can only be judged through the initiation and analysis of long-term follow-up monitoring data (Gibbs et al. 1999). The statistical aspects of monitoring efforts have been well vetted in recent works such as Buckland et al. (2001) and Elzinga et al. (2001). What has lagged is the application of these monitoring principles to specific conservation schemes. There is no single solution for maximizing power to detect population trends while minimizing monetary costs. For example, the most cost-effective monitoring scheme depends heavily on the behavior and life history of the species under management, and on the spatial configuration of areas to be sampled (Jackson et al. 2008, Witczuk et al. 2008). Here we utilize readily available statistical packages to explore the trade-offs between survey cost and statistical power when monitoring the response of grasshopper sparrows (*Ammodramus savannarum*) to enrollment of farmland in grassland conservation schemes.

Grasshopper sparrows and other grassland obligate bird species rely solely on prairie and hayfields for breeding and foraging. In recent decades, the majority of grassland bird species have suffered significant population declines due to habitat loss and agricultural intensification (Bollinger et al. 1990, Herkert 1994, Murphy 2003). Agricultural grasslands that remain in the landscape have become less suitable for breeding as hayfields, are cut earlier in the breeding season, and cutting rotations are shortened (Bollinger and Gavin 1992, Troy et al. 2005).

The growing conservation concern for grassland bird populations has led managers and conservationists to advocate for enrollment of agricultural grasslands into programs such as the Conservation Reserve Program (CRP) and Wildlife Habitat Incentives Program (WHIP). These private land enrollment activities, administered by the United States Department of Agriculture (USDA), offer financial incentives for farmers to manage environmentally sensitive agricultural land for the benefit of grassland birds. In most instances, the farmers agree to delay mowing their hayfields until after resident breeding birds have had time enough to fledge at least one clutch of young. The CRP is the largest of the private lands conservation programs in the US with over 11 million hectares enrolled in various types of grassland in 2007 alone (Barbarika 2007).

Despite the considerable amount of farmland enrolled in these programs and the subsequent potential benefit for grassland birds, long-term monitoring programs that evaluate the success of these programs are rare. Existing studies revealed that grassland birds were more abundant and nest densities higher in CRP farmland than in other habitat types such as cropland (Johnson and Schwartz 1993, Best et al. 1997). Other studies showed that mowing a hayfield during the breeding season reduced fecundity and survival in some grassland bird species (Bollinger et al. 1990, Perlut et al. 2006, 2008). However, these were short-term studies that did not determine the effect of farmland enrollment on grassland bird population trends. Long term studies (≥ 5 years) of the effect of CRP enrollment on grassland birds exist, however they are based on Breeding Bird Survey (BBS) trend data (Reynolds et al. 1994, Herkert 1998). The BBS has known limitations in terms of its ability to accurately detect population trends for species with low abundances and a tendency to avoid edges, such as grassland birds (Fletcher and

Koford 2003, Sauer et al. 2003, Renfrew et al. 2005). Further, population trends occurring on the scale at which BBS surveys are conducted may not accurately represent the population trends occurring at the scale of management (Sauer et al. 2003). To gain the most benefit from our conservation efforts we need cost-effective, long term monitoring programs that are implemented at the appropriate spatial scale and with grassland bird biology in mind.

In New Jersey, managing land for the benefit of grassland birds is particularly important as the state is experiencing rapid urbanization with losses in agricultural land greater than in any other land use type (Hasse and Lathrop 2008). The Central Piedmont (CP) Plains region of New Jersey contains some of the most extensive agricultural complexes left in the State, providing important habitat for several grassland bird species including the State-threatened grasshopper sparrow, a species that experienced a 15.8% decline in New Jersey between 1966 and 2007 (Sauer et al. 2008).

In a previous study, we simulated a CP Plains grasshopper sparrow metapopulation (96 hayfields) under management scenarios with increasing amounts of hayfield area enrolled in delayed mowing programs. Our results indicated that enrolling between 31 and 48% of the total hayfield area (total area = ~4,700 ha) in the landscape resulted in steady population persistence for at least 50 years. Further enrollment of land above 20% only minimally improved persistence (Seigel and Lockwood 2009). Lower enrollment scenarios resulted in a decreasing population trend with an associated relatively high probability of extinction within 50 years. Here we conduct a power analysis to determine the ability of six potential monitoring programs to detect the grasshopper sparrow metapopulation declines that occurred under the low- and mid-enrollment scenarios. There exists an effort to enroll CP Plains farmlands into conservation programs (mostly within WHIP), with a concomitant effort to monitor the status of grasshopper sparrows and other grassland birds in the area using citizen scientists (NJ Audubon 2008). If our recommendations for effective monitoring are applied to this citizen science program, we have the opportunity to use the resulting trend analyses to fine-tune our metapopulation model and the set of lands that are targeted for enrollment.

