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Effects of Hayfield Management on Grassland Songbirds: Behavioral Responses and Population Processes

A Dissertation Presented

by

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The Faculty of the Graduate College

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Specializing in Natural Resources

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ABSTRACT

Over the last 40 years North American grassland bird populations have declined more than any other bird guild. This trend is especially evident in Vermont, where species experiencing precipitous declines include the Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*). These declines are linked to habitat loss due to reforestation and suburbanization as well as the intensification of grassland management.

Modern grassland management includes earlier first-haying dates (late-May) and shorter intervals between haying events (35 days). These management practices have severe repercussions for songbird populations because 1) early-haying results in complete nest failure (99% Savannah Sparrow and 100% Bobolink nests), 2) the interval between the first and second haying is too short for birds to renest, and 3) intensively managed fields comprise a significant portion of the total available habitat (as much as 40%).

In 2002-2006, I examined how hayfield and pasture management affected grassland songbird ecological and evolutionary behavior in the agricultural landscape of the Champlain Valley, Vermont and New York. I studied songbirds in four grassland management types: *early-hayed* fields harvested in late-May or early-June and again in mid-July; *middle-hayed* fields harvested in late-June or early-July; *late-hayed* fields harvested after 1 August; r*otationally*-*grazed* pastures, a matrix of small paddocks where cows are moved after the grass in a paddock is eaten to a low point. I addressed the following objectives:

1. Determined the annual productivity, survival, and recruitment of Bobolinks and Savannah Sparrows in the four treatment types.
2. Identified the effects of early-haying on the social and genetic mating systems of Savannah Sparrows.
3. Conducted a population viability analysis for Bobolinks and Savannah Sparrows nesting in the Champlain Valley, assessing sensitivities of life-history parameters and identifying effective management alternatives.

This study provides information on how agricultural management affects the ecology, evolution, and viability of grassland birds. It will help inform landowners, managers, and law-makers about management practices and habitat requirements needed to sustain populations.

DEDICATION

To my wife, best friend, and inspiration, Stacey. Thank you for your endless support and encouragement, particularly every summer morning at 4 a.m.

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Foreword

Conservation biology is rooted in questions of how and why populations change. Here, *change* refers both to landscape-level alterations like population growth and decline as well as local and individually-based adaptations like mate choice and sexual selection. As such, the goal of this dissertation is to decompose landscape-level interactions into individually-based behaviors, as well as to aggregate individually-based behaviors into landscape-level interactions.

This work explores local, individually-based data on annual productivity, adult survival, recruitment, and mating systems, and applies these data to landscape-level questions of population growth. This research focuses on two grassland obligate species whose populations are declining, the Savannah Sparrow (*Passerculus sandwichensis*) and the Bobolink (*Dolichonyx oryzivorus*), both breeding in the Champlain Valley of Vermont and New York, USA.

With 146,000 ha of managed grasslands (NASS 1999), the Champlain Valley stands as one of the largest, most contiguous northeastern agricultural landscapes. This region mainly consists of small, privately owned parcels, complicating research and conservation which must therefore address the fragmented nature of both ownership and management interests. Given the Champlain Valley's complicated landscape, the fact that this region was historically forested, and that all grasslands must be maintained by management, it is reasonable to ask whether research and conservation efforts should instead be undergone within the species' historic ranges. For example, would species conservation be more effective in large, contiguous, single-owner regions such as in the federally owned Neal Smith National Wildlife Refuge, Iowa, where 3239 ha of tallgrass prairie is being restored; the Konza Prairie, a 3487 ha tallgrass prairie managed by Kansas State University and the Nature Conservancy; or the five ranches covering ~144,000 ha Ted Turner owns in Nebraska's Sandhills?

This dissertation begins with the understanding that research and conservation efforts for declining species should focus both in regions with significant populations and in historic regions where habitat and species can be restored. For example, although Illinois was once a core region for breeding Bobolinks, between 1966 and 2005, populations in that state declined by 8.6% annually (Sauer et al. 2005). The combination of such long-term population decline in traditional habitat and a simultaneous, though only moderate, degrading of northeastern habitats, has resulted in a Bobolink population in traditional breeding areas like Illinois that is one-quarter to one-third that of eastern hayfields (Bollinger and Gavin 1992). Considering these changing landscapes, it seems reasonable to study existing large, albeit declining, populations in non-traditional habitat, as such conservation may prevent species endangerment and act as a storing house for significant evolutionarily information. Finally, although this research examines the life-histories of two specialized species, its themes, analytical framework, questions asked, and questions answered will hopefully cross ecological and conservation boundaries.

Study Species

Bobolinks and Savannah Sparrows account for the vast majority (92%) of the Champlain Valley's obligate grassland nesting community (Shustack 2004). The differences and similarities between these two species provide an ideal model to examine management of the Champlain Valley. Bobolinks and Savannah Sparrows differ in the degree of within-species plumage dimorphism. Typical of icterids, Bobolinks are sexually dimorphic in size and alternate plumage. Males are larger and extremely conspicuous, with a black face and body and bright yellow skull cap. Females are more sparrow-like in appearance, yellowish with a buffy head stripe. With their characteristic yellow eye stripe, Savannah Sparrow plumage is not dimorphic, though males are larger than females (Wheelwright and Rising 1993). The courtship behavior of these species also differs. Bobolink males spend much of their time in courtship and mate defense, flying high, acrobatic patterns, and singing bubbly songs (Martin and Gavin 1995). Savannah Sparrow males sing and court from high posts, forbs or grasses within delineated nesting territories (Wheelwright and Rising 1993).

Breeding biology is similar between these two species, though critical differences are influenced by migration strategy and wintering location. Savannah Sparrow males generally arrive on the breeding grounds as much as one week prior to females (Bedard and Meunier 1983), though their shorter migration (wintering in southern U.S. and Mexico) leads to a mid- to late-April arrival. Savannah Sparrows generally attempt to raise two broods (Wheelwright et al. 1992). Bobolinks are long-distance migrants, making a round trip transequatorial flight of 20,000 km from northern Argentina/ southern Bolivia to the northern United States and southern Canada (Martin and Gavin 1995). Males arrive in early-May; females begin to arrive one week after males (Wittenberger 1980). As a result of the late breeding grounds arrival, Bobolinks generally raise one brood, though, will re-nest upon early failure (Gavin 1984).

Whereas the effects of migration clearly differentiate these two species, they are linked to grasslands through breeding natural history. Both species are opportunistic foragers during the breeding season, generally feeding on insects while walking along the ground. Females of both species use dried grass to build nests on the ground (Martin 1971, Bedard and Meunier 1983). Bobolink clutches average 5 eggs, incubating for 11 days (Martin 1971, Gavin 1984). Savannah Sparrows generally lay 4 eggs in a clutch (Weatherhead 1979) and incubate for 10 to 12 days (Bedard and Meunier 1983). These two species are not agonistic towards each other and often nest in close proximity.

North American grasslands and associated obligate birds

Since European settlement, native grasslands have been replaced throughout their natural range. Roughly 4% remains of the historic tall-grass prairie stretching from Canada and Minnesota south to Texas (Steinauer and Collins 1996). Three factors have caused this habitat decline: cool season grasses and forbs for agriculture replaced native prairie (Warner 1994); native grasslands were tilled and replanted with annual row crops (Herkert 1995, Warner 1994); finally, suburbanization paved fertile soils with roads and houses (Sampson and Knopf 1994).

These native habitat losses caused significant declines in the associated vertebrate groups, particularly grassland obligate birds. In fact, since the 1960's, throughout most of their range, grassland birds have declined more than any other North American bird guild (Peterjohn and Sauer 1999, Murphy 2003, Sauer et al. 2005). Interestingly, many grassland obligate species adapted well to introduced agricultural grasslands that replaced historic prairie between the settlement period and the early 1950's (Samson and Knopf 1994, Warner 1994). However, between 1956 and 1992, many grassland species suffered declines of up to 98% (Herkert 1997). The sources of decline included habitat loss to row crops and alfalfa monocultures (Best 1986, Warner 1994), higher predation rates caused by fragmentation (Herkert et al. 2003), increased brood parasitism by the Brownheaded Cowbird (*Molothrus ater*) (Johnson and Temple 1990, Herkert et al. 2003), and machinery related nest and adult mortality (Warner 1989, Frawley and Best 1991).

Although also in decline, northeastern United States grassland habitat and bird populations have a unique history and suite of pressures. Early 18th century land clearing for timber and agriculture created expansive grasslands that supported significant populations of breeding birds (Askins 1999). In the early 20th century, however, farm abandonment and fallout of the timber industry initiated a widespread regrowth of the northern forest. Since the 1930's, grassland habitat has declined by 60% in New England and New York (Askins 1999). The negative effects of 20th century reforestation on northeastern grassland bird populations and habitat are pronounced. From 1966 to 1994, data showed significant declines in 14 of 19 grassland bird species (Askins 1999), and five states now list nine grassland specialist species as threatened or endangered (Vickery et al. 1992). Regionally, the most precipitous annual declines include the Henslow's Sparrow (*Ammodramus henslowii*) (9%), Grasshopper Sparrow (*Ammodramus savannarum*) (6%), Eastern Meadowlark (*Sturnella magna*) (3%), Savannah Sparrow (1.7%) and Bobolink (1.4%). Species and habitat diversity is now low—in the Champlain Valley of Vermont and New York, 92% of all encountered grassland obligate birds were Savannah Sparrows and Bobolinks (Shustack 2004). Birds are now limited to smaller pockets of habitat, primarily breeding in managed hayfields (Bollinger and Gavin 1989, Shustack 2004).

Although habitat change is associated with population decline, the changing processes of grassland management in the Northeast have played an important role. Management changes include earlier first harvest dates and more frequent harvests

(Bollinger et al. 1990, Troy et al. 2004). Since the 1960's, hay farmers have advanced the initial cutting date from mid-summer to late-May or early-June (Bollinger et al. 1990); forage protein levels are higher early in the growing season (Cherney et al. 1993), resulting in increased production by lactating dairy cows (Bosworth and Stringer 1985).

Early hayfield management, however, occurs at a vulnerable time of the breeding cycle. In early June most birds are in the later part of the incubation stage or early to middle nestling stage. As ground-nesters, eggs and nestlings are vulnerable to being crushed by the harvest machinery. Some intact nests may survive the harvest process and females may continue caring for exposed nests. However, haying related nest failure can also occur by gull, crow, and small mammal predation (Bollinger et al. 1990). Additionally, a greater harvesting frequency results in a shorter window of opportunity (35 days) to renest in between haying events. For many grassland birds, the nesting cycle—including nest building, egg laying, incubation, and nestling feeding - lasts around 28 days. It is also critical to consider that during fledging, nestlings walk out of the nest; Wheelwright and Templeton (2003) estimated Savannah Sparrows require a minimum of 12 days for fledglings to acquire basic foraging skills. Therefore, young fledglings are also vulnerable to haying events. In terms of timing and interval, hayfield management clearly possesses a variety of risks to grassland nesting songbirds.

LITERATURE CITED

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

Bedard, J., and M. Meunier. 1983. Parental care in the Savannah Sparrow. Canadian Journal of Zoology 61:2836-2843.

Best, L. B. 1986. Conservation tillage: ecological traps for nesting birds? Wildlife Society Bulletin 14:308-317.

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping of eastern populations of the Bobolink. Wildlife Society Bulletin 18:143-150.

Bollinger, E. K., and T. A. Gavin. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk 106: 584-594.

Bollinger, E. K., and T. A. Gavin. 1992. Eastern Bobolink populations: ecology and conservation in an agricultural landscape. Pages 497-506 *in* J. M. H. III and D. W. Johnston, editors. Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, D.C.

Bosworth, S. C. and W. C. Stringer. 1985. Cutting management of alfalfa, red clover, and birdsfoot trefoil. Agronomy Facts 7, The Pennsylvania State University. 4 p.

Cherney, D. J. R., J. H. Cherney, and R. F. Lucey. 1993. In vitro digestion kinetics and quality of perennial grasses as influenced by forage maturity. Journal of Dairy Science 76:790-797.

Frawley, B. J., and L. B. Best. 1991. Effects of mowing on breeding bird abundance and species composition in alfalfa fields. Wildlife Society Bulletin 19:135-142.

Gavin, T. A. 1984. Broodedness in Bobolinks. The Auk 101:179-181.

Herkert, J. R. 1995. An analysis of midwestern breeding bird population trends, 1966-1993. American Midland Naturalist 134:41-50.

Herkert, J. R. 1997. Bobolink Dolichonyx oryzivorus population decline in agricultural landscapes in the midwestern USA. Biological Conservation 80:107-112.

Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmermann, 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, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Iowa Academy of Sciences 54:106-111.

Martin, S. G. 1971. Polygyny in the Bobolink: habitat quality and the adaptive complex. Ph.D. Dissertation. Oregon St. University, Corvallis, Oregon.

Martin, S. G. and T. A. Gavin. 1995. Bobolink (*Dolichonyx* oryzivorus). Birds of North America. 176: 1-24.

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

National Agricultural Statistics Service (NASS). 1999. USDA. http://www.nass.usda.gov/census/.

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

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2004. Version 2005.2.* USGS Patuxent Wildlife Research Center*, Laurel, MD.*

Shustack, D. P. 2004. Bobolink and Savannah Sparrow habitat selection in the Champlain Valley. Thesis. University of Vermont, Burlington, Vermont, USA.

Steinauer, E. M., and S. L. Collins. 1996. Prairie ecology: the tallgrass prairie. Pages 39-53 in F. B. Samson and F. L. Knopf, editors. Prairie conservation: preserving North America's most endangered ecosystems. Island Press. Washington, D.C.

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

Vickery, P. D., M. L. J. Hunter, and J. V. Wells. 1992. Is density an indicator of breeding success? Auk 109:706-710.

Warner, R. E. 1989. Hay cutting and the survival of pheasants: A long-term perspective. Journal of Wildlife Management 53:455-461.

Warner, R. E. 1994. Agricultural land use and grassland habitat in Illinois: future shock for Midwestern birds? Conservation Biology 8:147-156.

Weatherhead, P. J. 1979. Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. Auk 96:391-401.

Wheelwright, N. T., and J. D. Rising. 1993. Savannah Sparrow. Birds of North America 45:1-28.

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.

Wheelwright, N. T. and J. J. Templeton 2003. Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. Condor 105:279-287.

Wittenberger, J. F. 1980. Vegetation structure, food supply, and polygyny in Bobolinks (*Dolichonyx oryzivorus*). Ecology 61:140-150.

Chapter 1

Grassland songbirds in a dynamic management landscape: behavior responses and management strategies[1]

ABSTRACT

In recent decades, earlier and more frequent harvests of agricultural grasslands has been implicated as a major cause of population declines in grassland songbirds. From 2002-2005, in the Champlain Valley of Vermont and New York, USA, we studied the reproductive success of Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*) on four grassland treatments: 1) early-hayed fields cut before 11 June and again in early- to mid-July; 2) middle-hayed fields cut once between 21 June and 10 July; 3) late-hayed fields cut after 1 August; and 4) rotationally-grazed pastures. Both the number of fledglings per female/year and nest success (Logistic-exposure method) varied among treatments and between species. Although birds initiated nests earlier on early-hayed fields compared to others, haying caused 99% of active Savannah Sparrow and 100% of active Bobolink nests to fail. Both the initial cutting date and time between cuttings influenced renesting behavior. After haying, Savannah Sparrows generally remained on early-hayed fields and immediately renested (mean clutch completion 15.6 ± 1.28 days post-haying), while Bobolinks abandoned the fields for at least two weeks (mean clutch completion 33 ± 0.82 days post-haying). While female Savannah Sparrows fledged more offspring per year (1.28 ± 0.16) than female Bobolinks (0.05 ± 0.05), reproductive success on early-hayed fields was low. The

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[1] 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.

number of fledglings per female/year was greater on middle-hayed fields (Savannah Sparrows, 3.47 ± 0.42; Bobolinks, 2.22 ± 0.26), and late-hayed fields (Savannah Sparrows, 3.29 ± 0.30; Bobolinks, 2.79 ± 0.18). Reproductive success was moderate on rotationally-grazed pastures, where female Savannah Sparrows and female Bobolinks produced 2.32 ± 0.25 and 1.79 ± 0.33 fledgling/year respectively.

We simultaneously conducted cutting surveys throughout the Champlain Valley and found that 3-8% of hayfield habitat was cut by 1-4 June, 25-40% by 12-16 June, and 32-60% by 28 June - 2 July. Thus, the majority of grassland habitat was cut during the breeding season; however, late-hayed fields served as high-quality reserves for late-nesting female Bobolinks who were displaced from previously hayed fields. For fields first cut in May, a 65-day interval between cuts could provide enough time for both species to successfully fledge young.

INTRODUCTION

North American grassland songbird population declines from the 1960's to present are strongly associated with changes in agricultural land use (Bollinger and Gavin 1992, Sampson and Knopf 1994, Warner 1994, Herkert 1997, Askins 1999, Peterjohn and Sauer 1999, Warren 2005). This trend is especially apparent in the northeastern United States, where grassland songbird populations have declined rapidly. From 1966 to 1994, 14 of 19 grassland and savannah bird species significantly declined in northeastern North America (Askins 1999), and recent surveys indicate low species diversity (Shustack 2004).

The process of grassland management in the Northeast has changed in recent decades, with earlier first harvest dates and more frequent harvests (Bollinger et al. 1990, Troy et al. 2005). Since the 1960's, hay farmers have advanced the initial cutting date from mid-summer to late-May or early-June because forage protein levels are higher early in the growing season (Cherney et al. 1993), which in turn increases the milk production by lactating dairy cows (Bosworth and Stringer 1985). The effects of these changes are critical because in the Northeast, hayfields and pastures serve as the primary breeding habitat for obligate grassland songbirds (Bollinger and Gavin 1992, Shustack 2004).

Early hayfield management occurs at a vulnerable time in the breeding cycle of grassland songbirds. In early- to mid-June most birds are in the late incubation stage or have young nestlings. Since most grassland birds nest on the ground, the eggs and nestlings are vulnerable to being crushed by the harvest machinery. Although some intact nests may survive the harvest process, nest failure can also occur by abandonment or post-haying predation, as avian predators and small mammals often search recently hayed fields, preying on exposed eggs, nestlings, and fledglings (Bollinger et al. 1990). Additionally, greater harvesting frequency results in a shorter window of opportunity (35 days) to renest between haying events. For many grassland birds, the nesting cycle—including nest building, egg laying, incubation, and nestling feeding—lasts around 28 days. When fledging occurs, however, nestlings walk out of the nest and cannot fly. Therefore, young fledglings are also vulnerable to haying events. In terms of timing and cutting intervals, hayfield management is a clear threat to grassland nesting songbirds.

Modernized hayfield management has a strong negative effect on songbird demography, though only a few studies have examined this relationship. Both Nocera et al. (2005) and Dale et al. (1997) used point count data to determine whether delayed hay dates positively affected breeding songbirds. Only Warner and Etter (1989) and Bollinger et al. (1990) measured individual female demography relative to the types of management-defined grassland habitats they select. Their studies documented, however, only the immediate nest destruction of haying and did not consider whether the timing of management may impact species differently over the course of the nesting season.

Though these studies clearly demonstrated that haying causes high nest, nestling, and fledgling mortality, whether songbird demography varies under a diversity of haying regimes remains unclear. As a result, recommendations to increase songbird productivity in grassland-based agricultural landscapes have unanimously focused on the value of delaying hay harvest to mid-July or August (Bollinger and Gavin 1992, Nocera et al. 2005, Warren and Anderson 2005). Nonetheless, in agricultural regions, due to financial and nutritional needs, delaying initial hay harvest is not an option for most farmers (Troy et al. 2005). Therefore, in working landscapes, grassland management plans that balance both farmers' and birds' needs are critical for long-term conservation planning. Northeastern grassland landscapes and the populations they support are dynamic over time and space (Norment 2002). To understand the effects of grassland management on a larger breeding population, we need detailed demographic data that describe how multiple species of songbirds behave within diverse management scenarios that are representative of the agricultural landscape. Additionally, we need to gather information within a larger system about how hayfields are managed within and between seasons.

To address these questions, we initiated a demographic study of two obligate grassland songbirds breeding in agricultural grasslands within the Champlain Valley of Vermont, USA and New York, USA. Our objectives were to: 1) describe Bobolink (*Dolichonyx oryzivorus*) and Savannah Sparrow (*Passerculus sandwichensis*) nesting phenology and breeding behavior relative to four management-defined grassland treatments; 2) determine if nest success and nest survival differed among the four grassland treatment types; 3) evaluate the effect of delayed first harvest on nest success and the number of fledglings produced per female/year; 4) describe how hayfields are managed both within a year and between consecutive years throughout the Champlain Valley; 5) describe management scenarios that can provide high quality grassland songbird breeding habitat in the Champlain Valley.

METHODS

Study Area

Research took place from May to August 2002-2005 in the Champlain Valley, a relatively isolated system bordered by Vermont's Green Mountains on the east and New

York's Adirondack Mountains on the west. As the main dairy land for Vermont and eastern New York, the Valley includes 146,000 ha of mostly privately-owned managed grasslands (NASS 1999). Roughly 65% of these grasslands are managed as forage fields for dairy and beef cows.

Bobolinks and Savannah Sparrows account for the majority (72%) of the Champlain Valley's grassland nesting bird community (Shustack 2004). Other species nesting in low densities within the valley's grasslands include eastern meadowlark (*Sturnella magna*), red-winged blackbird (*Agelaius phoeniceus*), grasshopper sparrow (*Ammodramus savannarum*), upland sandpiper (*Bartramia longicauda*), northern harrier (*Circus cyaneus*), and horned lark (*Eremophila alpestris*).

Study Species

Bobolink and Savannah Sparrow life history strategies have both similarities and differences, which make them an ideal model to examine how management affects a community of grassland songbirds. On the breeding grounds, the two species have similar patterns of resource use. Both species are grassland obligates that feed on insects, use dried grass to build nests on the ground, and have nesting cycles lasting 23 to 25 days. However, differences in migration and wintering location influence breeding strategies. Savannah Sparrows are short-distance migrants (Wheelwright and Rising 1993), arriving on the Champlain Valley breeding grounds in mid- to late-April. Nesting spans from early-May to mid-August, which allows them enough time to attempt two broods (Wheelwright et al. 1992). In contrast, Bobolinks are long-distance migrants (Martin and Gavin 1995), arriving on their Champlain Valley breeding grounds in mid-May. Breeding occurs from late-May to mid-July. This brief window generally provides enough time to raise only one brood, although Bobolinks will occasionally renest after early failure (Martin 1971, Gavin 1984).

Experimental Design

To assess the impacts of grassland management on the population ecology of Bobolinks and Savannah Sparrows, we studied the four major grassland treatment types in the Champlain Valley:

- *Early-hayed fields* (EH): hayed between 27 May and 11 June, and generally again in early- to mid-July
- *Middle-hayed fields* (MH): hayed between 21 June and 10 July
- *Late-hayed fields* (LH): hayed after 1 August
- *Rotationally-grazed pastures* (RG): fields in which cows were rotated through a matrix of paddocks and moved after all of the grass in a paddock was eaten to a farm-specific height. The vegetation in each paddock is thereby given a multiple week "rest" between grazing events.

We established treatment fields in three study areas: (1) Shelburne, Vermont (2002-2005) (EH, LM, RG), (2) Hinesburg, Vermont (2003-2005) (EH, LH, MH, RG), and (3) Cumberland Head, New York (2002-2004) (MH, LH). We interviewed land owners and managers to identify fields whose long-term management fell into our treatment definitions. We then selected fields based on size (large enough to include a 10.5 ha focal study plot; field size ranged from 13.2 – 38.3 ha; mean = 21.1 ha), and proximity (>8 km) to other study areas. Land use within each study area was consistent for at least 10 years prior to the initiation of our study. Fields were composed of a mixture of cool season grasses and forbs. Early- and middle-hayed fields had greater forb composition than late-hayed fields or pastures, including alfalfa (*Medicago sativa* L.), red clover (*Trifolium pratense* L.), white clover (*Trifolium repens* L.), and dandelion (*Taraxacum officinale* Weber). Late-hayed fields and rotionally-grazed pastures were grass dominated, including orchard grass (*Dactylis glomerata* L.), timothy, (*Phleum pretense* L.), and bluegrass (*Poa* sp.), and reed canarygrass (*Phalaris arundinacea* L.*)*. However, late-hayed fields generally had significant "old field" communities, including sedge (*Carex* spp.), vetch (*Vicia* sp.), bedstraw (*Galium* sp.), and native forbs.

The two replicates of rotationally-grazed pasture were stocked with heifers and dry cows at 1-1.5 cow/ 0.4 ha ratio. The Hinesburg pasture was in management intensive grazing (MIG) practice, where the paddock was grazed to 5-10 cm, and the cows were rotated every 7 days. The Shelburne pasture was in a light grazing rotation, where grass was grazed to 10-20 cm, and cows were rotated every 7-14 days. All early- and middle-hayed fields were cut with disc mowers that left 5-10 cm grass stubble. After these fields were cut, the grass was treated with either a rake or conditioner, and then round-baled or chopped. In most years, liquid manure was spread on early-hayed fields 2 to 10 days after the first cut. Late-hayed fields were cut both with disc mowers and brush hogs (12-18 cm), and in some years the grass was left on the field in wide windrows.

Field methods

Beginning in early-May, we captured territorial birds with mist-nets, and put unique combinations of three color bands and a single metal U.S. Fish and Wildlife Service band on the legs of all adults of both species. Color-banded birds were continuously resighted throughout the breeding season. In mid-May we began intensive, season-long nest searching and nest monitoring to assess annual fecundity. Although we did not make rigorous density estimates on the fields, our impression was that densities were relatively consistent among treatments, with the exception of rotationally grazed fields which had lower densities of Bobolinks. We attempted to find nests of all females that bred on each treatment field. We located nests by observing adult behavior and by flushing incubating females off their nests while walking through the fields swishing bamboo sticks. The majority of nests were found during the incubation stage (64.9%); the rest were found during the nest building (1.8%), egg laying (15.1%), hatching (3.6%), and nestling stages (14.6%). After locating a nest, we immediately identified the associated female and male. If one or both adults were unbanded, we captured those individuals near the nest location. Females could typically be assigned to nests unambiguously through incubation and brooding behavior. We determined male nest association by observing territory defense, mate guarding, and food deliveries (Wheelwright and Rising 1993, Martin and Gavin 1995).

Each nest was marked with a single bamboo stake and colored flagging placed 2-5m from the nest. While nest markers can slightly increase avian predation of passerine nests (Gotmark 1992), we took care to minimize these effects by both setting random stakes throughout fields and by posting a 50 m X 50 m grid throughout each field. We visited nests every one to two days until fledging or failure. Nestlings were weighed and banded with a single metal U.S. Fish and Wildlife Service band on day six or seven. A nest was considered successful if at least one bird fledged.

On early- and middle-hayed fields, we monitored nests immediately before and after the nest area was hayed. Ring-billed gulls (*Larus delawarensis*), common ravens (*Corvus corax*), and American crows (*Covus brachyrhynchos*) followed the haying machinery and preyed upon revealed nests, fledglings, insects, mammals, and amphibians. We did not disturb the predators' foraging efforts. Behavioral observations of adults caring for known age fledglings and subsequent renesting patterns showed that young fledglings did not survive haying events. While we believe that juveniles seven days post-fledgling may not survive haying events, this study was not designed to precisely evaluate fledgling survival. However, in the absence of fledgling survival data, we conservatively considered nestlings that left a given nest within three days prior to a haying event as a failed nest. We measured annual nesting phenology and breeding behavior by following the maximum number of females available on each field throughout the reproductive year for as long as they remained on the respective field. We quantified the number of offspring produced in a breeding season by each adult female.

Analysis methods

Nesting phenology and breeding demographics

Nesting phenology was evaluated with both clutch completion and fledging dates. Clutch completion dates illustrated both spring settlement patterns as well as renesting patterns. Nest contents that survived either from egg-laying to incubation, incubation to hatching, or nestling to fledging, were included in the phenology analysis. For such eggs or chicks, we could obtain clutch completion dates by back-calculating from either the hatching or fledging date. We used all nests to analyze breeding demographics (number of offspring produced per female/year, clutch size, number of clutches per female) among treatments and between species with two-way ANOVA tests in PROC MIXED (SAS Institute Inc., Cary, North Carolina, USA).

Nest success and daily nest survival

We used the logistic-exposure method (hereafter, L-E, Shaffer 2004) to model nest success and daily nest survival. The logistic-exposure model is a likelihood-based modeling approach that allows unbiased estimation of daily nest survival and inclusion of covariates that may influence daily nest survival. Rather than treating each nest as a sample, the number of days between nest checks (an interval) is the primary focus. The model uses a binomial framework to estimate the probability that a nest will survive (or fail) through the interval. Given a large number of intervals, the number of days within each interval, and a specified model, the analysis finds the most likely daily survival estimates. Various competing models are then ranked and compared using an information theoretic approach. The L-E method is a powerful analytical tool for data sets with variable intervals between observations because nest-check intervals are weighted by the interval length. This method assumes that the fate of all nests is independent of other nests, and that daily survival probabilities are both homogenous across the nest cycle and are affected similarly by explanatory variables (Shaffer 2004). The three management treatments within this study all affect nest success and therefore bias the assumption of independence. However, the effects of predation and weather, both significant causes of nest failure, were independent. While most nest-check intervals were between one and two days, nests subjected to management (haying) were monitored just prior to haying and immediately after haying—intervals as short as 10 minutes. In order to use the information gathered from these precise visits, our L-E modeling occurred at hourly intervals later scaled up to daily intervals for nest survival estimates. While shorter intervals may increase observer-caused nest failure, the precise information gained from these observations was critical to the research objectives.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare alternative nest success models. Our *a priori* model set was developed from the data reported by Bollinger et al. (1990) and Bollinger and Gavin (1992). Their study found that hayfield management caused > 90% of active Bobolink nests to fail. However, because weather is a major determinant of when farmers begin haying in the Champlain Valley, we included year in the variable set to examine how treatment stochasticity affected nest success. Finally, because Bobolinks and Savannah Sparrows have distinct breeding strategies but are equally subject to both haying and annual stochasticity, we included species in model sets. Therefore, our ten individual, additive, and interaction models examine how grassland treatment type ($n = 4$), species ($n = 2$), and year ($n = 4$) affected nest success. The nest success models were: species only; year only, treatment only; year + species; treatment + year; treatment + species; treatment + species + year; treatment*species interaction; year*species interaction; treatment*year interaction. All statistical analyses were performed with SAS 8.0.

Daily nest survival was determined as DNS = exp (log-odds) / (1+exp (log-odds), where the model specific logit followed the linear equation:

$$\text{log-odds (DNS)} = \text{intercept} + \beta_1 (X_1) + \beta_2 (X_2) + \beta_3 (X_3) + \ldots. + \beta_X(X_X)$$

and X_i were the covariate values associated with the nest or the nest interval, and β_i was the corresponding effect size. Nest success was calculated as the daily nest survival raised to the exponent of the nest cycle length, and included the egg laying, incubation, and nestling stage. Nest cycles were 23 days for Savannah Sparrows and 25 days for

Bobolinks. Models that did not include species as a parameter were scaled to an average 24-day nesting period. We used model averaging to obtain overall nest success values. Here, we summed the products of the daily nest survival against their AIC_c weight (ω_i) for the top six ranking models, which accounted for >99% of model AIC_c weights. The model averaged 95% confidence intervals were calculated with the intercept (β_o) and coefficients (β_i) for the lower and upper estimates for each model.

Nest survival as a function of haying date

We observed haying six times on early-hayed fields (27 and 28 May, and 3, 5, 7 and 11 June) and on middle-hayed fields (21, 23, 24, and 27 June, and 2 and 10 July). The progressive nature of the haying dates granted an opportunity to model how nest success and nest survival varied as a function of the first haying date. Late-hayed fields were hayed after the nesting season, and were assigned a standardized haying date of 1 September. Renesting after a first cut was not included in this analysis because nest survival of the second nest was not directly affected by the first haying event.

Haying date was standardized with a Z-transformation based on the mean (15 June) and standard deviation (14.3 days) of all haying dates across all years. Since nest fates were standardized across years, this analysis ignored year effects that may have influenced nest fate (predation, weather) and log-odds (nest success) was modeled as a function of only haying date. We performed a Likelihood-ratio test to assess model fit by comparing this model to an intercept (null) model.

Cutting surveys

To better understand the population level implications of our plot-based study, from late-May to mid-July we conducted cutting surveys on privately owned fields throughout the valley. These surveys assessed within-year and between-year patterns of grassland management. In 2002, 69 randomly selected hayfields (560 ha) (Shustack 2004) were visited every 10-14 days to determine whether or not the field had been hayed. In 2003-05 we expanded the survey to include the original 69 fields as well as all fields visible from the road survey point (+278-355 fields; +804-1019 ha).

RESULTS

Nesting phenology

Nesting phenology varied by treatment and species (*n* = 576 Savannah Sparrow and 344 Bobolink nests). On the early- and middle-hayed treatments, haying interrupted clutch completion and fledging for Savannah Sparrows (Fig. 1a, b) and Bobolinks (Fig. 1b). For Bobolinks on early-hayed fields (Fig. 1a), the timing of first nests (initial clutch completion through 6 June) and presumed renests of new immigrants settling post-haying (clutch completion dates 25 June – 1 July) ensured that no nests successfully fledged young (with one exception, see below) before the second (early- to mid-July) haying. Early-haying resulted in substantial delays in fledging for Savannah Sparrows (Fig. 1a). With the exception of one nest that survived a first cut, Savannah Sparrows did not fledge young on early-hayed fields until after 26 June. On middle-hayed fields (Fig. 1b), no Bobolinks renested after the haying period, thus any successful nests fledged young (at least 3 days) prior to the first cut. By contrast, some Savannah Sparrows on middle-hayed fields fledged young prior to the cut (2-23 June) and some successfully renested or double-brooded after the cut (17 July-8 August). Patterns of clutch completion and fledging were similar within species between the late-hayed and pasture treatments as both species fledged young throughout the breeding season (through 11 August for

Savannah Sparrows and 28 July for Bobolinks; Fig. 1c, d). Savannah Sparrows showed greater within-season site fidelity after nest failure, thus their extended nesting period was a result of both renesting and double brooding.

Both species showed significant differences in the timing of the first 18 clutch completion dates among treatments (1-way ANOVA, Bobolinks: $F_{3,\,68}= 24.5$, $P < 0.01$, Savannah Sparrows: $F_{3,\,68}=14.98$, $P < 0.01$). We compared 18 nests because this is the maximum available on early-hayed fields for which to compare (subsequent nests failed to haying). We discriminated between pairs of treatments within ANOVA models with least-squares means tests (LSM). For Savannah Sparrows, mean clutch completion dates on early-hayed fields were significantly earlier than middle-hayed (LSM: $P < 0.01$), late-hayed (LSM: $P < 0.01$), and rotationally-grazed pastures (LSM: $P < 0.01$). Middle-hayed fields were not significantly different than late-hayed (LSM: $P = 0.12$) or rotationally-grazed pastures (LSM: $P = 0.55$). Late-hayed fields, however, were significantly earlier than pastures (LSM: $P = 0.03$). Analyses using first nests were similar to results obtained for mean nesting dates. Compared to late-hayed fields, Savannah Sparrow females began incubating nests nine days earlier on early-hayed fields, four days earlier on middle-hayed fields, and five days earlier on pastures. The earliest observed clutch completion date for Savannah Sparrows was 6 May and the latest was 30 July.

For Bobolinks, the first 18 clutch completion dates on early-hayed fields were significantly earlier than pastures (LSM: $P < 0.01$), while clutch completion dates on early- and late-hayed (LSM: $P = 0.54$) and early- and middle-hayed fields were not significantly different (LSM: $P = 0.42$). Bobolink clutch completion dates were significantly earlier on middle-hayed fields than pastures (LSM: $P < 0.01$) and late-hayed fields were earlier than pastures (LSM: $P < 0.01$). As compared to late-hayed fields, Bobolinks began incubating three days earlier on early-hayed fields, two days earlier on middle-hayed fields, and three days earlier on pastures. For Bobolinks, the earliest observed clutch completion date was 21 May and the latest was 9 July.

To understand if renesting patterns varied among treatments, we examined how long it took female Savannah Sparrows to renest following failure of their first nest. In this analysis, haying caused all first nests to fail on early-hayed fields, while all first nests on the other three treatments failed for non-haying related causes. Renesting patterns were significantly different among treatments (1-way ANOVA, $F_{3,78} = 4.03$, $P = 0.01$). Least-squares means tests between paired treatments showed that renesting was significantly slower on early-hayed fields than on all other treatments (LSM: middle-hayed: $P = 0.03$; late-hayed: $P < 0.01$; grazed: $P = 0.04$). Mean days to renest after failure were 15.6 ± 1.28 ($n = 48$) on early-hayed, 9.1 ± 0.83 ($n = 7$) on middle-hayed, 9.7 ± 1.3 ($n = 16$) on late-hayed fields, and 10.5 ± 0.90 ($n = 11$) on pastures. Interestingly, there is no significant difference in time to renest after a successful nest (1-way ANOVA, $F_{3,52} = 1.64$, $P = 0.19$). However, the mean number of days to renest was shorter on late-hayed fields (12.9 ± 1.57, $n = 24$) as compared to early-hayed fields (18 ± 3.29; $n = 7$, LSM: $P = 0.12$), middle-hayed fields (17.6 ± 2.02; $n = 12$, LSM: $P = 0.90$), and pastures (16.8 ± 1.97; $n = 13$, LSM: $P = 0.74$).

Breeding demographics

Within a season, female Savannah Sparrows laid significantly more eggs than female Bobolinks in the same field (1-way ANOVA: $F_{1,482} = 24.10$, $P < 0.01$, Table 1). Mean number of eggs laid ($F_{3,280} = 2.14$, $P < 0.10$) and nests per year ($F_{3,281} = 1.58$, $P <$

0.19) were similar among treatments for Bobolinks, although the standard deviation was greatest on pastures, which suggested that these females had a greater tendency to renest (Table 1). Bobolink clutches were significantly smaller on pastures as compared to all other treatments ($F_{3,\,294} = 4.17$, $P < 0.01$). Female Savannah Sparrows laid more eggs ($F_{3,\,326} = 3.81$, $P < 0.01$) and built more nests ($F_{3,\,326} = 3.28$, $P < 0.02$) in a season on early-hayed fields than other treatments. Females also laid more eggs on middle– than late-hayed fields (LSM: $P = 0.04$). Savannah Sparrow clutch size did not change significantly between nesting attempts on early-hayed fields ($F_{5,\,244} = 1.85$, $P = 0.10$) or pastures ($F_{3,\,107} = 1.58$, $P = 0.20$). Clutch size was significantly lower in late-hayed fields between the first and third attempts (LSM: $P < 0.01$) and decreased on middle-hayed fields between the second and third attempt (LSM: $P < 0.01$). Pooled among treatments, Bobolinks laid nearly one fewer egg in their second clutch than their first ($F_{2,\,295} = 5.01$, $P < 0.01$). These Bobolink data, however, should be interpreted with caution because only 5.4% of females ($n = 32$) renested on the same field within the same year (Fig. 2).