METHODS

We used MONITOR to evaluate the statistical power of our six monitoring options (Gibbs 1995). These options consider two possible hayfield enrollment scenarios (low- and mid-enrollment levels), with three possible designs within each. To calculate the power of each monitoring program, we first defined the following: (1) the number of hayfields to be monitored, (2) the mean annual grasshopper sparrow abundance in each hayfield (taken from previously published grasshopper sparrow metapopulation simulations, see below), (3) the within- and between-hayfield variation in abundance estimates, (4) the duration of monitoring, (5) the interval of monitoring, (6) the type of population trend (linear or exponential), and (7) the significance level associated with trend determination. Based on user-defined conditions, MONITOR generated many simulated sets of count data and randomly drawn sample counts and then calculated the proportion of trials in which population trends (determined by regression) differed significantly from zero. This proportion, measured from 0 (low power) to 1 (high power), was the power estimate and indicated how effective the specified monitoring program was at detecting a particular trend. We considered a monitoring program as successful when the specified population trend was detected with a power of 0.90 ($p \leq 0.05$).

Because the grasshopper sparrow metapopulation simulations of Seigel and Lockwood (2009) generated unique population trajectories under each of the two management scenarios (low- and mid-enrollment), we conducted two separate power analyses based on these results. We parameterized both analyses based on data from one simulation run under the respective management scenario. We randomly selected this run from ten runs reported by Seigel and Lockwood (2009) under each enrollment scenario.

Because our goal was to design a survey that could validate the conservation actions suggested by the simulations of Seigel and Lockwood (2009), we defined the trend to be detected (or the effect size) as the average inter-annual increase or decrease in the grasshopper sparrow CP Plains metapopulation over the 50-year time span of our simulations. In the low- and mid-enrollment scenarios, the simulated grasshopper sparrow metapopulation decreased at an annual rate of 7% and 2%, respectively. Therefore, we assessed how the power to detect a 7% decrease in abundance of grasshopper sparrows under the low-enrollment scenario and a 2% decrease under the high-enrollment scenario varied across different monitoring schemes. All population trajectories were exponential in nature.

MONITOR used interannual variation in abundance within hayfields, and also trend variation among hayfields, to calculate power. In the metapopulation simulations of Seigel and Lockwood (2009), each hayfield experienced a set degree of environmental stochasticity from year to year (within-hayfield variation), which affected the fecundity and survival rates of the grasshopper sparrows occupying that field. Thus to obtain interannual variation in abundance for each hayfield, we compared the 50-year simulated population trajectory that included environmental stochasticity with a simulated trajectory (based on the same inputs) that did not include environmental stochasticity. We then calculated the standard deviation of the annual differences in abundance between the two trajectories and incorporated it into MONITOR for each hayfield (min 1.92, max 12.65). Overall population trends also differed to varying degrees among hayfields due to spatial autocorrelation in environmental conditions. We used the coefficient of variation associated with the mean population trend across hayfields as a rough estimate of inter-site variability in local population trends (min 0.07, max 0.67). Population trend data was taken from the metapopulation simulations of Seigel and Lockwood (2009) (mean annual hayfield abundance min 5, max 40).

We varied three components of the monitoring program while holding all other variables constant to determine the minimum survey effort necessary in each case to achieve a power of 0.90: number of hayfields surveyed, duration of monitoring, and interval between surveys. For the first component, number of hayfields surveyed, we added randomly selected hayfields to the monitoring program until we reached the desired 0.90 power. Hayfields were chosen randomly regardless of their status as enrolled in a delayed mowing program or not. This decision is biologically warranted because grasshopper sparrows do not apparently distinguish between the two types of agricultural hayfields (enrolled or not) when selecting breeding habitat in the spring, and the population trends reported by Seigel and Lockwood (2009) were similar in both types of hayfields. For the second component, the duration of monitoring, we evaluated monitoring programs for the low-enrollment scenario that were 4 and 5 years in duration (Monitoring Programs 1 and 2); and for the mid-enrollment scenario, we evaluated programs that were 7 and 8 years duration (Monitoring Programs 4 and 5). We chose these lengths of time based on preliminary calculations that indicated that these were the minimum annual monitoring durations necessary to achieve the desired 0.90 power level. For the third component, interval between surveys, we lengthened the interval of monitoring from annual to every other year to determine if this would increase the efficiency (i.e. lower costs to achieve the same power) of a monitoring program (Monitoring Programs 3 and 6).

Sampling error decreases the precision of density estimates resulting in a lower probability of detecting a trend in a population (Diefenbach et al. 2003). To assess the degree that precision will vary between observers, especially for relatively untrained volunteers typical of a citizen science monitoring program, we had four observers conduct line transect distance sampling of grasshopper sparrows in one of the subpopulations of the CP Plains grasshopper sparrow metapopulation (Skeet Field) during the breeding seasons of 2004 through 2007. After the observers completed all surveys, we entered the data set into *Distance 5.0*, a program that fits detection function models to the distance sampling data to generate a density estimate (Buckland et al. 2001). We generated annual density estimates for the grasshopper sparrow population in Skeet Field based on the observers’ data combined (in 2004 and 2006 when two observers counted birds) and for the individual observers that counted sparrows in 2005 and 2007.

Our distance sampling results revealed a high degree of variation in density estimates among observers both between-years and within-years (see below). To determine how added variation from sampling error affected the power to detect population trends, we increased the inter-annual variation associated with each hayfield by 20% in the four-year and five-year power analyses. We chose a 20% increase because this was a conservative estimate of sampling error based on the between-observer variation we detected and may represent a realistic level of variation present in monitoring programs involving multiple observers (Diefenbach 2003).