The number of offspring fledged per female/year was significantly different between species (1-way ANOVA, $F_{1,\,484} = 16.35$, $P < 0.01$, Table 1). Savannah Sparrow females fledged consistently more offspring than Bobolink females because they renested after failure and sometimes raised two broods. Female fledging rates were significantly different among treatments ($F_{3,\,614} = 29.74$, $P < 0.01$), although the interaction between species and treatment was not significant ($F_{3,\,484} = 0.68$, $P = 0.57$). On early-hayed fields, females of both species fledged fewer offspring than those on middle (LSM: $P < 0.01$), late-hayed fields (LSM: $P < 0.01$), and pastures (LSM: $P = 0.01$). The number of fledglings produced per breeding season were similar between middle-hayed and late-hayed treatments for both species (LSM: *P* = 0.43) (Table 1).

Causes of nest failure

Nests failed because of haying activities, cows, predation, weather, infertility, abandonment, and adult (female) mortality. As expected, certain categories of failure were associated with the fields' respective treatment type (Fig. 3). For example, on pastures, cows caused 39% of failures by either eating or trampling (*n* = 38) nests. Cows were more detrimental to Bobolinks (65% of failures; *n* = 22) than Savannah Sparrows (25% of failures; *n* = 16).

On early-hayed fields, 129 of the 130 (99.2%) active nests at the time of haying failed. Haying machinery directly caused 78% of these nests to fail. Predation caused failure of the remaining 22% of nests, mainly by ring-billed gulls, common ravens, and American crows. Perhaps by chance, failure from predation was not an issue on middle-hayed fields, where predation caused only 1% of haying-related nest failure (99% of active nests were destroyed by machinery). We did not document or suspect any direct mortality of adults from haying machinery or predation.

Despite similar productivity by birds nesting on late- and middle-hayed fields, the causes of failure between the two treatments differed. Predation caused 67% of all nest failures on late-hayed fields, but only 19% of nest failures on middle-hayed fields. On middle-hayed fields, haying activity accounted for 55% of failed nests.

Weather, mainly flooding, accounted for a large proportion of Bobolink failures on the late-hayed fields (27%) and Savannah Sparrow failures on the grazed pastures (30%). Only 1% of Savannah Sparrow nests and 2% of Bobolink nests on early- and middle-hayed fields failed from weather-related causes. This low proportion of weather related failures is notable, considering post-haying nests were generally more exposed due to low vegetative structure. While post-haying renests were exposed to heat and rain they were more likely to fail due to predation.

Adult female mortality was extremely rare. We found three dead female Savannah Sparrows < 1m from their nests, but none showed any signs of injury. All cases of infertility were female Savannah Sparrows ($n = 2$) who laid multiple, infertile clutches within a given year.

Nest success and daily nest survival

Grassland management was the strongest factor affecting nest success and daily nest survival (Table 2). All models that received weight of support > 0.01 included field treatment as a variable. The treatment*species interaction model ranked highest ($\omega_i = 0.57$), with 2.1 times more weight of support than the next best ranking model. Models of lower rank and weight illustrated that year and species effects were also important. The treatment-only model received an AIC_c weight of only 0.03, which further suggested that treatment alone did not affect nest survival.

The coefficients within our L-E linear models indicate the strength and direction of the effect for each of the model factors relative to the reference factor (Append. 1).

The early-hayed treatment had the greatest negative effect on nest success of the four treatment types, with coefficients ranging from -0.99 to -1.75 across the six highest ranking models (Fig. 4a-b). Grazing had the second strongest negative effect. We have high confidence in the biological relevance of these effects because only one of the confidence intervals for the twelve coefficients (ranging from -0.35 to -0.70) for early-hayed and grazed treatments overlapped zero, and that estimate overlapped zero by a marginal amount (grazed: treatment*year: 95% CI = -1.16 - 0.08). Our data suggested no biologically meaningful difference in daily nest survival between middle-hayed and late-hayed treatments (Fig. 5).

In the three ranking models that included species as a parameter, the coefficient estimates clearly indicated that the effect of the grassland treatment was stronger on Bobolinks than Savannah Sparrows (Appendix 1). The Bobolink coefficients ranged from -0.17 to -0.63. While two of three coefficients overlapped zero, we have high confidence in these estimates because the overlap was marginal (treatment + species: 95% CI = -0.37 – 0.04; treatment + species + year: 95% CI = -0.37 – 0.03).

Apparent nest success

While we believe that the logistic-exposure method is the most appropriate technique with which to analyze our data, model results are not comparable to studies that report either apparent nest success (ANS) or Mayfield (Mayfield 1975) corrected nest success. Thus for comparative purposes Appendix 2 reports apparent nest success, which was in nearly all cases noticeably different, and generally greater, than our L-E nest success values.

Grassland management surveys

The Champlain Valley is a dynamic landscape with noticeable year to year variation in management, where the majority of available hayfield habitat was hayed at some time, during the breeding season. Hayfields represented between 58-63% of all agricultural lands and 75-80% of all surveyed grasslands. Pastures accounted for 16-20% of all agricultural lands and 20-25% of all grasslands in the Valley. By 1-4 June, between

3-8% of hayfield habitat was cut; by 12-16 June between 25-40% was cut; and by 28 June - 2 July 32-60% was cut (Fig. 6). In terms of our defined treatments, between 19-32% of hayfields were cut by the end of the early-hayed period (11 June); 27-49% of hayfields were cut by the beginning of the middle-hayed period (21 June); and 32-69% of hayfields were cut by the end of the middle-hayed period (10 July). Additionally, 59% of early-hayed habitat was hayed a second time during the breeding season.

DISCUSSION

Our results describe a gradient of demographic responses among four grassland habitats defined by management practices. For all response variables, early-hayed fields were low quality habitats for reproduction. Female Savannah Sparrows on middle- and late-hayed fields fledged 2.6 – 2.7 times more young each year than females on early-hayed fields, even though females on early-hayed fields built more nests and laid more eggs. The effects of early haying on phenology and breeding success did vary, however, between species and among years. For female Savannah Sparrows, the number of annual fledglings produced was > 1.0 on early-hayed fields because females remained on the fields and often renested immediately after haying. In fact, some females began laying eggs two days after haying in nests built in 10-12 cm of grass, but renesting patterns varied between years. When females were more immediate and synchronous in renesting after haying, they tended to fledge nests before a second cut in mid-July. In some years renesting was asynchronous, and nearly all nests failed with the second haying. When second hay cuts caused all nests to fail, some females remained on the field and renested again in late-July.

Predation rates between the first and second haying were highly variable. In extreme years, predation caused 59-69% of failures on early-hayed fields, while in other years only 9-18% of failed nests were depredated. High predation resulted in asynchronous renesting, which again caused more nests to be vulnerable to a second mid-July haying. This stochastic nature of predation resulted in some years in which the number of fledglings produced by female Savannah Sparrows on early-hayed fields was near 0.0 and others where the number of fledglings produced was near 2.0.

In contrast to Savannah Sparrows, the number of fledglings produced by female Bobolinks on early-hayed fields was near zero. Including nesting attempts before and after haying, only one Bobolink nest was successful on an early-hayed field. This nest was initiated after the first haying, where a female nested in a small, wet, uncut strip in the field. However, some Bobolinks may have emigrated and renested in other areas (see below). These results are similar to Bollinger et al. (1990), where mid-June haying resulted in ~94% nest failure.

We are confident that we did not miss successful Bobolink nests on the early-hayed treatments because all Bobolinks abandoned the field within two days following a haying event. Additionally, our Bobolink sample for the first cut on the early-hayed fields underestimates the actual number of breeding females because many were still in settlement, nest building, and egg laying stages. Our field observations and banding records indicated that these females were committed to territories even though not yet identified with an active nest. Regardless of their breeding stage at the time of haying, no banded female returned to nest in an early-hayed field after the field was cut (some returned between years). Perhaps most important to management options, the timing of the first haying influenced the probability that Bobolinks would repopulate early-hayed fields. In all years, no Bobolinks were present during the first two weeks after haying. Only novice (unbanded) female Bobolinks repopulated fields cut before 2 June (n = 3) within the same year. This information suggests that early-hayed fields were sinks and most likely the post-cut breeders using them were recruited from other areas.

These nesting patterns contrast the behaviors observed by Bollinger et al. (1990). In their study, 24% (5 of 21) of female Bobolinks renested in unmowed sections of the field in which mowing caused nest failure. Like late-nesting females in this study, Bollinger et al.'s (1990) renests all failed to subsequent haying. A critical difference between studies, though, is that only novice females repopulated fields hayed *prior to 2 June*, as early-hayed fields rarely have unmowed sections.

Middle-hayed fields offered high quality breeding habitat similar to late-hayed fields. In fact, the number of fledglings produced by Savannah Sparrow females was greater on middle-hayed fields than late-hayed fields (+0.18 fledglings/ year, Table 1; +5% nest success, Fig. 4). This trend was not, however, true for Bobolinks (-0.57 fledglings/year, Table 1; -11% nest success, Fig. 4), although the number of fledglings produced was above female-female replacement and nest success was relatively high on middle-hayed fields. The relatively high levels of success for both species on middle-hayed fields is particularly surprising because it is contrary to the current hay-land conservation dogma in the Northeast, where fields cut during the breeding season are considered poor quality and conservation organizations advise landowners to delay hay harvest until at least 1 August (Massachusetts Audubon Society 2003, Natural Resources Conservation Service 2005).

Late-hayed fields have other values not observed on middle-hayed fields. Savannah Sparrow fledging took place over a 67-day and 64-day window on the middle- and late-hayed treatments, respectively. However, from 2 July to 17 July (15-day window), 0.0% of nests fledged on middle-hayed fields while 26% of all nests fledged on late-hayed fields (Fig. 1). Lack of fledging during this window is a product of the nest failure caused by middle-haying dates and subsequent renesting cycles. As Savannah Sparrow renesting behavior between early, middle, and late-hayed fields was similar, they had the full 64-day window to nest on late-hayed fields while they only had a 52-day window on middle-hayed fields. The longer window on late-hayed fields provided additional time for females to renest after predation or weather events—including both females already on the field, as well as immigrants from other fields whose nests had likely failed due to cutting.

This hypothesis can be inferred from Bobolink phenology and banding data. The first Bobolink nest fledged three days earlier on middle- than late-hayed fields. Bobolinks fledged during a 16-day window on middle-hayed and a 42-day window on late-hayed fields (Fig. 1). Integrating phenology data with the banding data showing that only 'novice' Bobolinks repopulated very early-hayed fields, suggests that given appropriate habitat, Bobolinks will continue to build nests and lay eggs into late June. However, only 7% of successful and unsuccessful Bobolinks stayed and renested on late-hayed fields; evidence that most late nesting females must be new to their respective fields. Therefore, the late nesting females on the late-hayed fields presumably settled initially in other habitats in which their first nests failed or they failed to gain a territory. It is unlikely that females failed to gain territories, however, because Bobolinks in

Vermont generally have a polygynous social structure where males pair with multiple females (Perlut unpub. data). Thus, most first nests of late or repopulating females must have failed due to weather, predation, or grassland management. In fact, 39% of all successful nests on late-hayed fields fledged after 29 June—the last date of observed fledging on middle-hayed fields. Thus, late-hayed fields can serve as high-quality habitats for these late-nesting, displaced females.

Hayfield management is highly variable between years, however, the majority of hayfields were cut during the breeding season. As much as 32% and as little as 19% of hayfield habitat was mowed by 11 June, the end of the early-hayed period. Additionally, 59% of the early-hayed habitat was cut a second time within the breeding season. For comparison, Bollinger and Gavin (1992) observed similar cutting trends in central New York. Over a four year period, they observed between 10-30% area harvested by 11 June, but somewhat greater areas harvested by mid-July (60-78% central New York; 32-69% Vermont). One noticeable difference between these data and Bollinger and Gavin (1992) is a greater annual variation in Vermont. Our demographic results within the context of the cutting survey help explain Savannah Sparrow (-0.17% / year) and Bobolink (-3.05% / year) population declines in Vermont (1966-2004; Sauer et al. 2005).

Comprising 20-25% of all grasslands in the Champlain Valley, pastures are important nesting habitats to consider within this agricultural landscape. Our research, however, should be interpreted cautiously, as these results may not apply to other (non-rotational) grazing regimes. Among the four treatments, nest success (28% Savannah Sparrow, 21% Bobolinks) was moderate on pastures – and similar or higher than the Mayfield and apparent nest success results of other natural and simulated nest success studies (Jensen 1990, Paine 1996, Temple 1999, Lapointe et al. 2000, Ignatiuk and Duncan 2001). Female responses to nest failure on pastures were similar to the three hayed habitats. Savannah Sparrows remained on the field and quickly renested. While most female Bobolinks did not renest, they were more likely to renest on pastures than any other treatment. The consistent timing of cow-rotation created a mosaic of grass heights within a given farm. This diverse habitat likely caused more female Bobolinks to remain on the field and renest rather than to leave and search for suitable habitat elsewhere. This study may be the first to document annual, individual female breeding characteristics within rotationally-grazed pastures, as we were unable to identify any comparable studies.

Management implication

The difference in the reproductive timing between these two species creates a complex community for land managers trying to balance birds' requirements for successful reproduction with farmers' resource demands. Our results strongly endorse the value of late- and middle-haying as management options that create "source" breeding grounds for Bobolinks and Savannah Sparrows. The question land managers face, however, is how to turn early-hayed fields into more stable habitats where females can, at a minimum, reproduce at replacement. Our data indicate that the key variable is the timing of the second haying event. While Savannah Sparrows gained modest reproductive success on early-hayed fields, a 45-day window between 28 May and 12 July was insufficient for Bobolinks to fledge young. At the time of second haying, most nests were in the middle to late nestling stage. Wheelwright and Templeton (2003) estimated Savannah Sparrows require a minimum of 12 days for fledglings to acquire basic foraging skills. Therefore, given an additional 8 days to complete fledging and 12 days for fledglings to become sufficient foragers, we suggest cutting intervals of 65 days may be sufficient to support both Bobolink and Savannah Sparrow reproduction within an early-hayed system. However, if the first haying occurs after 2 June, the probability of Bobolink repopulation may be low to zero. Therefore, for a 65-day window between first and second cuts to benefit both species, farmers should attempt to cut early-hayed fields as early as possible. The ability to delay the second cut will be a farm-by-farm decision, mainly determined by livestock nutritional needs. An initial May harvest will produce a moderate volume of high-quality, protein rich forage. A delayed second harvest will produce comparatively lower protein-rich forage, though with a greater volume. This early-haying plan will therefore be most applicable to farms that house some combination of lactating dairy cows, heifers, beef cows, dry cows, or horses which often have diverse nutritional needs. The timing of cuts on middle-hayed fields is critical to the potential reproductive success of Bobolinks. In this management option, farmers producing hay for horses have the greatest flexibility to conduct first cuts during this period. As both species show relatively strong fidelity to breeding sites (Perlut unpubl. data), interannual consistency in management practices is a critical factor in maintaining habitat quality over the long-term.

ACKNOWLEDGMENTS

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LITERATURE CITED

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

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping of eastern populations of the Bobolink. Wildlife Society Bulletin **18**:143-150.

Bollinger, E. K., and T. A. Gavin. 1992. Eastern Bobolink populations: ecology and conservation in an agricultural landscape. Pages 497-506 *in* J. M. H. III and D. W. Johnston, editors. Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, D.C.

Bosworth, S.C. and W.C. Stringer. 1985. Cutting management of alfalfa, red clover, and birdsfoot trefoil. Agronomy Facts 7, The Pennsylvania State University, State College, Pennsylvania, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference, second edition. Springer, New York, New York, USA.

Cherney, D. J. R., J. H. Cherney, and R. F. Lucey. 1993. In vitro digestion kinetics and quality of perennial grasses as influenced by forage maturity. Journal of Dairy Science **76**:790-797.

Dale, B. C., P. A. Martin, and P. S. Taylor. 1997. Effects of hay management on grassland songbirds in Saskatchewan. Wildlife Society Bulletin **25**:616-626.

Gavin, T. 1984. Broodedness in Bobolinks. The Auk **101**:179-181.

Gotmark, F. 1992. The effects of investigator disturbance on nesting birds. Pages 63-104 *in* D. M. Power, editor. Current Ornithology Volume 9. Plenum Press, New York, New York.

Herkert, J. R. 1997. Bobolink *Dolichonyx oryzivorus* population decline in agricultural landscapes in the midwestern USA. Biological Conservation **80**:107-112.

Ignatiuk, J. B., and D. C. Duncan. 2001. Nest success of ducks on rotational and season-long grazing systems in Saskatchewan. Wildlife Society Bulletin **29**:211-217.

Jensen, H. P., D. Rollins, and R. L. Gillen. 1990. Effects of cattle stock density on trampling loss of simulated ground nests. Wildlife Society Bulletin **18**:71-74.

Lapointe, S., J. F. Giroux, L. Belanger, and B. Filion. 2000. Benefits of rotational grazing and dense nesting cover for island-nesting waterfowl in southern Quebec. Agriculture Ecosystems & Environment **78**:261-272.

Martin, S. G. 1971. Polygyny in the Bobolink: habitat quality and the adaptive complex. Thesis. Oregon State University, Corvallis, Oregon, USA.

Martin, S. G. and T. A. Gavin. 1995. Bobolink (Dolichonyx oryzivorus). Birds of North America. **176**: 1-24.

Massachusetts Audubon Society. 2003. http://www.massaudubon.org/Birds_and_Beyond/grassland/large.php#conservation.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin **87**:456-466.

National Agricultural Statistics Service (NASS). 1999. USDA. http://www.nass.usda.gov/census/.

Natural Resources Conservation Service (NRCS). 2005. Conservation Practice Standards. http://www.nrcs.usda.gov/technical/efotg/.

Nocera, J. J., G. J. Parsons, G. R. Milton, and A. H. Fredeen. 2005. Compatibility of delayed cutting regime with bird breeding and hay nutritional quality. Agriculture Ecosystems & Environment **107**:245-253.

Norment, C. 2002. On grassland bird conservation in the Northeast. The Auk **119**:271-279.

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.

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

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, Results and Analysis 1966 - 2004. Version 2005.2. USGS Patuxent Wildlife Research Center, Laurel, MD.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. The Auk **121**:526-540.

Shustack, D. P. 2004. Bobolink and Savannah Sparrow habitat selection in the Champlain Valley. Thesis. University of Vermont, Burlington, Vermont, USA.

Temple, S. A., B. M. Fevold, L. K. Paine, D. J. Undersander, and D. W. Sample. 1999. Nesting birds and grazing cattle: accommodating both on midwestern pastures. Studies in Avian Biology **19**:196-202.

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

Warner, R. E., and S. L. Etter. 1989. Hay cutting and the survival of pheasants: a long-term perspective. Journal of Wildlife Management **53**:455-461.

Warner, R. E. 1994. Agricultural land use and grassland habitat in Illinois: future shock for Midwestern birds? Conservation Biology **8**:147-156.

Warren, K. A., and J. T. Anderson. 2005. Grassland songbird nest-site selection and response to mowing in West Virginia. Wildlife Society Bulletin **33**:285-292.

Wheelwright, N. T., and J. D. Rising. 1993. Savannah Sparrow. Birds of North America **45**:1-28.

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.