We assessed cost-effectiveness of monitoring programs by calculating the survey time in hours required to successfully reach our desired power level. We assigned a survey time to each hayfield based on its size: small hayfields (0-50ha) = 3 hours, 14 minutes; medium hayfields (51-100ha) = 6hrs, 28min; large hayfields (101-150ha) = 9hrs, 42min; and extra large hayfields (>150ha) = 12hrs, 56min. Times were calculated based on the average amount of time it took to conduct distance sampling at Skeet Field, a medium sized hayfield. Total survey time required for each monitoring program consisted of the total survey time for all fields multiplied by the number of survey occasions.

RESULTS

The estimated density of grasshopper sparrows within Skeet Field differed among observers and years (Table 1). The overall high (51 male sparrows) and low (19 males sparrows) density estimates occurred within the same year (2004). The coefficient of variation for density estimates by Observers 1 and 2 in 2004 was 0.22, and 0.65 for density estimates by Observers 3 and 4 in 2006.

The power to detect a 7% population decline increased with increasing numbers of hayfields surveyed in both the four and five year monitoring programs (Monitoring Programs 1 and 2; Fig. 1). We found that by decreasing the survey frequency from annual to bi-annual in Monitoring Program 1, an additional two years were necessary to reach the target power of 0.90 (Table 2). Monitoring Program 2 required the fewest time units and hayfields surveyed to reach target power.

The power to detect a 2% population decline (mid-enrollment management scenario) increased as the number of hayfields surveyed rose in both the seven and eight year monitoring programs (Monitoring Programs 4 and 5; Fig. 2). We found that by decreasing the survey frequency from annual to bi-annual in Monitoring Program 4, an additional three years were necessary to reach a power of 0.90 (Table 2). Monitoring Program 6 required the fewest time units to reach a power of 0.90 (Table 2).

We were able to detect the 7% population decline in the low enrollment scenario with less effort and in a shorter time frame than we could detect the 2% decline in the mid-enrollment scenario. When we included an additional year of surveys in Monitoring Program 1, power to detect a 7% decline increased at a higher rate as hayfields were added to the monitoring protocol (Fig. 1). This result did not hold true for the Monitoring Programs of the mid-enrollment scenario; both programs reached 0.90 at a similar rate despite there being a difference in monitoring duration of one year (Fig. 2).

By incorporating a 20% increase in interannual variation due to sampling error (low precision), the power to detect a 7% annual decrease (low enrollment management scenario) in population abundance by Monitoring Program 1 decreased from 0.91 to 0.79 (Fig. 3). An additional year of surveying was necessary to reach power of 0.90 under this assumption, thereby increasing the total number of hours from 970 to 1164. In Monitoring Program 2, power decreased from 0.91 to 0.81 when interannual variation was increased by 20%. To reach the desired power of 0.90, an increase in the total hours surveyed from to 698 to 815 is required. When we increased interannual variation by 20% in Monitoring Programs 4 and 5 the power to detect a 2% population decrease fell from 0.90 to 0.81 and from 0.91 to 0.87 (Fig. 3). Although in both cases an extra year of surveys is necessary, the total hours required are less than the equivalent results when detecting a 7% decline.

DISCUSSION

Monitoring programs frequently provide the information on which management decisions are based, and as such, their ability to accurately represent population dynamics is critical to the success of conservation efforts (Gibbs et al. 1999, Field et al. 2007, Martin et al. 2007). We explored the effectiveness of a monitoring program at two scales by: (1) evaluating the accuracy of the data being collected at the level of the individual survey and (2) determining the ability of multiple monitoring designs to provide the statistical power necessary to detect a biologically significant population trend. Although we used grassland bird monitoring as an example, our approach and broad conclusions are applicable to any type of biological monitoring program.

To avoid making inappropriate management decisions, monitoring programs should be evaluated based on their cost-effectiveness and statistical power to detect a population trend. Based on the Marsh and Trenham (2008) survey of over 300 people involved in monitoring, most monitoring programs last from 3 to 10 years, and over half of the people said that their monitoring program was limited by lack of money and/or time, thereby indicating the importance of cost-effectiveness. Further, if a monitoring program is not able to detect a biologically significant population trend with reasonable statistical power, the financial and human resources used for that program have been wasted and the need to implement necessary management for a species has been missed (e.g., Zorn et al. 2003).

We found that by adding one additional year of surveys to Monitoring Program 1, we could reduce the amount of survey effort necessary to achieve 90% power by 28%. We also found that, by increasing the duration of Monitoring Program 3 by three years, we reduced the monitoring effort required to reach our power goal by 25%. The tradeoff between time and monitoring resources (i.e. money) however, is not always straightforward. Biologists and managers must decide on a case-by-case basis whether it is more important to reduce the amount of time or the amount of devoted resources necessary to detect a declining trend in a population.

We found a considerable amount of variation in density estimates among observers. In one instance, the difference between estimates was greater than 2-fold. A high level of inter-observer variability such as that found in our study reduces the probability of detecting real trends in population numbers across space or through time. When we included a conservative estimate of inter-observer variability in our power analysis, the statistical power to detect the desired population trend decreased by as much as 13%, with a stronger effect occurring in the low enrollment management scenario.

This decrease is not trivial when dealing with the conservation of threatened and endangered species, such as the grasshopper sparrow. If a declining trend is not detected, appropriate management aimed at reversing or slowing the decline may not be implemented. Further, there is a tradeoff between monitoring precision and monitoring effort. Monitoring effort must be increased to overcome the effect of sampling error on the power to detect a trend, requiring more funding to obtain the necessary data. For example, for Monitoring Program 1 we estimated that an additional 194 survey hours would be necessary to overcome the effect of sampling error on power. Although the number of observers in our study was low, we believe their range of skills may be typical of differences among observers in any other grassland bird study and suggests caution when drawing conclusions from density data collected using even the best counting methodologies.

We were able to detect the 7% population decline with almost half the monitoring effort necessary to detect the 2% decline. A larger effect size is “easier” to detect because it creates more separation between the null hypothesis of zero change in population abundance and the alternative hypothesis that there is a population trend occurring. Larger effect size reduces Type I error or the probability that a significant trend will be falsely detected. This is a characteristic of monitoring that is advantageous for conservation efforts; as a population decline increases in magnitude, the time necessary to detect that decline decreases.

We used the widely accepted alpha level of 0.05 in our power analysis. However, some have argued that alpha may be relaxed in order to gain a savings in monitoring effort in cases where there is a strong *a priori* expectation that a decline is occurring

(Field et al. 2007). In doing so, we are increasing the probability of Type I error, or the probability that a significant population trend would be detected when it is not actually occurring. We were conservative with what we considered to be a satisfactory power level (0.9), however, a power of 0.8 is frequently considered acceptable (Freilich et al. 2005). Reducing the power level (or increasing Beta) increases the probability of not detecting a trend when one is actually occurring, or Type II error. Alpha and Beta levels should be defined based on the potential consequences associated with making both types of errors. In our case of monitoring a grasshopper sparrow metapopulation under delayed mowing grassland management, a Type I error, or detecting a significant declining population trend when one was not occurring, could lead to further enrollment of additional hayfields into delayed mowing management. A Type II error, or not detecting a significant population trend when one was occurring in reality, would result in continued population decline because no further management actions would be taken. It is up to managers to decide on the relative importance of Type I and II errors. Simulations such as ours can provide managers with a transparent schema for balancing these concerns.

ACKNOWLEDGEMENTS

We thank Brian Clough, Matthew Sileo, Thomas Almendinger, Tabby Fenn, and Ryan Sklar for their participation in field data collection. We thank Troy Ettel for input on the logistics of farm enrollment and other insights into management. Partial funding for this work was provided by the Duke Farms Foundation and Rutgers University to JLL.

LITERATURE CITED

ANDERSON, D. R., K. P. BURNHAM, B. C. LUBOW, L. THOMAS, L., P. S. CORN, P. A. MEDICA, AND R. W. MARLOW. 2001. Field trials of line transect methods applied to estimation of desert tortoise abundance. Journal of Wildlife Management 65: 583-597

BARBARIKA, A. 2007. Conservation Reserve Program Summary and Enrollment Statistics, Fiscal Year 2007. http://www.fsa.usda.gov/Internet/FSA_File/annual_consv_2007.pdf

BEST, L. B., H. CAMPA III, K. E. KEMP, R. J. ROBEL, M. R. RYAN, J. A. SAVIDGE, H. P. WEEKS, JR., AND S. R. WINTERSTEIN. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. Wildlife Society Bulletin 25: 864-877

BOLLINGER, E. K., P. B. BOLLINGER, AND T. A. GAVIN. 1990. Effects of hay-cropping on eastern populations of the bobolink. Wildlife Society Bulletin 18: 142-150

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, United Kingdom.

DIEFENBACH, D. R., D. W. BRAUNING, AND J. A. MATTICE. 2003. Variability in grassland bird counts related to observer differences and species detection rates. Auk 120: 1168-1179

ELZINGA, C. L., D. W. SALZER, J. W. WILLOUGHBY, AND J. P. GIBBS. 2001. Monitoring Plant and Animal Populations. Blackwell Science, Inc. Malden, MA.

FIELD, S. A., P. J. O'CONNOR, A. J. TYRE, AND H. P. POSSINGHAM. 2007. Making monitoring meaningful. Austral Ecology 32: 485-491

FLETCHER, R. J. AND R. R. KOFORD. 2003. Spatial responses of bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. Auk 120: 799-810

FREILICH, J. E., R. J. CAMP, J. J. DUDA, AND A. E. KARL. 2005. Problems with sampling desert tortoises: a simulation analysis based on field data. Journal of Wildlife Management 69: 45-56

GIBBS, J.P. 1995. MONITOR 7.0: Software for estimating the statistical power of population monitoring programs. USGS-Patuxent Wildlife Research Center, Laurel, MD. http://www.mbr-pwrc.usgs.gov/software/monitor.html

GIBBS, J.P., H. L. SNELL, AND C. E. CAUSTON. 1999. Effective monitoring for adaptive wildlife management: Lessons from the Galapagos Islands. Journal of Wildlife Management 63: 1055-1065

HANNAFORD, M. J., M. T. BARBOUR, AND V. H. RESH. 1997. Training reduces observer variability in visual-based assessments of stream habitat. Journal of the North American Benthological Society 16: 853-860