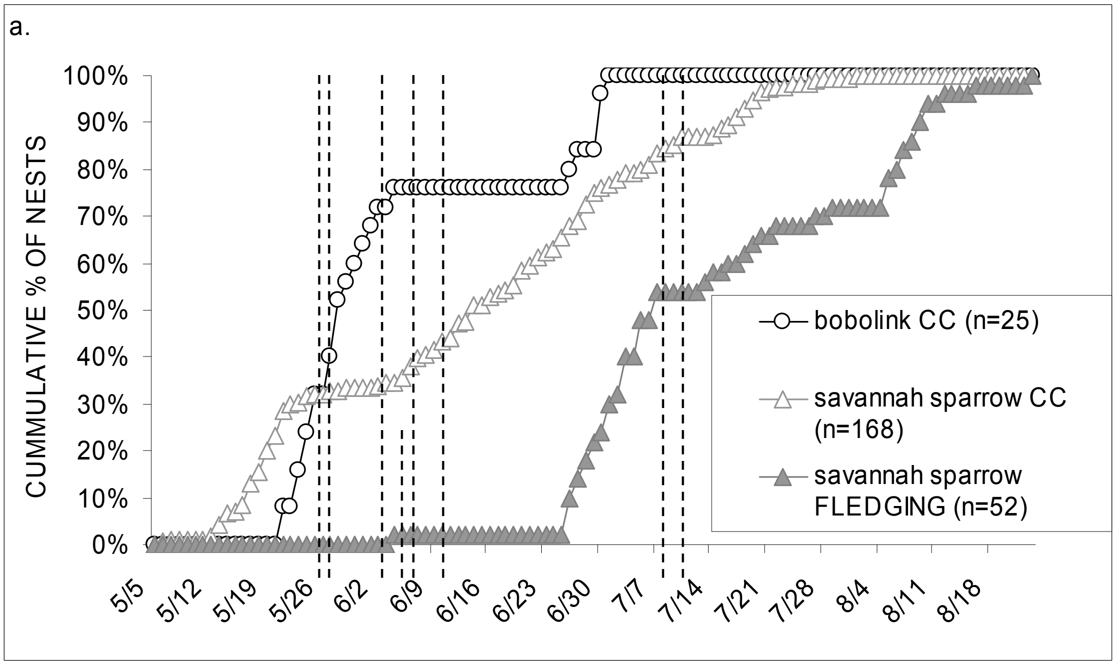
Table 1: Fledglings produced per female/year, number of nests, and number of eggs laid by species and treatment type in the Champlain Valley (NY, VT) 2002-2005. Standard error presented in parenthesis.

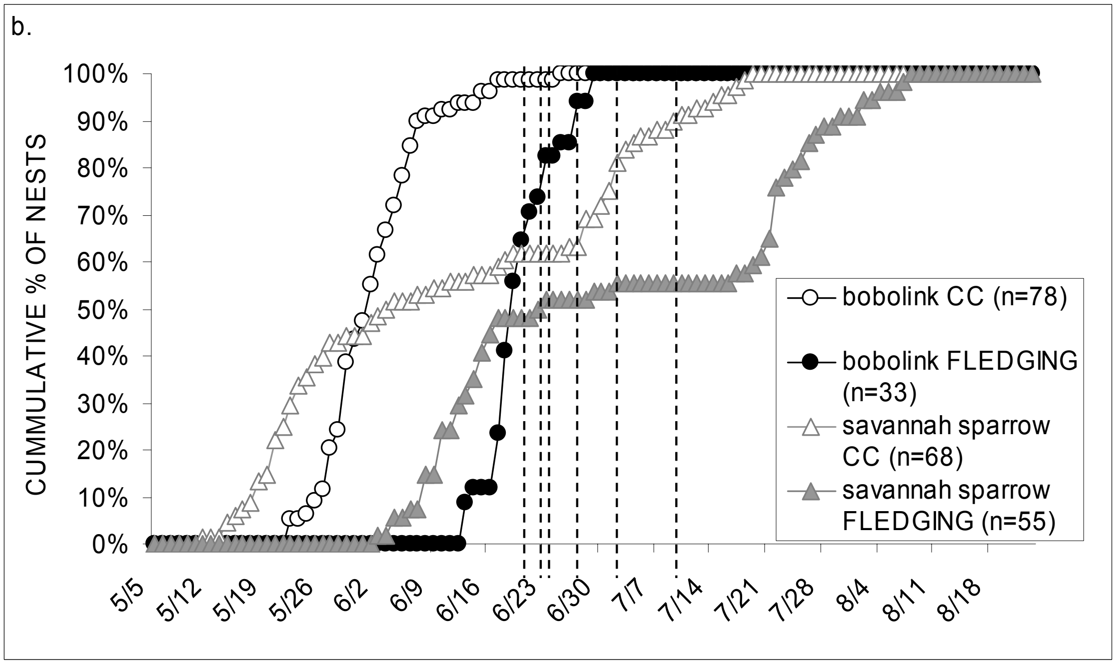
PARAMETER	SPECIES	TREATMENT			
		EARLY-HAYED	MIDDLE-HAYED	LATE-HAYED	GRAZED
# FLEDGLINGS/ FEMALE/ YEAR	BOBOLINK	0.05 (0.05)	2.22 (0.26)	2.79 (0.18)	1.79 (0.33)
	SAVANNAH SPARROW	1.28 (0.16)	3.47 (0.42)	3.29 (0.30)	2.32 (0.25)
# NESTS/YEAR	BOBOLINK	1.00 (0.00)	1.03 (0.02)	1.05 (0.02)	1.09 (0.06)
	SAVANNAH SPARROW	1.87 (0.10)	1.64 (0.08)	1.64 (0.08)	1.52 (0.08)
# EGGS/YEAR	BOBOLINK	4.71 (0.18)	5.28 (0.13)	5.05 (0.11)	5.05 (0.29)
	SAVANNAH SPARROW	7.35 (0.39)	6.44 (0.55)	6.58 (0.33)	5.73 (0.32)

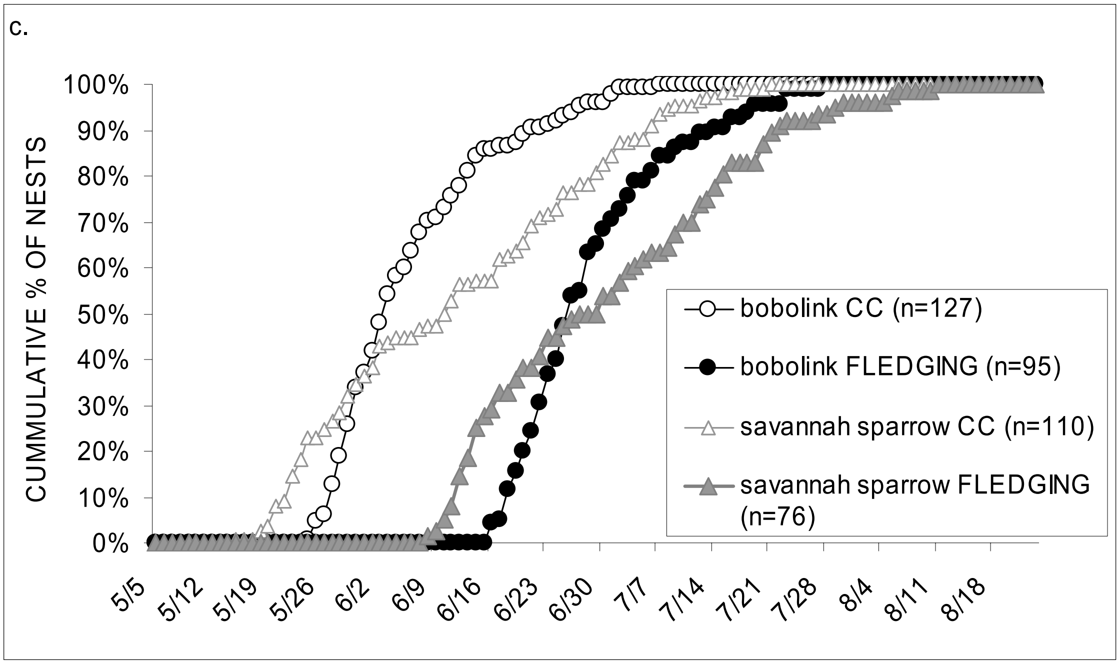
Table 2: Logistic-exposure nest success model set with corresponding ranking values for Savannah Sparrow and Bobolink nests in the Champlain Valley (NY, VT) 2002-2005 (K is the number of estimated parameters; DEVIANCE is the -2logl; AIC_c is a second order correction for AIC which is computed as DEVIANCE – 2K; Δ_i measures the difference between AIC_c between $model_i$ and the best fitting model; ω_i is the AIC_c weight, interpreted as the probability of being the best model in the model set).

RANK	MODEL	K	DEVIANCE	AIC_C	Δ_i	ω_i
1	treatment * species interaction	8	4050.41	4066.43	0.00	0.57
2	treatment * year interaction	15	4037.82	4067.90	1.47	0.27
3	treatment + species + year	8	4055.20	4071.23	4.79	0.05
4	treatment + species	5	4061.80	4071.81	5.37	0.04
5	treatment + year	7	4057.97	4071.99	5.55	0.04
6	Treatment	4	4064.36	4072.37	5.94	0.03
7	year * species interaction	8	4134.95	4150.98	84.54	0.00
8	year + species	5	4170.71	4180.72	114.29	0.00
9	Year	4	4176.38	4184.39	117.95	0.00
10	Species	2	4185.97	4189.97	123.53	0.00

Figure 1. Nesting phenology for Savannah Sparrows and Bobolinks in Champlain Valley (NY, VT) 2002-2005 was different among treatments and between species (a: early-hayed, b: middle-hayed, c: late-hayed, d: rotationally-grazed pasture). Phenologies are presented on each field both in terms of clutch completion dates (CC), indicating spring settlement and renesting behavior, as well as fledging phenology (where available). Figures include all nesting attempts that survived at least one change of state from egg-laying to incubation, incubation to hatching, or nestling to fledging. Vertical bars on early- and middle-hayed figures illustrate the observed haying events.


a.
CUMMULATIVE % OF NESTS
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30
7/7
7/14
7/21
7/28
8/4
8/11
8/18
bobolink CC (n=25)
savannah sparrow CC (n=168)
savannah sparrow FLEDGING (n=52)


b.
CUMMULATIVE % OF NESTS
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30
7/7
7/14
7/21
7/28
8/4
8/11
8/18
bobolink CC (n=78)
bobolink FLEDGING (n=33)
savannah sparrow CC (n=68)
savannah sparrow FLEDGING (n=55)


c.
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
CUMMULATIVE % OF NESTS
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30
7/7
7/14
7/21
7/28
8/4
8/11
8/18
bobolink CC (n=127)
bobolink FLEDGING (n=95)
savannah sparrow CC (n=110)
savannah sparrow FLEDGING (n=76)

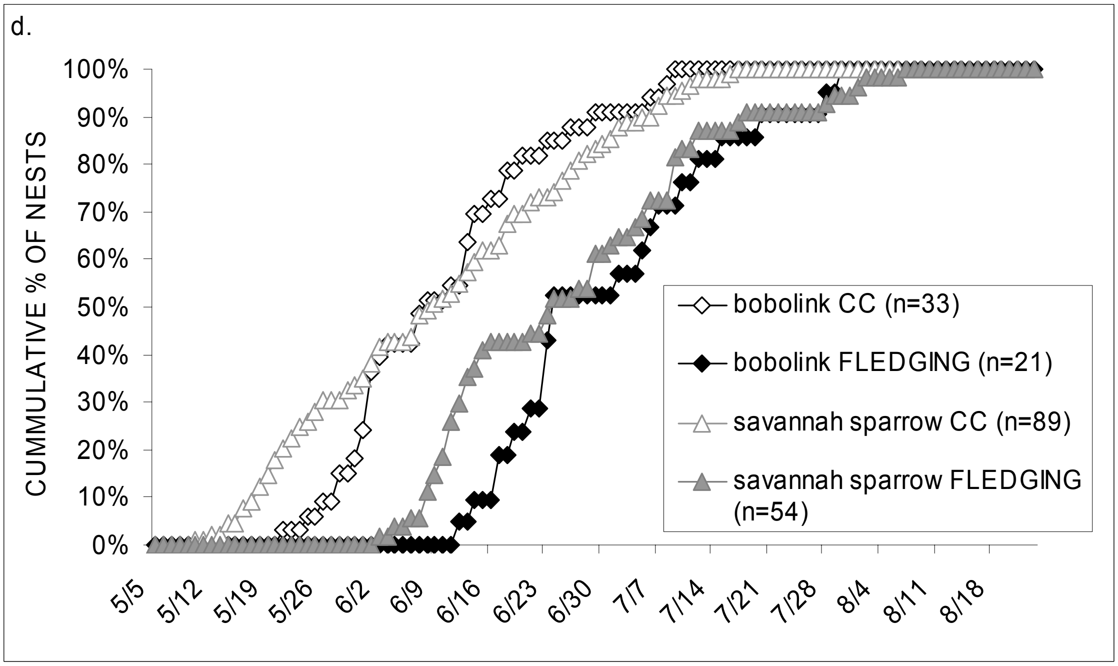
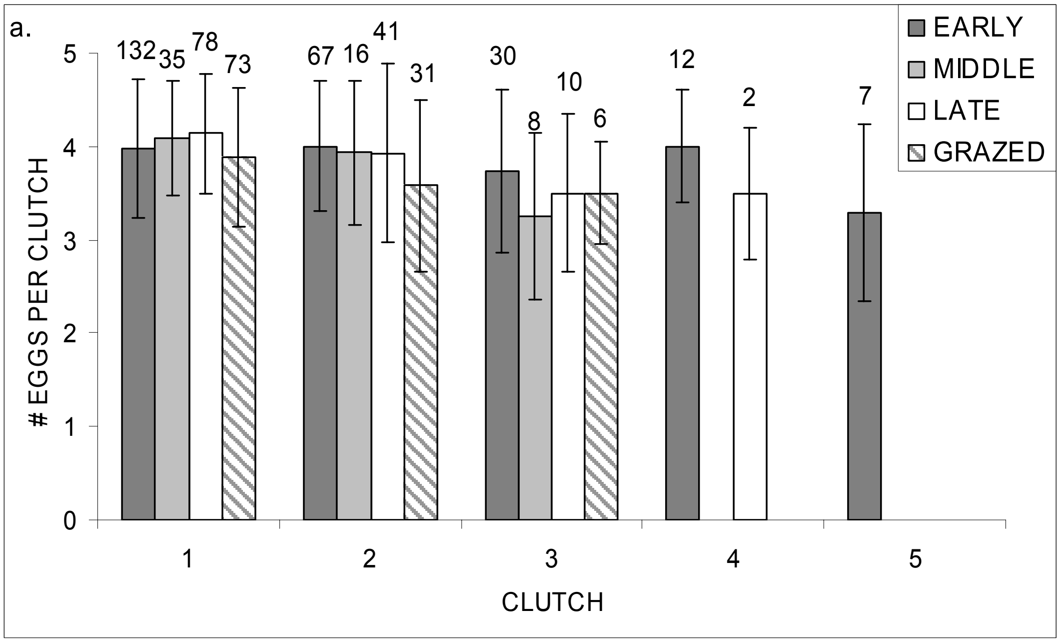

d.
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
CUMMULATIVE % OF NESTS
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30
7/7
7/14
7/21
7/28
8/4
8/11
8/18
bobolink CC (n=33)
bobolink FLEDGING (n=21)
savannah sparrow CC (n=89)
savannah sparrow FLEDGING (n=54)

Figure 2a-b: The number of Savannah Sparrow (a) and Bobolink (b) eggs laid per clutch in the Champlain Valley (NY, VT) 2002-2005. Second Bobolink clutches had nearly one fewer egg, though samples were low because few marked females laid replacement clutches. Error bars indicate 95% confidence intervals and numbers above each bar represent sample size.


a.
EGGS PER CLUTCH
0
1
2
3
4
5
CLUTCH
1
2
3
4
5
132
35
78
73
67
16
41
31
30
8
10
6
12
2
7
EARLY
MIDDLE
LATE
GRAZED

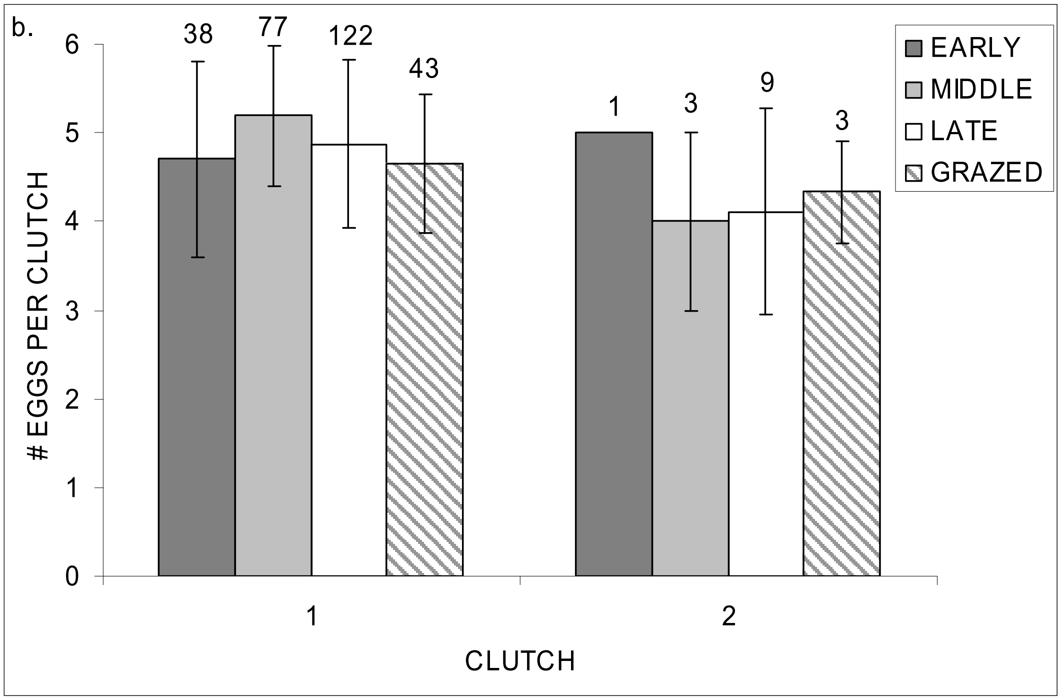

b.
EGGS PER CLUTCH
0
1
2
3
4
5
6
CLUTCH
1
2
38
77
122
43
1
3
9
3
EARLY
MIDDLE
LATE
GRAZED

Figure 3: Causes of failure for all failed Savannah Sparrow and Bobolink nests in the Champlain Valley (NY, VT) 2002-2005 (sample sizes included above bars). Types of failures were generally associated with treatment type. Note that failure due to haying includes nest loss during hay harvest and secondary losses due to predation, or abandonment.

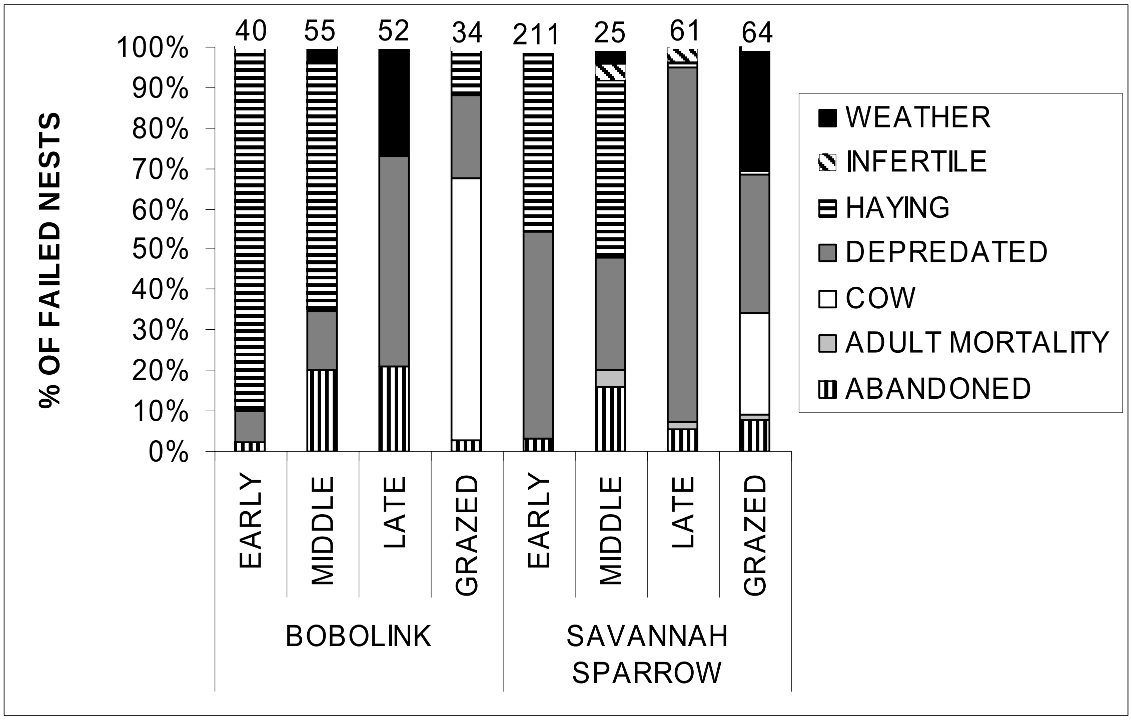


Figure 4a-b: Savannah Sparrow (a) and Bobolink (b) logistic-exposure model averaged nest success in the Champlain Valley (NY, VT) 2002-2005. Error bars indicate 95% confidence intervals. Values indicate mean value for treatment.