HASSE, J. AND R. G. LATHROP. 2008. Tracking New Jersey's dynamic landscape: Urban growth and open space loss 1986-1995-2002. Center for Remote Sensing and Spatial Analysis, Rutgers University, New Brunswick, NJ. http://www.crssa.rutgers.edu/projects/lc/urbangrowth/

HERKERT, J.R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461-471

HERKERT, J. R. 1998. The influence of the CRP on grasshopper sparrow population trends in the mid-continental United States. Wildlife Society Bulletin 26: 227-231

JACKSON, A. L, A. C. BRODERICK, W. J. FULLER, F. GLEN, G. D. RUXTON, AND B. J. GODLEY. 2008. Sampling design and its effect on population monitoring: How much monitoring do turtles really need? Biological Conservation 141: 2932-2941

JOHNSON, L., R. J. CAMP, K. W. BRINCK, AND P. C. BANKO. 2006. Long-term population monitoring: Lessons learned from an endangered passerine in Hawaii. Wildlife Conservation 34:1055-1063

JOHNSON, D. H. AND M. D. SCHWARTZ. 1993. The Conservation Reserve Program and grassland birds. Conservation Biology 7:934-937

KEPLER, C. B. AND J. M. SCOTT. 1981. Reducing bird count variability by training observers. Studies in Avian Biology 6: 366-371

MARSH, D. M, AND P. C. TRENHAM. 2008. Current trends in plant and animal population monitoring. Conservation Biology 22: 647-655

MARTIN, J., W. M. KITCHENS, AND J. E. HINES. 2007. Importance of well-designed monitoring programs for the conservation of endangered species: Case study of the snail kite. Conservation Biology 21:472-481

NEW JERSEY AUDUBON SOCIETY. Grassland Survey Results. http://www.njaudubon.org/Research/CitizenScience/Grass_2005_results.html Accessed February 23, 2008

PERLUT, N. G., A. M. STRONG, T. M. DONOVAN, AND N. J. BUCKLEY. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications 16:2235-2247

PERLUT, N. G., A. M. STRONG, T. M. DONOVAN, AND N. J. BUCKLEY. 2008. Grassland songbird survival and recruitment in agricultural landscapes: implications for source-sink demograpy. Ecology 89:1941-1952

RENFREW, R.B., C. A. RIBIC, AND J. L. NACK. 2005. Edge avoidance by nesting grassland birds: A futile strategy in a fragmented landscape. Auk 122: 618-636

REYNOLDS, R. E., T. L. SHAFFER, J. R. SAUER, AND B. G. PETERJOHN. Conservation Reserve Program: benefit for grassland birds in the Northern Plains. Transactions of the North American Wildlife Resources Conference 59: 328-336

SAUER, J. R., J. E. FALLON, AND R. JOHNSON. 2003. Use of North American Breeding Bird Survey data to estimate population change for Bird Conservation Regions. Journal of Wildlife Management 67: 372-389

SAUER, J. R., J. E. HINES, AND J. FALLON. 2008. The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. Version 5.15.2008. *USGS Patuxent Wildlife Research Center*, Laurel, MD

SEIGEL, A. B. AND J. L. LOCKWOOD. 2009. How increasing levels of private land enrollment in conservation agreements affect the population viability of grassland birds. Ecological Applications *In review*

THOMPSON, A. A. AND B. D. MAPSTONE. 1997. Observer effects and training in underwater visual surveys of reef fishes. Marine Ecology Progress Series 154: 53- 63

TROY, A. R., A. M. STRONG, S. C. BOSWORTH, T. M. DONOVAN, N. J. BUCKLEY, AND M. L. WILSON. 2005. Attitudes of Vermont dairy farmers regarding adoption of management practices for grassland songbirds. Wildlife Society Bulletin 33: 528-538

WITCZUK, J., S. PAGACZ, AND L. S. MILLS. 2008. Optimising methods for monitoring programs: Olympic marmots as a case study. Wildlife Research 35: 788-797

ZORN, P., T. LINKE, M. SMITH, AND V. BLAZESKI. 2003. Optimizing limited monitoring capacity: Applying power analysis as a management tool for the ecological integrity program at Point Pelee National Park. Science and Management of Protected Areas Association 5th International Conference. Victoria, British Columbia, Canada

Table 1. Estimated density (males per hectare) and population size of grasshopper sparrows in a medium-sized agricultural field within the focal metapopulation for four observers. Population size is the number of individuals estimated to be in this field based on its area (70 ha) and the density estimate.

Year		**Density (ind./ha)**	**Population size**
2004	Observer 1	0.849	51
	Observer 2	0.312	19
	Observers 1 + 2	0.592	36
2005	Observer 3	0.493	30
2006	Observer 3	0.053	32
	Observer 4	0.072	44
	Observers 3 + 4	0.656	39
2007	Observer 4	0.624	37

Table 2. Attributes of three monitoring programs that achieve a power of 0.90 to detect a 7% population decline in the CP Plains grasshopper sparrow metapopulation, and attributes of another three monitoring programs that achieve a power of 0.90 to detect a 2% decline. Attributes varied between monitoring programs include: duration of monitoring in years, number of survey occasions, number of hayfields surveyed with percent of total number of hayfields in the metapopulation in parentheses, and time in hours required for completion of entire monitoring program.