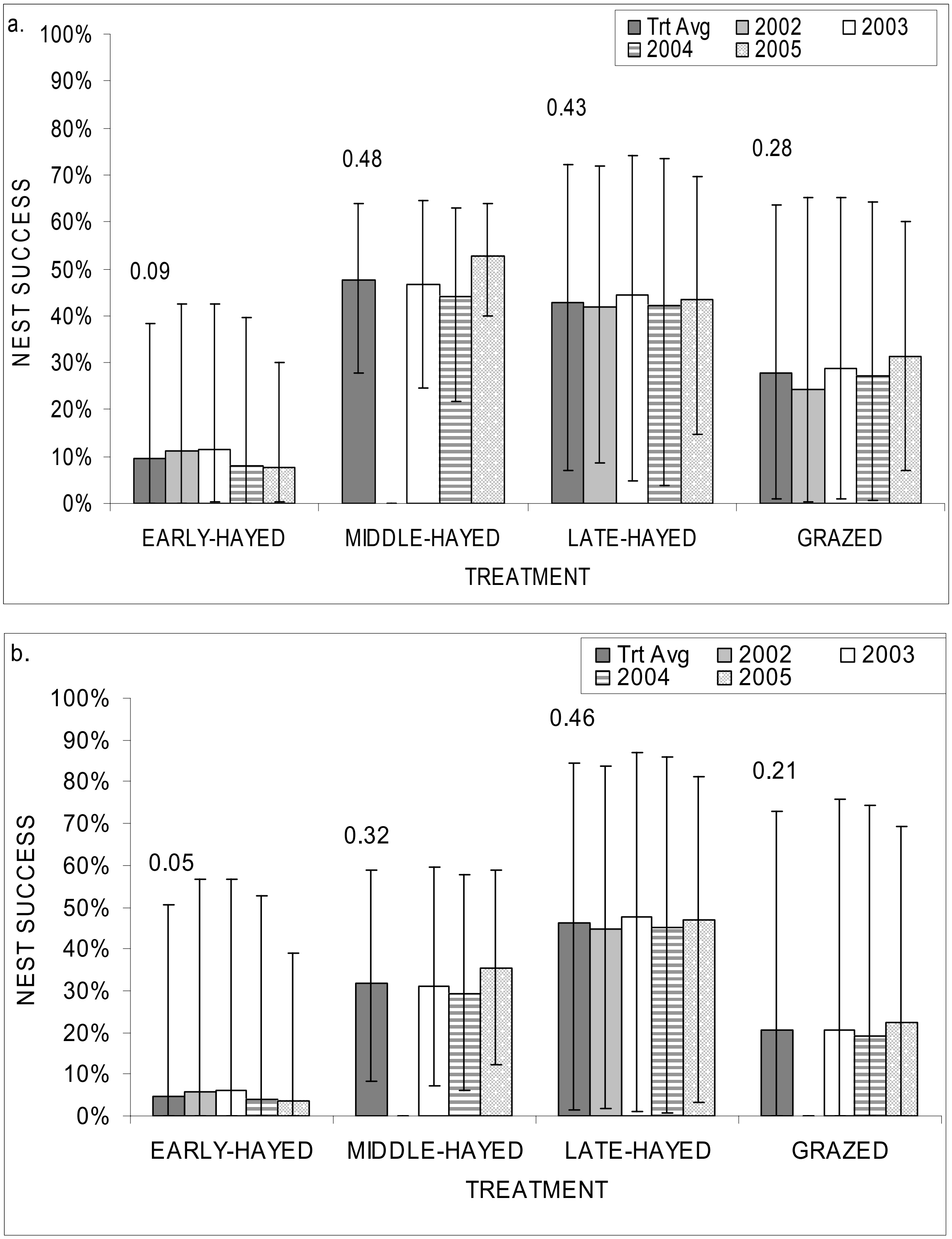


Figure 5: Bobolink and Savannah Sparrow logistic-exposure model averaged daily nest survival in the Champlain Valley (NY, VT) 2002-2005. Error bars indicate 95% confidence intervals.

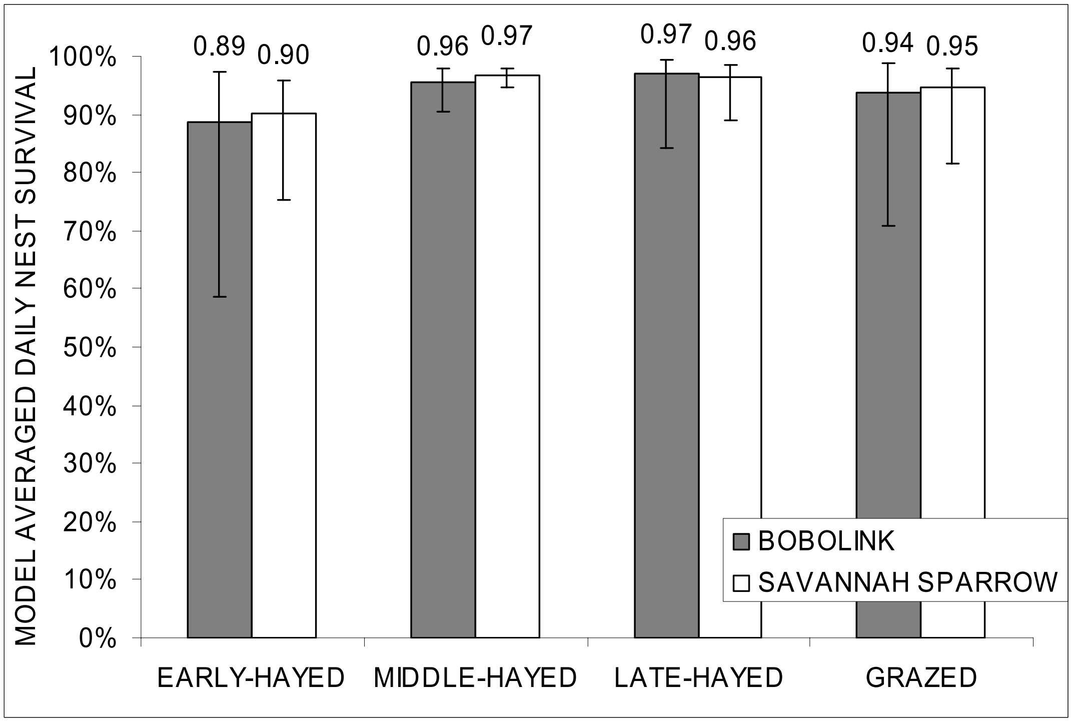
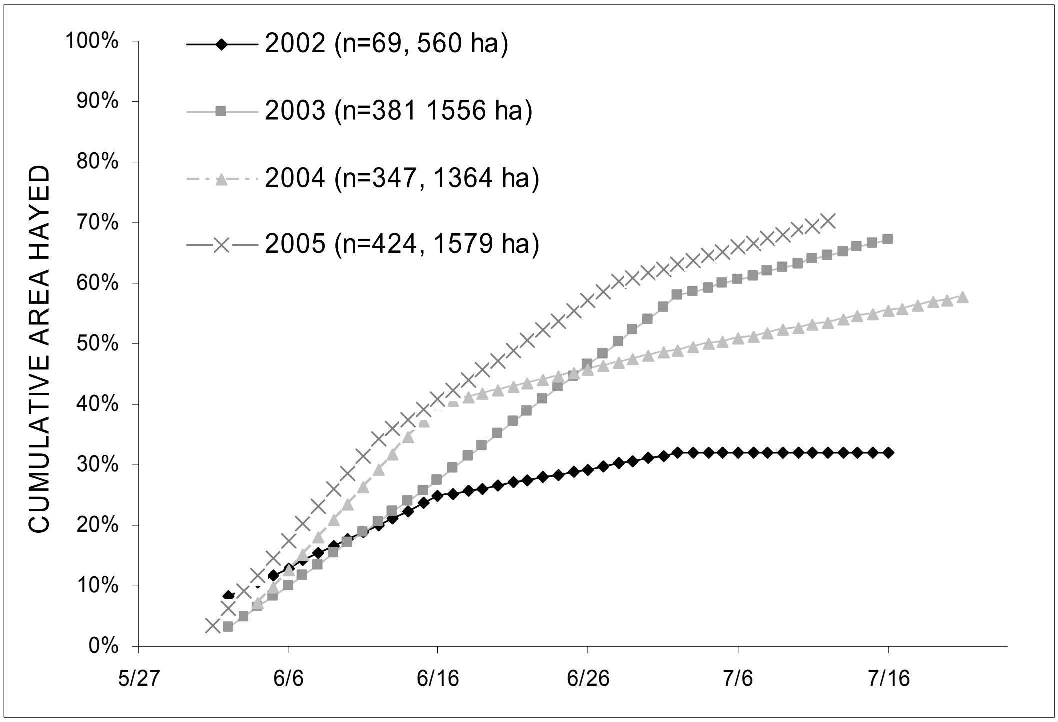


Figure 6: Cumulative area hayed, Champlain Valley, VT 2002-2005. By 1-4 June, between 3-8% of hayfield habitat was cut; by 12-16 June between 25-40% of hayfield habitat was cut; and 32-60% was cut by 28 June - 2 July. Additionally, 59% of hayfields cut before 11 June were cut a second time during the breeding season.



Chapter 2

Agricultural management affects evolutionary processes in a migratory songbird

ABSTRACT

Seventy-two percent of the world's temperate grasslands are affected by agriculture or human development. Because little native habitat remains, populations that are dependent on agriculturally-managed grasslands to carry out their life cycles are declining. For example, hay-harvests have detrimental effects on breeding grassland songbirds, where the harvest process results in complete nest failure. Although such ecological effects of agriculture are well-documented, the effect on evolutionary processes is uninvestigated. Here, we show that early-season harvest of grass forage has both ecological and evolutionary implications for a ground-nesting songbird, the Savannah sparrow (*Passerculus sandwichensis*). We explored how hay-harvest affects social and genetic mating systems, two key components driving evolutionary change. On an unharvested field, 55% of females were in polygynous associations, and social polygyny was associated with greater rates of extra-pair paternity. In contrast, on an early-harvest field, simultaneous nest failure caused by haying increased social monogamy and decreased extra-pair paternity. Haying-mediated changes in social and genetic mating systems resulted in greater than two-fold increase in the opportunity for sexual selection. Because up to 40% of available habitat in our system is in early-harvest management, these data demonstrate a strong population-level effect of agricultural management on sexual selection, and consequently, evolutionary processes.

INTRODUCTION

As humans exert greater influences on ecological systems (Hannah *et al.* 1995), coevolved relationships between vertebrates and their breeding habitats can become decoupled. Although human-mediated effects on ecological processes have been well documented (Vitousek *et al.* 1997; Parmesan & Yohe 2003), in general, little is known about the evolutionary consequences of anthropogenic activities on vertebrate populations. One widely cited example of negative ecological effects but unknown evolutionary effects is that of agricultural grasslands and the songbirds that use these habitats for breeding (Bollinger *et al.* 1990; Bollinger & Gavin 1992; Perlut *et al.* 2006). In fact, breeding in agricultural grasslands is thought to be a main contributor to long-term grassland bird population declines (Bollinger & Gavin 1992; Peterjohn & Sauer 1999; Murphy 2003), as all or nearly all active nests are destroyed during harvest (Bollinger *et al.* 1990; Perlut *et al.* 2006). In this study, we explore the evolutionary consequences of agricultural management practices on breeding songbirds.

Hay-harvests, by altering the distribution of resources and the synchrony of breeding females, may influence mating systems, and hence evolutionary processes (Verner & Willson 1966; Emlen & Oring 1977; Fishman & Stone 2005). Most polygynous avian species, in which males establish social pair bonds with multiple mates, are found in habitats with high resource variation among territories, with the best territories holding sufficient food resources for multiple mates (Emlen & Oring 1977). When a small percentage of males monopolize resources and multiple females, a greater opportunity for sexual selection and increased variance in male fertilization success arises (Emlen & Oring 1977). However, if females become highly synchronous (with overlapping fertile periods; Kempenaers (1993)), the rate of social monogamy may increase because males have little opportunity to seek additional mates (Emlen & Oring 1977), resulting in low variance in male fertilization success. Thus, while resource abundance and distribution define a habitat's polygyny potential, female synchrony may determine whether this potential is realized.

Variance in male fertilization success, however, is not always explained by the social mating system. At the individual pairing level, social mating systems are often incorrectly assigned as a result of extra-pair paternity (EPP), which occurs when an egg is fertilized by a male other than the social mate. EPP defines the genetic system of a breeding population and female breeding synchrony is a critical component either increasing or decreasing the EPP rate (Stutchbury & Morton 1995). Synchrony increases EPP if females can assess male quality simultaneously and mate accordingly (Stutchbury *et al.* 1997); offspring are sired by a small proportion of available males, increasing variance in fertilization success. Alternatively, synchrony decreases EPP if males increase time spent mate guarding, decreasing the amount of time seeking copulations (Kempenaers 1997; Weatherhead 1997); high synchrony results in low social and genetic polygyny, lowering variance in fertilization success.

Because the extent of social and genetic polygyny influences variation in male fertilization success, mating systems can affect evolutionary processes. The extent of variation in male fertilization success effects the magnitude of sexual selection (Webster *et al.* 1995); therefore, mating systems can directly influence the strength of selection on phenotypes important to male-male competition and female choice. Changes in the ecological conditions that shape social and genetic mating systems may alter the characteristics that define sexual selection, thereby influencing a species' evolutionary trajectory.

Birds breeding in managed agricultural systems provide a unique opportunity to determine how altering resource distribution and breeding synchrony influence both ecological and evolutionary processes. We studied the Savannah sparrow (*Passerculus sandwichensis*), a species with a mixed-mating strategy, asynchronous settlement, and biparental care (Wheelwright & Rising 1993; Perlut et al. 2006). Our objective was to identify plasticity in Savannah sparrows' social and genetic mating systems as a result of hay-harvest and to determine the evolutionary significance of these behavioural responses.

From 2002-05, we studied Savannah sparrows in one early-harvest field, first harvested ~1 June, and one unharvested field. In the early-harvest field, we compared the social and genetic mating systems pre- and post-cutting (two discrete 'haying intervals') and quantified changes in breeding synchrony and resource distribution between the two periods. In the unharvested field, we followed settlement patterns throughout the season and determined how breeding synchrony, resource distribution, the social mating system, and the genetic mating system changed over time.

METHODS

Our research took place in the Champlain Valley of Vermont, USA, which contains 146,000 ha of managed grasslands (NASS 1999). We monitored nests in one early-harvest field and one unharvested field, each 10.5 ha. Adult birds were captured with mist nets and fitted with unique combinations of coloured leg bands and one metal U.S. Fish and Wildlife Service band. We measured standard morphology and obtained a small (20-60uL) sample of blood. Nestlings were bled, and banded with a single metal band.

We attempted to find the nests of all females on each field, and visited each nest every one to two days until the young fledged or the nest failed. The social mating system was determined through intensive nest observations. Since incubation is a female-only behaviour, female association was identified by flushing incubating birds off the nest. Male association was identified by feeding and territory defense behaviour (Wheelwright & Rising 1993).

Female breeding synchrony was calculated with Kempenaers' (1993) breeding synchrony index. SI determines the average proportion of fertile females on a given day within a population, requiring information on the breeding stage of every nesting female on a field. Females whose nest contents survived either from egg-laying to incubation, incubation to hatching, or nestling to fledging, were included within the synchrony analysis because these nests could be back-dated to a clutch completion date. In order to determine the effects of haying, female breeding synchrony on the early-harvest field was evaluated with the first post-harvest renest for each female. If females failed within an interval, we ignored future renests, as their inclusion would confound the effects of predation within haying-mediated synchrony analyses.

Paternity analysis was performed with four hypervariable microsatellite loci: *Psa*12, *Passerculus sandwichensis* (Freeman-Gallant *et al.* 2005); *Escu*6, *Emberiza schoeniclus* (Hanotte *et al.* 1994); *Mme*1 and *Mme*8, *Melospiza melodia* (Jeffery *et al.* 2001). All molecular and paternity assignment methods followed Freeman-Gallant *et al.* (2005). We sampled a total of 107 broods (*n* = 352 nestlings), including 24 (*n* = 90 nestlings) pre-harvest and 42 (n = 124 nestlings) post-harvest broods on the early-harvest field, and 41 (n = 140 nestlings) broods on the unharvested field. Paternity analysis for both fields combined showed high EPP rates, where 72% of broods had at least one extra-pair offspring (n = 77 broods). Females sought extra-pair sires for a majority of the offspring in each brood (54%, n = 191 nestlings). The opportunity for sexual selection was determined following Webster *et al.* (1995). With this method, sexual selection is a function of the variation in the number of social mates obtained, variation in mate quality, and/or variation in success at obtaining both within-pair and extra-pair fertilizations.

Invertebrates were sampled in 2004-05 on the early-harvest and unharvested fields. Insects were collected both pre- and post-harvest with ten sweep net samples at ten randomly selected locations throughout the field. Length-mass regression equations were constructed to convert invertebrate length into estimates of dry biomass for 12 taxonomic groups. To construct the equations, we measured the lengths (to the nearest 0.01 mm) of selected invertebrates obtained from sweep net samples. In 2004, all invertebrates >3 mm in length that were captured were identified into one of 12 prey categories and counted in the field. In 2005, invertebrates were collected and put in a forced-air drying oven at 100°C for 24 hours and later weighed on an electronic balance (precision ± 0.01mg). For both years, mass was regressed versus length using a power function of the form: $\text{mass} = a * \text{length}^{b}$.

RESULTS

Hay-harvest decreased the social polygyny rate. On the unharvested field, the social mating system showed a mixed strategy, with 55% of females in polygynous pairings and 45% of females in monogamous pairings over all years (figure 1). These proportions were stable over the breeding season. On the early-harvest field, before haying, 33% of females were in polygynous associations and 67% of females were monogamous. The pre-harvest monogamy rate was upwardly biased due to the fact that the early-harvest field was cut when polygynous males were just beginning to establish social bonds with secondary females. However, the unharvested field was an adequate control; the monogamy rate of the unharvested field's first broods prior to June 16 was not different than pre-harvest monogamy rate (Least-square means (LSM): $P = 0.096$). Early-harvest caused 99% ($n = 72$) of all first nests to simultaneously fail and females renested immediately (Perlut *et al.* 2006). The monogamy rate increased significantly post-harvest (LSM: $P < 0.01$), where 17% of females were in polygynous associations and 83% of females paired monogamously (figure 1). The monogamy rate on the unharvested field was significantly lower than the monogamy rate on the early-harvest field after cutting (LSM: $P = 0.002$).

Hay-harvest also influenced the genetic mating system. On the unharvested field, EPP was associated with the social mating system, where socially monogamous females had 62% lower EPP rates than socially polygynous females ($Z = 4.49$, $P < 0.001$; figure 1). These rates were consistent across the breeding season (first broods vs. second broods: $X^2 = 1.22$, $df = 1$, $P = 0.27$; second broods vs. third broods: $X^2 = 0.89$, $df = 1$, $P = 0.340$). On the early-harvest field, EPP decreased significantly ($X^2 = 649.81$, $df = 1$, $P < 0.001$) after the first harvest in both mating systems; monogamous females had 51% and polygynous females had 66% fewer extra-pair young than pre-harvest females (figure 1).