Management scenario	**Monitoring Program**	**Duration (years)**	**Number of survey occasions**	**Number of hayfields surveyed**	**Time (hrs)**
Low-enrollment (7% decline)	1	4	5 annual	29 (30)	970
	2	5	6 annual	18 (19)	698
	3	6	4 bi-annual	29 (30)	776
Mid-enrollment (2% decline)	4	7	8 annual	34 (35)	1630
	5	8	9 annual	28 (29)	1659
	6	10	6 bi-annual	34 (35)	1222

FIGURE LEGEND

Fig. 1. Power analysis of two monitoring programs for a grasshopper sparrow metapopulation with a low-enrollment of hayfield in delayed mowing management. Lines indicate the power of 4-year (5 survey occasions) and 5-year (6 survey occasions) monitoring programs with increasing numbers of annually surveyed hayfields to detect a 7% decrease in sparrow abundance. Horizontal line indicates power of 0.90.

Fig. 2. Power analysis of two monitoring programs for a grasshopper sparrow metapopulation with a high-enrollment of hayfield in delayed mowing management. Lines indicate the power of 7-year (8 survey occasions) and 8-year (9 survey occasions) monitoring programs with increasing numbers of annually surveyed hayfields to detect a 2% decrease in sparrow abundance. Horizontal line indicates power of 0.90.

Fig. 3. Effect of a 20% increase in interannual variation due to sampling error on power to detect declining population trends (dark bars) and the number of survey hours necessary to reach a power of 0.90 (light bars). Monitoring Programs 1 and 2 were designed to detect a 7% population decrease in the low enrollment management scenario. Monitoring Programs 4 and 5 were designed to detect a 2% population decrease in the mid-enrollment management scenario.

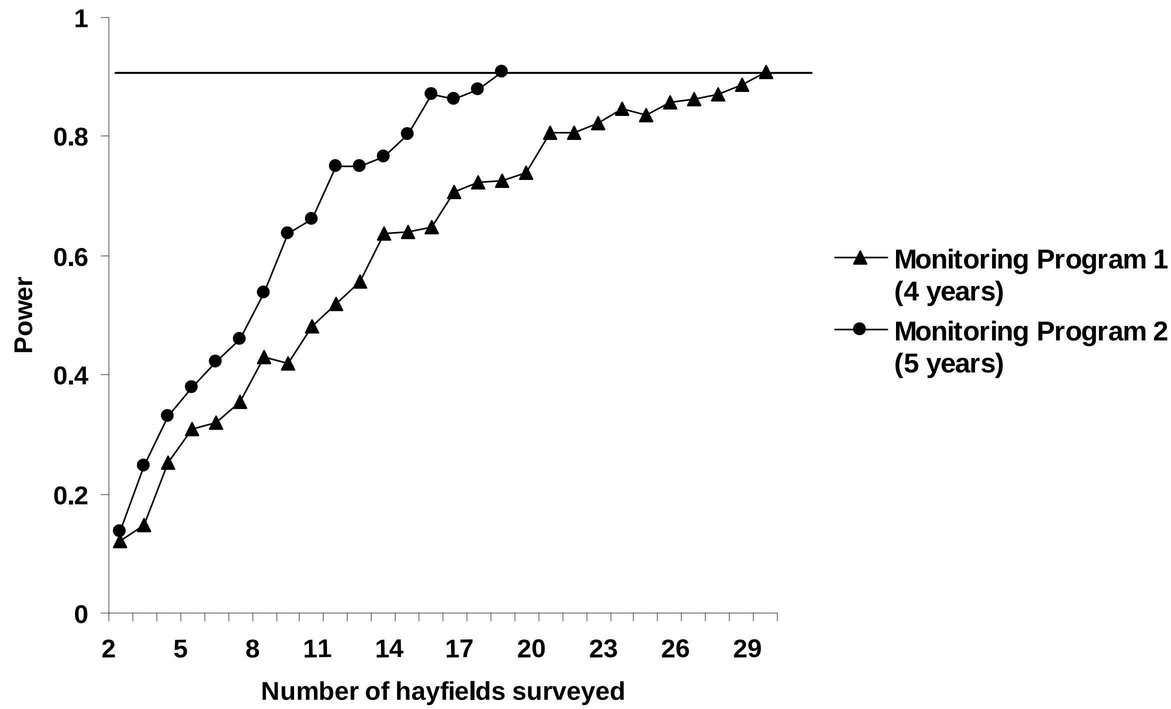
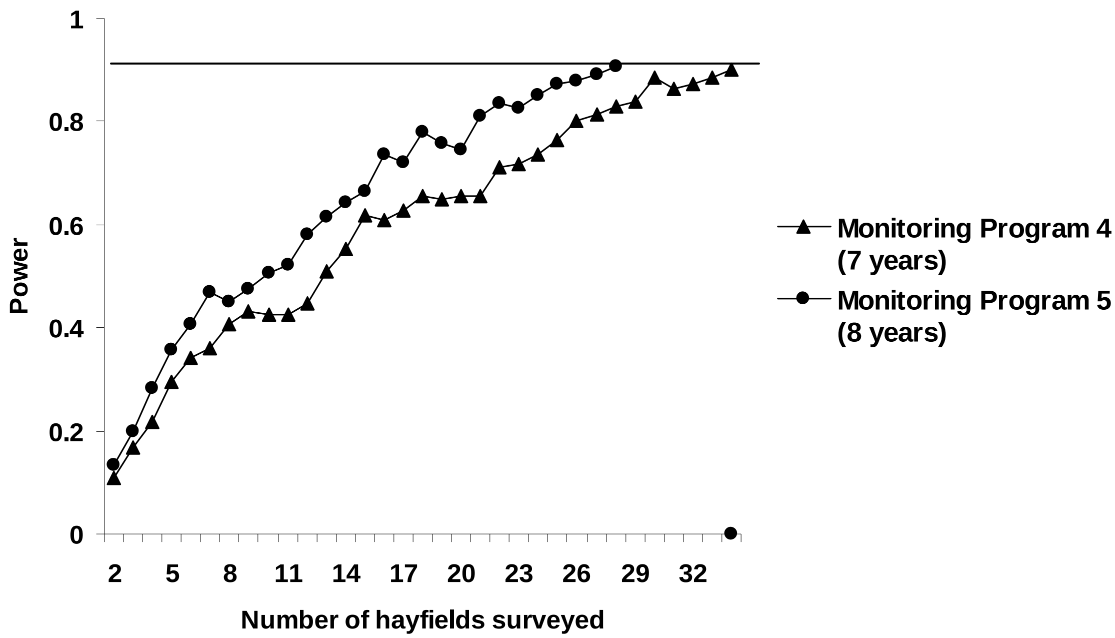