Post-harvest changes in the genetic mating system may result from the joint effects of changes in social mating system through putative changes in resource distribution and changes in breeding synchrony. On the early-harvest field, EPP was also associated with the social mating system ($Z = -3.13$, $P < 0.002$); post-harvest pairings were mainly monogamous, and monogamous nests had less extra-pair paternity. This change in social mating system may have resulted from haying-mediated changes in food resources which decreased the total food biomass by 460% and the variance in food biomass by 417% (figure 2). Thus, post-harvest, males' inability to monopolize resources contributed to their inability to attract multiple females.

The effects of hay-harvest on synchrony and the genetic mating system were less clear. Synchrony was higher on the early-harvest field (Synchrony Index (SI) = 0.68 ± 0.04 (s.e.m.), $n = 52$; Kempenaers 1993) prior to haying than post-harvest (SI = 0.60 ± 0.03, $n = 57$; LSM: $P = 0.11$), though not statistically different. However, post-harvest nests were significantly more synchronous than nests on the unharvested field (SI = 0.48 ± 0.03, $n = 44$; LSM: $P = 0.01$). On the early-harvest field, synchrony did not explain EPP ($Z = 1.46$, $P = 0.14$), although like the monogamy rate, the pre-harvest estimate of synchrony on the early-harvest field is potentially upwardly-biased. By contrast, EPP on the unharvested field was associated with female breeding synchrony, where more synchronous females had higher extra-pair paternity ($Z = 4.35$, $P < 0.001$). Together, these results support the social mating system, perhaps mediated through changes in food resources and breeding synchrony as the mechanism for decreased EPP post-harvest.

Despite the fact that early haying resulted in increased social and genetic monogamy, early-harvest more than doubled the total opportunity for sexual selection, I (table 1). This doubling occurred in two ways. First, relative to the unharvested field, there was a 30% increase in the variance associated with within-pair fertilization success.

This effect arose, in part, from increased variance associated with the number (+10%, M_{wp}) and quality (+110%, N_{wp}) of social mates following simultaneous nest failure caused by haying. Second, early-haying ameliorated the strong, negative covariance between a male's within-pair and extra-pair fertilization success. Overall, fertilizations were thereby distributed less evenly through the population.

DISCUSSION

Because harvesting influenced both the social and genetic mating systems, haying altered the opportunity for sexual selection, thus potentially influencing the evolution of Savannah sparrows. In the unharvested field, high extra-pair paternity occurred at the expense of within-pair fertilizations, greatly constraining the variance in male reproductive success and the overall opportunity for sexual selection. Here, the polygyny rate was high, and polygynous pairing had greater EPP. In the early-harvest field, by contrast, males accumulated both within-pair and extra-pair fertilizations. This result, however, occurred after haying constrained males to accept monogamous pairings. Taken together, these results suggest that the strength and target of selection might be affected by haying, to the extent that different fitness components are associated with different phenotypes (Yezerinac & Weatherhead 1997). By disrupting this process, hay-harvest could alter the evolutionary trajectory that leads to ecologically and sexually selected forms—an active process within natural populations of this species as evidenced by its 13 recognized subspecies (Wheelwright & Rising 1993).

When viewed from the landscape perspective in which up to 40% of available habitat is in early-harvest management (Perlut et al. 2005), these data indicate a strong evolutionary pressure applied by agriculture. Early-harvest offset the resource distribution and to a lesser degree, breeding synchrony that enabled social polygyny, causing the population to become more socially and genetically monogamous. These changes doubled the strength of sexual selection, and as a consequence, altered evolutionary processes of the population. We know of no other vertebrate studies that have identified both ecological and evolutionary effects linked to human influenced agricultural management.

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LITERATURE CITED

Bollinger, E. K., Bollinger, P. B. & Gavin, T. A. 1990 Effects of hay-cropping on

Eastern populations of the Bobolink. *Wildlife Soc. B.* 18, 143-150.

Bollinger, E. K. & Gavin, T. A. 1992 Eastern bobolink populations: ecology and conservation in an agricultural landscape. In *Ecology and Conservation of Neotropical Migrant Landbirds* (eds J. M. Hagan III, D. W. Johnston), pp. 497-506. Washington D.C.: Smithsonian Institute Press.

Emlen, S. T. & Oring, L. W. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215-223.

Fishman, M. A. & Stone, L. 2005 Fertility assurance and breeding synchrony. *Bull. Math Biol.* 67, 875-883.

Freeman-Gallant, C. F., Wheelwright, N. T., Meicklejohn, K. E., States, S. L. & Sollecito, S. V. 2005 Little effect of extra-pair paternity on the opportunity for sexual selection in Savannah sparrows (*Passerculus sandwichensis*). *Evolution* 59, 432-440.

Hannah, L., Carr, J. L. & Lankerani, A. 1995 Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity Conserv.* 4, 128-155.

Hanotte, O., Zanon, C. & Pugh, A. 1994 Isolation and characterization of microsatellite loci in a passerine bird - the reed bunting *Emberiza-Schoeniclus*. *Mol. Ecol.* 3, 529-530.

Jeffery, K. J., Keller, L. F. & Arcese P. 2001 The development of microsatellite loci in the Song Sparrow, *Melospiza melodia* (Aves) and genotyping errors associated with good quality DNA. *Mol. Ecol. Notes* 1, 11-13.

Kempenaers, B. 1993 The use of a breeding synchrony index. *Ornis. Scand.* 24, 1.

Kempenaers, B. 1997 Does reproductive synchrony limit male opportunities or enhance female choice for extra-pair paternity? *Behaviour* 134, 551-562.

Murphy, M. T. 2003 Avian population trends within the evolving agricultural landscape of Eastern and Central United States. *Auk* 120, 20-34.

National Agricultural Statistics Service USDA. 1999 http://www.nass.usda.gov/census.

Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.

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

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

Stutchbury, B. J. & Morton, E. S. 1995 The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* 132, 675-690.

Stutchbury, B. J., Piper, W. H., Neudorf, D. L., Tarof, S. A., Rhymer, J. M., Fuller, G. & Fleischer, R. C. 1997 Correlates of extra-pair fertilization success in hooded warblers. *Behav. Ecol. Sociobiol.* 40, 119-126.

Verner, J. & Willson, M. F. 1966 The influence of habitats on mating systems of North American passerine birds. *Ecology* 47, 143-147.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. 1997 Human domination of the earth's ecosystems. *Science* 277, 494-499.

Weatherhead, P. J. 1997 Breeding synchrony and extra-pair mating in red-winged blackbirds. *Behav. Ecol. Sociobiol.* 40, 151-158.

Webster, M. A., Pruett-Jones, S., Westneat, D. F. & Arnold, S. J. 1995 Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution* 49, 1147-1157.

Wheelwright, N. T. & Rising, J. D. 1993 Savannah Sparrow. *Birds of North America* 45, 1-28.

Yezerinac, S. M. & Weatherhead, P. J. 1997 Reproductive synchrony and extra-pair mating strategy in a socially monogamous bird, *Dendroica petechia*. *Anim. Behav.* 54, 1393-1403.

Table 1: Post-haying variance in male reproductive success, including both within-pair (WP) and extra-pair (EP) components, increased the opportunity for selection. Both within-pair and extra-pair variance includes the number of mates a male attracts (M), the number of young produced per mate (N), and the percentage of these young he sires (P). Estimates for the unharvested field include only first clutches. Standardized values were computed as the variance/mean^2.

	Unharvested field	Early-harvest field post-harvest
Source	Standardized value	Standardized value
Total variance	0.339	0.773
Total WP variance	0.192	0.249
M_{wp}	0.182	0.201
N_{wp}	0.024	0.050
P_{wp}	0.048	0.028
Total EP variance	0.167	0.174
M_{ep}	0.136	0.133
N_{ep}	0.014	0.024
P_{ep}	0.036	0.049
Total WP & EP covariance	-0.192	-0.079

Figure 1: The social and genetic mating system post-harvest was significantly different than both the pre-harvest period and unharvested field. EPP did not differ between pre-harvest nests and first-brood nests found on the unharvested field before the latest observed harvest late (June 11) ($X^2 = 0.26$; *df* = 1; $P = 0.608$). However, EPP did differ between pre- and post- harvest ($X^2 = 12.88$; *df* = 1; $P < 0.001$); and EPP differed between first broods on the unharvested field and post-harvest renests ($X^2 = 7.16$; *df* = 1; $P = 0.007$). On the unharvested field, by June 16, 60% of females were in monogamous pairings. At this early stage, the unharvested field monogamy rate was not statistically different than pre-harvest monogamy rate (LSM: $P = 0.096$). However, the unharvested field monogamy rate was lower than post-harvest (LSM: $P = 0.002$); and pre-harvest monogamy rate was lower than post-harvest (LSM: $P = 0.04$). Sample sizes indicated; error bars represent standard error values.

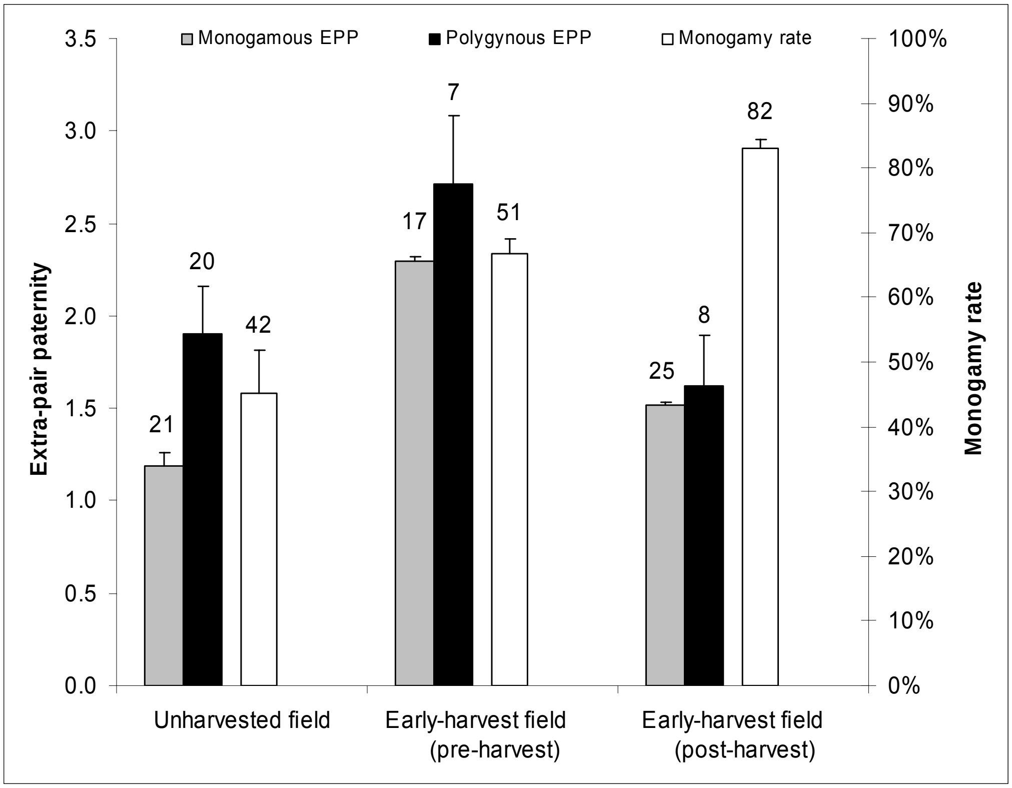
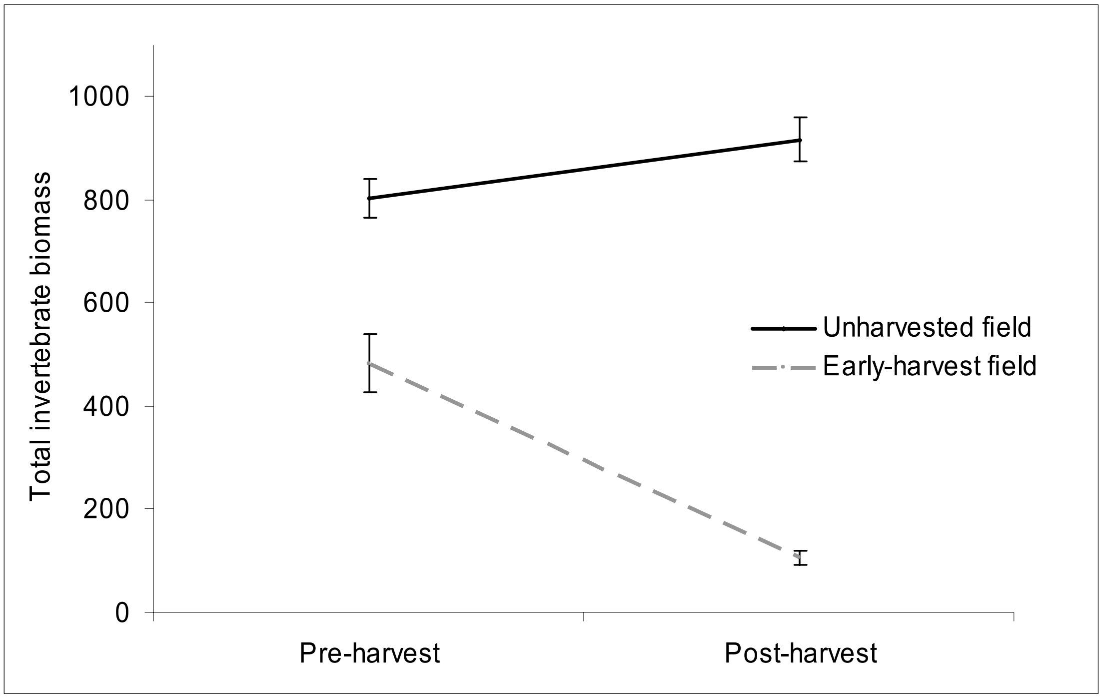


Figure 2: The total amount of invertebrate biomass and the within-field variance decreased by >400% after haying. This decrease in amount and distribution of biomass resulted in a change in the social mating system on the early-harvest field, significantly increasing the monogamy rate (LSM: $P < 0.01$). Error bars indicate the standard deviation of these samples.



Chapter 3

Grassland songbird survival and recruitment in heterogeneous agricultural landscapes: implications for source-sink demography

ABSTRACT

Population growth and decline is sensitive to changes in three key life-history parameters: annual productivity, juvenile survival, and adult survival. However, for many species these parameters remain unknown. For example, although grassland songbirds are imperiled throughout North America, within this guild, only a small number of studies have assessed these parameters. From 2002-2006, in the agricultural landscape of the Champlain Valley of Vermont and New York, USA, we studied Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*) demography on four grassland treatments: 1) early-hayed fields cut before 11 June and again in early- to mid-July; 2) middle-hayed fields cut once between 21 June and 10 July; 3) late-hayed fields cut after 1 August; and 4) rotationally-grazed pastures. We assessed whether these treatments affected adult apparent survival (ϕ) and recruitment (*f*), how sensitive these parameters were to the presence of non-breeders and local dispersal, and the populations' ability to persist in these four habitats.

On average, birds using late-hayed fields had > 25% higher apparent survival than those on the more intensively managed early-hayed, middle-hayed, and grazed fields; male ϕ was 36% higher than female ϕ; Savannah Sparrow ϕ was 64% higher than Bobolink ϕ. Across all analyses and among the four treatments, apparent survival estimates ranged from 0.58 – 0.85 for male and 0.48 – 0.71 for female Savannah Sparrows, and 0.52 – 0.70 for male and 0.19 – 0.55 for female Bobolinks. For males of

both species, potential non-breeders decreased the precision of and lowered apparent survival estimates by 25%; though, female estimates showed little variation with the inclusion of non-breeders. Inclusion of local dispersal observations increased apparent survival estimates and in many cases increased precision, though the effect was stronger for Savannah Sparrows than Bobolinks, and for males than females. High Savannah Sparrow apparent survival rates resulted in stable or near stable populations ($\lambda \sim 1$), particularly in late-hayed and grazed fields, while low Bobolink apparent survival rates resulted in strongly declining populations ($\lambda < 1$) in all treatments.

INTRODUCTION

Population ecology is centered on questions of how and why populations grow and decline. Answers are often found within sensitivities of key demographic parameters—including annual productivity, juvenile survival, and adult survival (Crouse et al. 1987, Donovan et al. 1995, Anders and Marshall 2005). These life-history parameters, though, are difficult to quantify because their estimation is dependent on individually-based, long-term field data. Therefore, demographic parameters for many species remain unknown. For example, though grassland songbirds are known to be imperiled throughout North America (Peterjohn and Sauer 1999, Murphy 2003, Brennan and Kuvlesky 2005, Sauer et al. 2005), within this guild, only a small number of studies have assessed annual productivity (Bedard and LaPoint 1985, Bollinger et al. 1990, Kershner et al. 2004, Walk et al. 2004, Perlut et al. 2006), juvenile survival (*indicates return rates; *Wheelwright and Mauck 1998, Kershner et al. 2004, Adams et al. 2006), and adult survival (*Bedard and LaPoint 1984, *Bollinger and Gavin 1989, *Warner and Etter 1989, Perkins et al. 2003, Hagen et al. 2005, Fletcher et al. 2006). Though the pace of assessing grassland songbird life-history parameters has clearly increased, only Fletcher et al. (2006) estimated multiple parameters and examined how sensitivities within these parameters affected population growth.

The need to assess grassland songbirds' life history parameters is particularly important because > 70% of the world's remaining grassland habitat is devoted to agriculture and other human use (Hannah et al. 1995). Management intensity of agricultural grasslands has increased in recent years, where farmers harvest hay earlier and more frequently in a season (Troy et al. 2005). However, management intensity varies throughout agricultural landscapes, resulting in a mosaic of management-defined habitats. To date, only annual productivity has been quantified within these heterogeneous agricultural landscapes. Results show that annual productivity varies dramatically among management-defined grasslands, where less-intensively managed fields have high annual productivity and are potentially population sources (sensu Pulliam 1988), and more intensively managed fields have little to no annual productivity and are population sinks (Bollinger et al. 1990, Perlut et al. 2006). Importantly, the strength of these effects varies among species (Perlut et al. 2006). For example, Savannah Sparrow (*Passerculus sandwichensis*) productivity on fields that are harvested early in the breeding season is ~1 offspring per adult female per year, whereas Bobolink (*Dolichonyx oryzivorus*) productivity on those same fields is ~0 offspring per adult female per year. In contrast, both species fledge ~3 young per adult female per year on fields where haying is delayed until after the breeding season (Perlut et al. 2006). Though we are beginning to understand how annual productivity correlates with agricultural management, no study has looked at survival costs associated with selecting various management-defined habitats within a landscape (but see Bollinger and Gavin (1989) for return rates), and no study has investigated the ability of populations to persist in these habitats.

Survival and recruitment are key parameters in understanding how populations grow or decline over time. Apparent survival, ϕ, is the probability than an individual survives, returns, and is detected; recruitment, f, is the number of individuals entering a population through birth or immigration per surviving individual already in the population. However, estimation of these parameters is largely dependent on field methodology, which in turn affects inferences about population viability (Pradel 1996, Cooch and White 2007). Two population-level behaviors known to affect parameter estimation are local dispersal (between-year movement of individuals off of a study site) and the presence of non-breeding individuals, floaters, that move on and off a study site without being constrained by parental care at a nest. Field methodologies that do not account for these behaviors may result in biased parameter estimates. For example, by moderately expanding resight efforts off study sites, survival estimates, estimate precision, and the probability of detection can increase significantly (Cilimburg et al. 2002). In contrast, inclusion of non-breeding individuals can lower survival estimates of breeding populations (Pradel et al. 1997).

To quantify survival and recruitment, the behavioral factors that affect these estimates, and how these parameters affect inferences about population growth, we conducted a demographic study of two obligate grassland songbird species breeding in agricultural grasslands within the Champlain Valley of Vermont and New York, USA. The goal of this study was to address whether four discrete grassland treatments uniquely affected adult apparent survival and recruitment for two songbird species, and to assess how sensitive these estimates are to changes in field methodologies. We 1) estimated survival and recruitment of birds known to be breeding within the boundaries of nine fields that represent the four treatment types that constitute breeding habitat in the Champlain Valley, 2) determined the sensitivity of survival and recruitment estimates to the effects of non-breeders, 3) determined the sensitivity of survival estimates to effects of local-scale dispersal off the treatment fields, and 4) assessed the finite rate of increase (λ, realized lambda) for each of the four treatment types within the sampling period.

METHODS

Experimental design

We studied four grassland treatment types common in the Champlain Valley:

1. *Early-hayed fields* (EH): hayed between 27 May and 11 June, and generally again in early- to mid-July;
2. *Middle-hayed fields* (MH): hayed between 21 June and 10 July;
3. *Late-hayed fields* (LH): hayed after 1 August;
4. *Rotationally-grazed pastures* (RG): fields in which cows were rotated through a matrix of paddocks and moved after all of the grass in a paddock was eaten to a farm-specific height. Each paddock was thereby given a multiple week "rest" between grazing events.

We established treatment fields in three study areas: (1) Shelburne, Vermont (2002-2006 EH, LH, RG), (2) Hinesburg, Vermont (2003-2006 EH, LH, MH, RG), and (3) Cumberland Head, New York (2002-2005 LH; 2003-2005 MH). Each treatment field was a minimum of 10.5 ha, and study areas were > 8 km apart. Land use within each study area was consistent for > 10 years prior to the initiation of our study. Fields were composed of a mixture of cool season grasses and forbs (see Perlut et al. 2006 for details on vegetation, management, and study area).

Field methods

Beginning on 8 May, we captured birds with mist-nets, and put unique combinations of three color bands and a single metal U.S. Fish and Wildlife Service band on the legs of all adults of both species. Color-banded birds were continuously resighted throughout the breeding season. In mid-May we began intensive, season-long nest searching and nest monitoring (*n* = 733 Savannah Sparrow, 447 Bobolink nests). After locating a nest, we immediately identified the associated female and male. If one or both adults were unbanded, we captured and banded those individuals near the nest location. Resight-recapture efforts concluded each year when the last nest fledged or failed (23 July to 23 August). These nest associations provided important resight-recapture data because the breeding status of these individuals was known.

In 2005 and 2006 we supplemented field efforts within the Shelburne and Hinesburg study areas to explore how between-year, local breeding dispersal off study fields affected the sensitivity of adult survival estimates. In 2005 we opportunistically searched all fields within a 1.5 km radius of the three Shelburne treatment fields, one to two times each (including treatment fields, *n* = 57 fields, 457.2 ha). In 2006 we opportunistically searched all fields within a 1.5 km radius of the Shelburne treatment fields one to two times and Hinesburg treatment fields once (including treatment fields, *n* = 257 fields, 1081 ha). Searches occurred on precipitation-free days between the hours of 0500 and 1400. Both individually and in pairs, we walked through fields swishing 1.5 m bamboo stakes through the grass, flushing birds. We identified each bird as banded or unbanded, recorded its identity, species, and sex, and marked the location of color-banded individuals with a GPS unit. Although singing males were easy to detect and identify, we made a concerted effort to look for and identify less conspicuous females.

From these combined field efforts we created six non-mutually exclusive data sets, consisting of capture-recapture observations (Table 1, sample sizes in Appendix 1).

- Objective 1: To quantify ϕ and *f* for known breeders, we used the BREEDERS, ON PLOT dataset, including only those individuals on the nine study fields who were socially associated with at least one known nest in any year.
- Objective 2: To quantify ϕ and *f* for all breeding and non-breeding individuals, the ALL ADULTS, ON PLOT dataset consisted of all adults banded on the nine study fields.
- Objective 3: We used data collected in Vermont to assess ϕ for individuals who were socially associated with at least one known nest in any year, BREEDERS, WITH DISPERSERS, on the seven Vermont study fields as well as resight data from off-study field searches. BREEDERS, NO DISPERSERS only included adults who were socially associated with at least one known nest in any year on the seven Vermont study fields. ALL ADULTS, WITH DISPERSERS consisted of all individuals banded on the seven Vermont study fields as well as data from off-study field searches. Last, ALL ADULTS, NO DISPERSERS included only individuals banded on the seven Vermont study fields.

Analysis methods

Objective 1: Survival and recruitment of known breeders

We used the Pradel model (Pradel 1996) to assess apparent yearly survival and recruitment in Program MARK (White and Burnham 1999). This analysis focused on survival and recruitment of all individuals who were socially associated with at least one nest in any year and who were marked and resighted within the boundaries of nine study fields (BREEDERS, ON PLOT), for which estimates from Objectives 2 were compared (see below). Bobolink arrival dates on early-hayed fields complicated this analysis.

Because Bobolinks returned to the study sites later in the spring (mid- to late-May) than Savannah Sparrows (late-April to early-May), early-haying generally occurred while Bobolinks were in the early courtship or egg-laying stage, disrupting breeding before many nests were identified and breeding status could be ascertained. Bobolinks abandoned early-hayed fields immediately after cutting (Perlut et al. 2006), became non-breeders, renested elsewhere, or left the Champlain Valley (Strong unpubl data). To account for these possible effects caused by the timing of haying, all Bobolinks banded on early-hayed fields before cutting remained in the BREEDERS, ON PLOT set even if they did not have an identified nesting attempt. Finally, breeding observations were made only during nest-monitoring years, therefore BREEDERS, ON PLOT includes NY 2002-04, all Shelburne fields 2002-06, and all Hinesburg fields 2003-05. In non-nest-monitoring years (all NY 2005; Hinesburg middle- and late-hayed fields 2006), all resighted-recaptured individuals were included in the data set for those specific years.

Our *a priori* models were developed from data reported in Perlut et al. (2006), where breeding biology varied among the four grassland treatment types, and the magnitude of these effects varied between Savannah Sparrows and Bobolinks. Because the number of successful nesting attempts, number of clutches laid per female, and variance in male fertilization success (Chapter 2) varied among treatments, we added sex to the model set to determine if grassland management affected males and females differently. Therefore, with treatment, species, and sex as explanatory variables of ϕ and f, the candidate model set included all combinations of two-way additive, two-way interactive, and three-way additive models for both ϕ and f ($n = 50$ models). Our data could not support a three-way interactive model. Finally, because management was consistent within a given field over the course of the study we treated ϕ and f as constant across all years. Although environmental variation may also have minor effects on ϕ and f, we believe that management consistency overshadowed these effects.

The resight probability, p, potentially varied among years and sites because nest searching efforts resulted in greater time spent on a given field as compared to non-nest searching years, and field crew sizes and experience varied between the New York and Vermont sites. To account for this variability, p was modeled as a function of state (NY vs. VT) and nest search effort (nest-search vs. no nest-search) for all Objective 1 models.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare and rank alternative models, and model averaged to obtain overall survival and recruitment estimates for each species, treatment, and sex. We obtained model averaged parameter estimates (ϕ and f) and 95% confidence intervals by summing the products of the estimates and their AIC_c weight (ω_i) for all models. We determined the relative importance of each factor (treatment, species, sex) by summing the products of the survival and recruitment estimates and their AIC_c weight (ω_i) for the top models which accounted for > 99% of model AIC_c weights. Confidence intervals for the β coefficients that did not include zero were considered biologically significant. The coefficients within our linear models indicate the strength and direction of the effect for each of the model factors relative to the reference factor. The reference factors for treatment, species, and sex were late-hayed fields, Savannah Sparrows, and males, respectively.

To our knowledge, there is currently no method to assess model fit for the Pradel method in Program MARK. Therefore, to assess model fit, we estimated ϕ with the Cormack-Jolly-Seber method (Lebreton et al. 1992) in Program MARK, and tested goodness-of-fit (GOF) for the BREEDERS, ON PLOT set with Program RELEASE (Burnham et al. 1987).

Objective 2: Sensitivity of ϕ and f to non-breeders

The ALL ADULTS, ON PLOT set was used to quantify survival and recruitment of all adults banded over the course of the study. BREEDERS, ON PLOT (Objective 1) included 85.4% of the marked individuals; the additional 14.6% of individuals may have been migrants, floaters, adults whose nests failed before we detected their association, or non-breeders (for sample sizes see Appendix 1). These individuals, referred to as 'non-breeders', were captured and resighted only in a single year and were never associated socially with a nest. This analysis included the same candidate model set (n = 50 models) and the same constraints for p as used in Objective 1.

Objective 3: Sensitivity of ϕ to local scale dispersal

To address the effects of local dispersal (1.5 km radius from the treatment fields) on survival, we added the 2005 and 2006 data collected during off-study field searches to capture histories within subsets of the ALL ADULTS, ON PLOT and BREEDERS, ON PLOT sets. These subsets excluded New York data, as off-site searches were conducted only in Vermont (Table 1, see Appendix 1 for sample sizes).

To assess ϕ, we used the Cormack-Jolly-Seber method (Lebreton et al. 1992) in Program MARK, and Program RELEASE to evaluate GOF. With treatment, species, and sex, the candidate model set included all combinations of two-way additive, two-way interactive, and three-way additive model (n = 8). Because recruitment should not be affected by the inclusion of emigrants from our study sites, f was not included in the candidate model set, substantially decreasing the number of models used in Objectives 1 and 2. Our data could not support a three-way interactive model.

Recapture-resight probabilities included data gathered only in Vermont and search effort varied among years. Here, p was a function of nest search effort (nest-search vs. no nest-search) and year (off-site observations vs. no off-site observations).

Objective 4: Finite rate of increase (λ, realized lambda) for the four treatments

In order to understand source-sink dynamics in the Champlain Valley, we assessed the populations' finite rate of increase for each of the four treatment types. Realized lambda (λ), the observed growth rate of the population between sampling occasions, can be estimated with survival and recruitment values, $\lambda = \phi + f$ (Pradel 1996, Cooch and White 2007). Although this method provides an estimate of λ, we cannot identify the relative contributions of death and emigration in the estimation of ϕ, nor the relative contributions of births versus immigration in the estimation of f. Here, over the course of the study, $\lambda > 1$ indicates that the population size increased, $\lambda < 1$ indicates the population size decreased, and $\lambda = 1$ indicates the population size was stable. Males and females have 12 estimates of λ for each treatment, including all combinations of the two recruitment estimates and six survival estimates derived from Objectives 1-3 (ϕ BREEDERS, ON PLOT + f BREEDERS, ON PLOT; ϕ BREEDERS, ON PLOT + f ALL ADULTS, ON PLOT etc.) As such, λ is presented as a 12-value range rather than our assessment of a best estimate. This objective, therefore, assessed which treatment-defined habitat types allowed population persistence.

RESULTS

Objective 1: Survival and recruitment of known breeders

BREEDERS, ON PLOT included capture histories for 725 Savannah Sparrows and 519 Bobolinks. The top ranking model, $\phi_{\text{treatment+species+sex}}\ f_{\text{treatment+species+sex}}$ ($\omega_i = 0.76$; Table 2), had six times more weight of support than the second ranked model, $\phi_{\text{treatment+species+sex}}\ f_{\text{treatment*species}}$ ($\omega_i = 0.11$), and 13 times more weight of support than the third ranked model, $\phi_{\text{treatment*species}}\ f_{\text{treatment*species}}$ ($\omega_i = 0.06$). The observed field data fit the CJS modeling framework ($\chi^2 = 21.35$, df = 16, $P = 0.17$).

<u>Savannah Sparrow ϕ</u>: Model-averaged survival estimates for male Savannah Sparrows ranged from 0.64 ± 0.09 on early-hayed to 0.78 ± 0.03 on late-hayed fields (Fig. 1A). Female survival rates were lower than males and ranged from 0.48 ± 0.11 on early-hayed to 0.65 ± 0.07 on late-hayed fields. Overall, ϕ increased with decreasing management intensity for both sexes ($\phi_{\text{late-hayed}} > \phi_{\text{middle-hayed}} > \phi_{\text{grazed}} > \phi_{\text{early-hayed}}$).

<u>Bobolink ϕ</u>: Survival rates of Bobolinks were lower than Savannah Sparrows in all treatments and for both sexes. Model-averaged estimates for male Bobolinks ranged from 0.43 ± 0.11 on early-hayed fields to 0.63 ± 0.08 on late-hayed fields (Fig. 1B). Female rates were lower than males, ranging from 0.27 ± 0.09 on early-hayed fields to 0.46 ± 0.11 on late-hayed fields. As with Savannah Sparrows, survival increased with decreasing management intensity.

<u>Savannah Sparrow f</u>: Recruitment was higher in early-hayed, middle-hayed, and grazed fields, than late-hayed fields. Model-averaged recruitment estimates for male Savannah Sparrows ranged from 0.20 ± 0.02 on late-hayed fields to 0.26 ± 0.05 to 0.27 ±

0.05 on the remaining fields (Fig. 2A). Female f was higher than male f and ranged from 0.24 ± 0.03 on late-hayed fields to 0.31 ± 0.06 to 0.32 ± 0.07 on the remaining fields.

Bobolink f: Across all treatments, Bobolink recruitment estimates were higher than Savannah Sparrow recruitment estimates. Model-averaged recruitment estimates for male Bobolinks ranged from 0.25 ± 0.04 on late-hayed fields to 0.36 ± 0.09 on middle-hayed fields (Fig. 2B). Female recruitment rates were higher than males and ranged from 0.30 ± 0.06 on late-hayed fields to 0.41 ± 0.11 on middle-hayed fields.

Objective 2: Sensitivity of ϕ and f to non-breeders

The ALL ADULTS, ON PLOT set included capture histories for 850 Savannah Sparrows and 606 Bobolinks. The top ranked model, $\phi_{treatment*species}\ f_{treatment*species}$, had 11 times more weight of support ($\omega_i = 0.86$, Table 2) than the second ranked model, $\phi_{treatment*species}\ f_{treatment+species}$ ($\omega_i = 0.08$). Comparing estimates with BREEDERS, ON PLOT, non-breeders caused ϕ to decline and f to increase in 12 of 16 comparisons. In general, ϕ estimate precision also decreased considerably (Fig 1A-B).

Savannah Sparrow ϕ: Model-averaged survival estimates for male Savannah Sparrows ranged from 0.52 ± 0.10 on middle-hayed fields to 0.58 ± 0.09 to 0.59 ± 0.10 on remaining fields. Thus, the inclusion of non-breeders decreased survival estimates by ~ 0.08 to 0.20 (-10 to -26%). The effects of management intensity and sex also decreased with the inclusion of additional adults in the dataset (Fig. 1A).

Bobolink ϕ: As with Savannah Sparrows, the inclusion of non-breeders decreased survival estimates for male Bobolinks ~ 0.08 to 0.24 (-13 to -55%). However, unlike Savannah Sparrows, female survival decreased on the more intensively managed fields (early-hayed and grazed), but increased on the moderate and less intensively managed fields (middle-hayed and late-hayed). Thus, for male and female Bobolinks, the importance of grassland habitat management on ϕ was magnified with the inclusion of potential non-breeding adults (Fig. 1B).

Savannah Sparrow *f*: For male Savannah Sparrows, *f* increased by 0.05 to 0.07 (18 to 21%) with the inclusion of non-breeders, except on middle-hayed fields where recruitment decreased by 0.03 (-11%) (Fig. 2A). Female estimates of recruitment were relatively unchanged, with the exception of middle-hayed fields, where *f* decreased by 0.08 (-33%).

Bobolink *f*: The addition of non-breeders on Bobolink recruitment estimates generally had the same impact as on Savannah Sparrow estimates: recruitment increased for males, and stayed the same for females (Fig. 2B).

Objective 3: Sensitivity of ϕ to local scale dispersal

To assess the sensitivity of ϕ to the inclusion of birds dispersing outside the study fields, we compared Cormack-Jolly-Seber model averaged estimates derived from four different datasets, all collected in Vermont: (1) BREEDERS, WITH DISPERSERS, (2) BREEDERS, NO DISPERSERS, (3) ALL ADULTS, WITH DISPERSERS, and (4), ALL ADULTS, NO DISPERSERS (Fig. 3A-B). In datasets 1-3, model $\phi_{\text{treatment+species+sex}}$ had >90% of the model weights (Table 3), and ranked second in set 4 ($\omega_i = 0.17$).

Savannah Sparrows: For male Savannah Sparrows in all treatments, local dispersal (<1.5 km off study fields) data increased estimates of survival rates as well as estimate precision. Male survival rates were highest for BREEDERS, WITH DISPERSERS and lowest for ALL ADULTS, NO DISPERSERS. Regardless of which dataset was used, estimates of ϕ were notably higher for males on less intensively managed fields (late-hayed) than moderate (middle-hayed) and intensively (early-hayed, grazed) managed fields. Females showed a similar pattern with respect to grassland management effects on ϕ; however, within each treatment, females showed less variation among the four datasets than males (Fig. 3A).

Bobolinks: As with Savannah Sparrows, the inclusion of off-site dispersers increased survival estimates for male Bobolinks in all treatments. These effects were especially strong on intensively managed fields (early-hayed, grazed) using the two ALL ADULTS datasets (Fig. 3B). Female Bobolink ϕ was consistently low across intensively and moderately managed fields, regardless of which of the four datasets were analyzed.

Objective 4: Finite rate of increase (λ, realized lambda) for the four treatments

With results from Objectives 1-3, we generated 12 estimates of lambda for each species, treatment, and sex. The amount of variation among lambda estimates differed among species, treatments, and sexes (Fig. 4). Compared to females, males of both species showed greater variation among λ estimates. Only male Savannah Sparrows in all treatments showed potential population increases within the sampling period. Ranges with maximum values for male Savannah Sparrows included late-hayed ($\lambda = 1.10$ to 0.80) and grazed fields ($\lambda = 1.08$ to 0.86). All estimates for female Savannah Sparrows were < 1, with highest estimates again on late-hayed ($\lambda = 0.96$ to 0.82) and grazed fields ($\lambda = 0.92$ to 0.83). For male Bobolinks, highest estimates were also on late-hayed ($\lambda =$ 0.98 to 0.81) and middle-hayed fields ($\lambda = 0.97$ to 0.74). Showing the overall fastest rates of decline, λ estimates for female Bobolinks were highest on late-hayed ($\lambda = 0.84$ to 0.74) and middle-hayed fields ($\lambda = 0.81$ to 0.73).

DISCUSSION

The results for Objective 1 showed that birds breeding in less-intensively managed grasslands incurred higher apparent survival than those breeding in intensively managed grasslands. Management-mediated low ϕ results from either increased mortality or failure to return to the study area. Survival was greater for males than females and greater for Savannah Sparrows than Bobolinks. Birds using late-hayed fields had > 25% higher survival than those on more intensively managed early-hayed, middle-hayed, and grazed fields; male survival was 36% higher than female survival; Savannah Sparrow survival was 64% higher than Bobolink survival.

Recruitment was highest on both intensively and moderately managed fields, perhaps as a result of lower apparent survival on these fields. Higher recruitment and lower survival on intensively managed fields indicates greater population turnover relative to less-intensively managed fields. Compared to late-hayed fields, populations on intensively or moderately managed fields included 33-34% more individuals who entered the system through birth or emigration for each surviving adult. Because intensively managed fields have little productivity, populations are likely dependent on receiving immigrants. Bobolink recruitment was 23% greater than Savannah Sparrow recruitment. Contrary to the survival trends, recruitment was consistent between sexes of a given species. Together, the survival and recruitment patterns suggest that if annual productivity results in a balanced sex ratio, through death and emigration, this population of Bobolinks, and to a lesser extent Savannah Sparrows, may be male-biased.