1
0.8
0.6
0.4
0.2
0
Power
2
5
8
11
14
17
20
23
26
29
Number of hayfields surveyed
Monitoring Program 1 (4 years)
Monitoring Program 2 (5 years)

Fig. 1



1
0.8
0.6
0.4
0.2
0
Power
2
5
8
11
14
17
20
23
26
29
32
Number of hayfields surveyed
Monitoring Program 4 (7 years)
Monitoring Program 5 (8 years)

Fig. 2

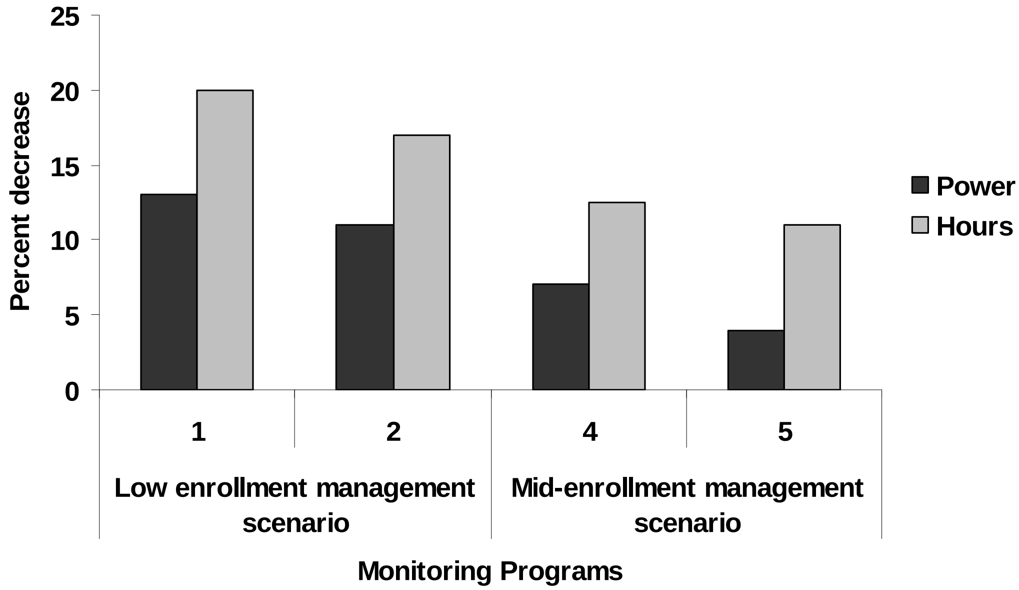

25
20
15
10
5
0
Percent decrease
Power
Hours
1
2
4
5
Low enrollment management scenario
Mid-enrollment management scenario
Monitoring Programs

Fig. 3

CONCLUDING REMARKS

The overarching goal of my research was to explore factors influencing the effectiveness of hayfield management for grassland bird conservation. There are numerous regions throughout the United States where declining grassland bird populations depend on fragmented agricultural grasslands for breeding habitat. If we are to succeed in our efforts to reverse population declines it is critical to maximize the effectiveness of grassland management in these regions by developing informed, landscape-scale conservation plans. My research specifically addressed how grasshopper sparrow metapopulation persistence was affected by the total area of managed grassland in the landscape, the number of grasslands in the landscape, and grassland size and isolation. I also emphasized the importance of developing effective monitoring programs to evaluate the response of grassland bird populations to management.

In Chapter 1, I built a spatially-explicit, stage-structured, stochastic model of a grasshopper sparrow metapopulation based on field data and published data. I used this model to study how increasing the total area of managed hayfields in a landscape affected the extinction risk of a grasshopper sparrow metapopulation. I found that the probability of extinction of the grasshopper sparrow metapopulation decreased considerably as more grassland area was enrolled in a delayed mowing management program. However, after between 31 to 48% of the total hayfield area in the landscape was under delayed mowing management, any additional enrollment only produced minimal reduction of extinction risk. This result is important in that it demonstrates that grassland bird populations can persist without having to protect or manage all remaining grassland habitat in the landscape.

I also unexpectedly found that the number of enrolled grasslands in a landscape had a significant effect on metapopulation persistence; all else constant, grasshopper sparrows had a lower risk of extinction in landscapes with higher numbers of enrolled hayfields. This result directed my attention to the effect of local source and sink subpopulations on the overall persistence of the metapopulation. Hayfields that are mowed during the breeding season produce sink populations, which have a detrimental effect on metapopulation persistence. Increasing the number of enrolled hayfields (i.e. population sources) in the landscape effectively decreases the number of population sinks and therefore the probability of metapopulation extinction decreases as well.

In Chapter 2, I modified the Chapter 1 model to examine how patch size may affect grasshopper sparrow metapopulation persistence by incorporating a direct relationship between grassland size and grasshopper sparrow fecundity. I found that while probability of extinction still decreased as more hayfield was enrolled in delayed mowing management, a patch size effect increased the risk of extinction at all levels of hayfield enrollment. According to published studies, there is no universal rule regarding the effect of grassland size on grasshopper sparrow fecundity. This relationship appears to vary in its intensity and according to geographic region. Because a patch size effect has the potential to increase the risk of extinction of a grassland bird metapopulation as shown in my research, it is critical to understand and consider this relationship in the region being targeted for conservation.

I also took a landscape scale approach to hayfield management by testing the effect of hayfield isolation on metapopulation persistence. I found that grasshopper sparrow probability of extinction was significantly higher when managed hayfields were dispersed throughout the landscape than when they were spatially clumped. I believe clumping source populations (i.e. managed hayfields) enables greater population growth because dispersing juveniles have a higher chance of selecting another managed hayfield as breeding habitat than selecting sink habitat.

In Chapter 3, I evaluated the cost-effectiveness of potential grasshopper sparrow monitoring programs using statistical power analysis. I found that the program most cost-effective in detecting a 7% population decline included 18 hayfields surveyed six times annually over five years. Monitoring programs that aimed to detect a lesser population decline were more costly. Grasshopper sparrow surveys conducted in the field by multiple observers revealed a large amount of variability in density estimates due to sampling error. At least one additional year of sampling would have to be added to a monitoring program to overcome this variability.

My research shows that it is possible to maintain viable grassland bird metapopulations in fragmented agricultural landscapes by enrolling hayfields in delayed mowing management programs. To support a grasshopper sparrow metapopulation specifically, 31 to 48% of hayfield area should be enrolled with more area required if there is a decrease in fecundity with decreasing hayfield size. When the total enrolled grassland area in a landscape is relatively low (1 to 5% of all grassland area) priority should be placed on enrolling more land. However, when the total amount of enrolled land is closer to 8% or higher, priority should also be placed on maximizing the number of hayfield parcels enrolled. Increasing the number of enrolled hayfields decreases the number of sink habitat patches in the landscape and therefore decreases the probability of extinction. Finally, regardless of the proportion of enrolled grassland in a landscape, hayfields in close proximity to existing enrolled land should be targeted first as metapopulation persistence is highest when managed hayfields are spatially clumped.

Grassland management decisions are frequently based on metapopulation models. As a result, monitoring is a critical part of grassland bird conservation because it provides abundance data that can be used to validate and then improve upon the metapopulation models. The improved models can provide the data necessary to generate more effective management strategies and thus the goal of adaptive management is achieved. Monitoring resources (e.g. funding) are frequently limited, however, making cost-effectiveness a priority. Power analysis is a valuable tool in designing a cost-effective monitoring program for grassland birds.

Population viability analysis is a powerful conservation tool for use in evaluating the effectiveness of a range of grassland management scenarios. Future research should focus on obtaining more precise vital rates of grassland birds including fecundity and survival in grasslands of different sizes and adjacent to various land uses. We can use this data to improve the accuracy of metapopulation models and therefore improve management decisions directed at reversing the declines of grassland birds.

Curriculum Vitae

Alison Seigel

Education

Institution	Degree	Year
Emory University, Atlanta, GA	B.S. Biology	1999
Rutgers University, New Brunswick, NJ	M.S. Ecology and Evolution	2006
Rutgers University, New Brunswick, NJ	Ph.D. Ecology and Evolution	2009

Publications

Seigel, A. and J. Lockwood. 2006. Phase I results: Conservation of Threatened Birds on Agricultural Grasslands at Duke Farms. Doris Duke Foundation.

Seigel, A., C. Hatfield, and J.M. Hartman. 2005. Avian Response to Restoration of Urban Tidal Marshes in the Hackensack Meadowlands, New Jersey. Urban Habitats 3: 87-116

Seigel, A. 2003. Avian survey at the Harrier Meadow Wetlands Mitigation site in Hartman, J.M. 2003. Harrier Meadow Wetlands Mitigation Site Fifth Annual Monitoring Report. New Jersey Meadowlands Commission, Lyndhurst, New Jersey