Our results provide strong evidence for the importance of knowing the breeding status of individuals when conducting demographic analyses. The presence of non-breeders significantly decreased survival estimates and increased recruitment estimates for these species (Objective 2). For males of both species, the presence of non-breeders decreased the precision of and lowered survival estimates by ~25%. Differing by ~1%, female estimates of ϕ showed little variation with non-breeders; suggesting that female settlement decisions are made quickly, and once settled, females attempt to breed. Like ϕ, female recruitment estimates were largely unchanged by the potential group of non-breeders. Although large sample sizes are critical for survival analyses, results may be compromised by including a large proportion of non-breeders, who may be substantially more nomadic than those tied to a breeding site.

Local dispersal data increased survival estimates and in many cases increased precision, though the effect was stronger for Savannah Sparrows than Bobolinks, and for males than females (Objective 3). Although we consciously attempted to detect both males and females, these results may be slightly male-biased, as females, especially Savannah Sparrows during the incubation stage, were inconspicuous. Nonetheless, these results provide an important contrast to the only comparable study that explored the role of local dispersal in estimating apparent survival. With search radii similar to this study, Cilimburg et al. (2002) found that local dispersal data increased ϕ in the Yellow Warbler (*Dendroica petechia*) from 0.42 to 0.49 for males and 0.35 to 0.41 for females. In some cases, the effect of including dispersal data was greater in this study. Male Savannah Sparrow and Bobolink ϕ in late-hayed fields increased from 0.60 to 0.85 and 0.57 to 0.70 respectively—effect-sizes more than three times that observed by Cilimburg et al. (2002).

Dispersal data complicated the interpretation of estimates of female ϕ on the intensively and moderately managed fields. Dispersal observations increased survival estimates for female Bobolinks on early-hayed and grazed fields but did not affect survival estimates for female Savannah Sparrows. Paired with nesting observations, these results make intuitive sense. Bobolinks abandoned early-hayed fields immediately after haying, and Savannah Sparrows remained and immediately renested (Perlut et al. 2006). Therefore, during post-haying dispersal, Bobolinks may assess local breeding habitats for opportunities in both the current and future years. This behavior is potentially an ecologically 'good' decision, as reproductive success on early-hayed fields is near zero, and is low on pastures (Perlut et al. 2006). Alternatively, local dispersal had little to no effect on survival estimates for middle-hayed and late-hayed fields, where reproductive success was moderate to high, respectively.

Like return rates from Bollinger and Gavin (1989), these results suggest that surviving females who select high quality fields return to their previous breeding site or disperse at a larger scale, > 1.5 km. Some males, however, appear to disperse locally regardless of previous years' habitat and reproductive success. This behavior may be a product of a polygynous social mating system, where males with the highest quality territories monopolize up to three social mates (Perlut unpub. data), leaving some males with no social mates. For females, large-scale dispersal could also be mediated by the polygynous social mating system, where males bear the cost of territory establishment and defense, and females select among males based on resources (Greenwood 1980). Females whose nests fail may have weak bonds to the given location, and potentially disperse in search of higher-quality territories. However, females on late-hayed fields are equally likely to return to the previous year's location regardless of nest success (Fajardo unpubl. data). Therefore, we suspect that dispersal >1.5 km may be a joint effect of individual nest failure, population (field-level) nest failure, and habitat destruction.

Although the effects of both non-breeders and local dispersal on survival estimates are notable, as evidenced in lambda ranges, Bobolinks paid a significant cost in survival when they selected fields managed during the breeding season. Along with low productivity, treatment-specific survival costs are likely limiting the population—as high recruitment rates (here, primarily immigration) were unable to offset low survival rates to maintain stable populations. Some portion of adults likely emigrate further than our dispersal effort could detect (Strong unpubl data), however, it is unlikely that this group would be large enough to increase survival estimates to late-hayed fields' level. For example, in a related breeding dispersal study, of detected individuals, nearly 90% of Bobolinks and 93% Savannah Sparrows returned to their previous field regardless of nest success in the previous year or available habitat within 1.5 km radii (Fajardo unpubl. data). Therefore, we expect that the number of > 1.5km dispersers to be > 0, though small enough such that if all individuals were detected, survival estimates would not equal those observed on late-hayed fields.

Migration and wintering constraints affect survival, though these processes relate to the entire population regardless of the treatment-type in which individuals breed. As such, two breeding ground scenarios may account for the increased mortality on intensively managed fields: 1) haying-mediated within-season dispersal may increase predation risk; and 2) haying-mediated within-season dispersal may limit access to resources when preparing for migration. In both cases, within-season dispersal increases mortality rates. Birds on intensively managed fields can disperse to less intensively managed fields which likely increases productivity; however, potential gains in productivity come at the expense of decreased apparent survival. Given low Bobolink λ ranges, within-season movement likely results in little added productivity. Interestingly, these results appear contrary to Fletcher et al. (2006), whose population growth models for Bobolinks breeding in restored grassland in Iowa, USA, suggested that factors during the non-breeding season appeared to affect ϕ more than those during the breeding season.

Grassland management also strongly effected recruitment. First-time breeders and new emigrants settled more frequently in low-quality (early-hayed and grazed) or moderate-quality fields (middle-hayed) than in high-quality fields (late-hayed). Though this study was not designed to identify the mechanism driving recruitment trends, two factors may contribute. First, breeders in late-hayed fields have high survival and philopatry; therefore, these fields are likely to be at a density dependent carrying capacity and offer fewer free territories each year (Pulliam and Danielson 1991), particularly for males. Here, increased survivorship comes with the added benefit of high productivity; however, despotic behavior comes with the cost of denying your progeny high-quality breeding sites. Alternatively, upon spring arrival, the short, green structure of early-hayed, middle-hayed, and grazed fields may be more attractive to novice individuals when making settlement decisions. Grass and stubble is removed from these fields in the autumn, thereby promoting a ‘greener’ spring appearance which may imitate co-evolved cues that otherwise suggest high habitat quality (Robertson and Hutto 2006). In this scenario, populations are limited by the density-dependent factors created by management, with more vacant territories in more intensively managed fields. However, in the Champlain Valley, for surviving breeders from late-hayed fields, habitat structural cues are less important than knowledge of past breeding success, as they clearly choose to return to late-hayed fields rather than select these other habitats. In a less intensively-managed study system, Bobolinks used the number of young produced as 'public information' to assess field quality (Nocera et al. 2005)—a trend that appears true for experienced breeders in this population though contrary for novice breeders.

These results strongly suggest that Bobolinks and to a lesser extent, Savannah Sparrows, illustrate classic source-sink dynamics within the mosaic of treatment-defined grassland habitat types in the Champlain Valley. High-quality habitats produce more offspring and adults who maintain territories on these fields both survive longer and have higher field-level philopatry than low-quality habitats. Treatment-specific ranges for λ show that populations may be close to stable on late-hayed fields, and significantly declining the other three treatments. Reproductive data show that late- and middle-hayed fields also produce offspring at a rate higher than female-female replacement (Perlut et al. 2006). Of critical management and long-term population interest, though, is how these data apply to the behavioral characteristic that separates a source-sink system from an ecological trap. In both a sink and a trap, habitat characteristics result in low productivity, however, in a trap, individuals show preference for low-quality habitats. Here we show that individuals entering the system through birth and immigration disproportionately select low-quality fields over high-quality fields. These data, along with the fact that both species initiate nesting activities earlier on low-quality fields (Perlut et al. 2006), may indicate preference (Robertson and Hutto 2006) for low-quality fields, and be evidence that intensively managed fields are ecological traps.

Bobolinks, with low adult survival, attraction to fields with low productivity, and a landscape increasingly devoted to intensive management, illustrate the need for serious conservation management. Though the effects are less strong for Savannah Sparrows, conservation measures that improve habitat quality will support both species. To further understand processes regulating the Champlain Valley's grassland songbirds, the next step is to apply survival and productivity parameters to the relative proportion of the four dominant habitat types. Understanding the landscape-level characteristics of grassland management will allow us to use these life-history parameters to model habitat requirements that would stabilize populations before these species face endangerment.

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LITERATURE CITED

Adams, A. A. Y., S. K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology **87**:178-188.

Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conservation Biology **19**:66-74.

Bedard, J., and G. LaPointe. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. Wilson Bulletin **96**:196-205.

Bedard, J., and G. LaPointe. 1985. Influence of parental age and season on Savannah Sparrow reproductive success. Condor **87**:106-110.

Bollinger, E. K., and T. A. Gavin. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk **106**:584-594.

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping of eastern populations of the Bobolink. Wildlife Society Bulletin **18**:143-150.

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

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference, second edition. Springer, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Bethesda, Maryland, USA.

Cilimburg, A. B., M. S. Linderberg, J. J. Tewksbury, and S. J. Hejl. 2002. Effects of dispersal on survival probabilities of adult Yellow Warblers (*Dendroica Petechia*). Auk **119**:778-789.

Cooch, E. G. and G. C. White (2007). Program MARK A Gentle Introduction. 5th edition. http://www.phidot.org/software/mark/docs/book/.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412–1423.

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.

Fletcher, R. J., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. Journal of Wildlife Management. **70**:145-157.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior **28**:1140-1162.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2005. Age-specific variation in apparent survival rates of male Lesser Prairie-Chickens. Condor **107**: 78-86.

Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation **4**:128-155.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Breeding-season decisions, renesting, and annual fecundity of female Eastern Meadowlarks (*Sturnella magna*) in Southeastern Illinois. Auk **121**:796-805.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. Auk **121**:1146-1154

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs **62**:67-118.

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

Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2005. Inadvertent social information in breeding site selection of natal dispersing birds. Proc Royal Society B **273**:349-355.

Perkins, D. W., P. D. Vickery, W. G. Shriver. 2003. Spatial dynamics of source-sink habitats: Effects on rare grassland birds. Journal of Wildlife Management. **67**:588-599.

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.

Pradel, R. 1996. Utilization of mark-recapture for the study of recruitment and population growth. Biometrics **52**:703-709.

Pradel, R., J. E. Hines, J. D. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. Biometrics **53**:60-72.

Pulliam, H. R. 1988. Sources, sinks, and population regulations. American Naturalist **132**:652-661.

Pulliam H. R. and B. J. Danielson. 1991. Sources, sinks, and habitat selection - a landscape perspective on population-dynamics. American Naturalist **137**:S50-S66.

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

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2004. Version 2005.2.* USGS Patuxent Wildlife Research Center*, Laurel, MD.*

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

Walk, J. W., K. Wentworth, E. L. Kershner, E. K. Bollinger, and R. E. Warner. 2004. Renesting decisions and annual fecundity of female Dickcissels (*Spiza americana*) in Illinois. Auk **121**:1250-1261.

Warner, R. E. and S. L. Etter. 1989. Hay cutting and the survival of pheasants: a long-term perspective. Journal of Wildlife Management **53**:455-461.

Wheelwright, N. T. and R. A. Mauck. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. Ecology **79**:755-767.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**:S120-S139.

Table 1: Data sets used to examine effects of grassland management of Savannah Sparrow and Bobolink survival and recruitment.

			OBSERVATIONS				
DATASET	OBJECTIVE	PARAM	ON PLOT	OFF PLOT	BREEDERS ONLY	NON-BREEDERS	STUDY SITES
BREEDERS, ON PLOT	1	ϕ and f	x		x		VT and NY
ALL ADULTS, ON PLOT	2	ϕ and f	x		x	x	VT and NY
BREEDERS, WITH DISPERSERS	3	ϕ	x	x	x		VT
BREEDERS, NO DISPERSERS	3	ϕ	x		x		VT
ALL ADULTS, WITH DISPERSERS	3	ϕ	x	x	x	x	VT
ALL ADULTS, NO DISPERSERS	3	ϕ	x		x	x	VT

Table 2: All candidate models with Δ $\text{AIC}_c < 10$ for BREEDERS, ON PLOT and ALL ADULTS, ON PLOT analyses. Model factors include four grassland treatments (early-hayed, middle-hayed, late-hayed, grazed), two species (Savannah Sparrow, Bobolink), and both sexes.

DATA SET	MODEL	Δ AIC_c	AIC_c WEIGHTS	# PARAMETERS
BREEDERS, ON PLOT	$\phi_{\text{treatment+species+sex}}\ f_{\text{treatment+species+sex}}$	0.000	0.764	17
	$\phi_{\text{treatment+species+sex}}\ f_{\text{treatment*species}}$	3.777	0.116	19
	$\phi_{\text{treatment*species}}\ f_{\text{treatment*species}}$	5.130	0.059	21
	$\phi_{\text{treatment+species+sex}}\ f_{\text{treatment+sex}}$	7.961	0.014	16
	$\phi_{\text{treatment*species}}\ f_{\text{treatment+species}}$	8.312	0.012	18
	$\phi_{\text{treatment+species+sex}}\ f_{\text{species*sex}}$	8.672	0.010	15
	$\phi_{\text{treatment+species+sex}}\ f_{\text{treatment+species}}$	8.893	0.009	16
	$\phi_{\text{treatment*species}}\ f_{\text{treatment+species+sex}}$	9.529	0.007	19
ALL ADULTS, ON PLOT	$\phi_{\text{treatment*species}}\ f_{\text{treatment*species}}$	0.000	0.860	21
	$\phi_{\text{treatment*species}}\ f_{\text{treatment+species}}$	4.765	0.079	18
	$\phi_{\text{treatment*species}}\ f_{\text{treatment+species+sex}}$	5.430	0.057	19

Table 3: Including only data from the Vermont study fields, candidate models for BREEDERS WITH DISPERSERS, BREEDERS NO DISPERSERS, and ALL ADULTS WITH DISPERSERS analyses showed overwhelming support for model $\phi_{treatment+species+sex}$; this model was ranked second in ALL ADULTS, NO DISPERSERS (for sample sizes see Appendix 1). Model factors include four grassland treatments (early-hayed, middle-hayed, late-hayed, grazed), two species (Savannah Sparrow, Bobolink), and both sexes.

SET	MODEL	Δ AIC_c	AIC_c WEIGHTS	# PARAMETERS
ALL ADULTS, NO DISPERERS	$\phi_{treatment*species}$	0.000	0.818	11
	$\phi_{treatment+species+sex}$	3.085	0.175	9
	$\phi_{species+sex}$	10.280	0.005	6
	$\phi_{species*sex}$	12.103	0.002	7
	$\phi_{treatment+species}$	13.975	0.001	8
	$\phi_{treatment*sex}$	27.613	0.000	11
	$\phi_{treatment+sex}$	27.616	0.000	8
	$\phi.$	45.853	0.000	4
ALL ADULTS, WITH DISPERERS	$\phi_{treatment+species+sex}$	0.000	0.904	9
	$\phi_{species+sex}$	5.275	0.065	6
	$\phi_{species*sex}$	7.255	0.024	7
	$\phi_{treatment*species}$	10.393	0.005	11
	$\phi_{treatment*sex}$	13.602	0.001	11

	$\phi_{treatment+sex}$	14.590	0.001	8
	$\phi_{treatment+species}$	15.987	0.000	8
	$\phi.$	37.560	0.000	4
BREEDERS, NO DISPERSERS	$\phi_{treatment+species+sex}$	0.000	0.941	9
	$\phi_{treatment*species}$	5.575	0.058	11
	$\phi_{species+sex}$	13.726	0.001	6
	$\phi_{species*sex}$	15.752	0.000	7
	$\phi_{treatment+species}$	21.916	0.000	8
	$\phi_{treatment*sex}$	36.452	0.000	11
	$\phi_{treatment+sex}$	36.719	0.000	8
	$\phi.$	67.948	0.000	4
BREEDERS, WITH DISPERSERS	$\phi_{treatment+species+sex}$	0.000	0.989	9
	$\phi_{species+sex}$	9.732	0.008	6
	$\phi_{species*sex}$	11.560	0.003	7
	$\phi_{treatment*species}$	19.368	0.000	11
	$\phi_{treatment*sex}$	26.657	0.000	11
	$\phi_{treatment+sex}$	26.784	0.000	8
	$\phi_{treatment+species}$	27.946	0.000	8
	$\phi.$	62.392	0.000	4

Figure 1A-B: Savannah Sparrow (A) and Bobolink (B) survival (ϕ) in relation to grassland management. The four treatments are ordered by management intensity, from highest intensity (early-hayed) to lowest intensity (late-hayed). Error bars indicate SE.

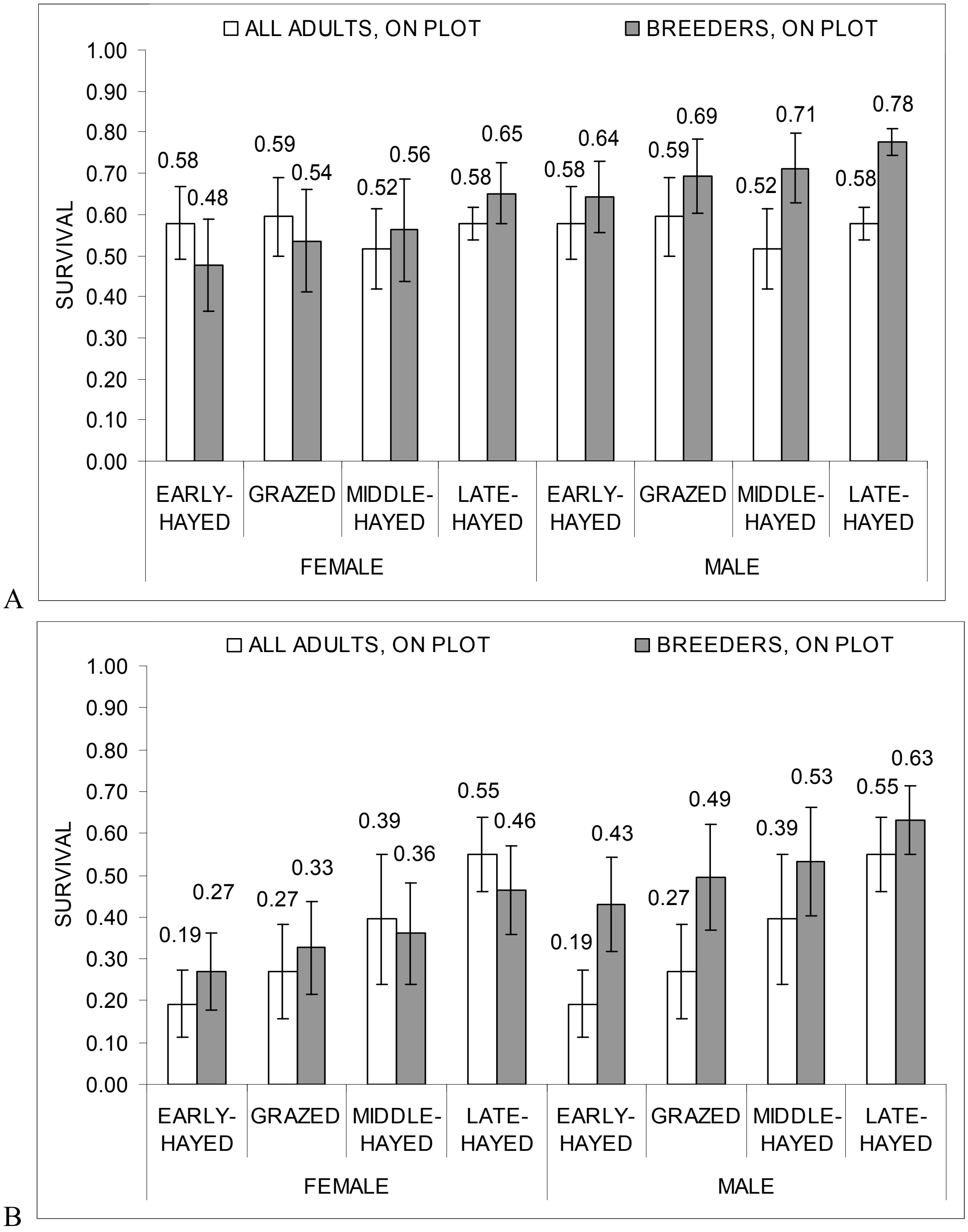
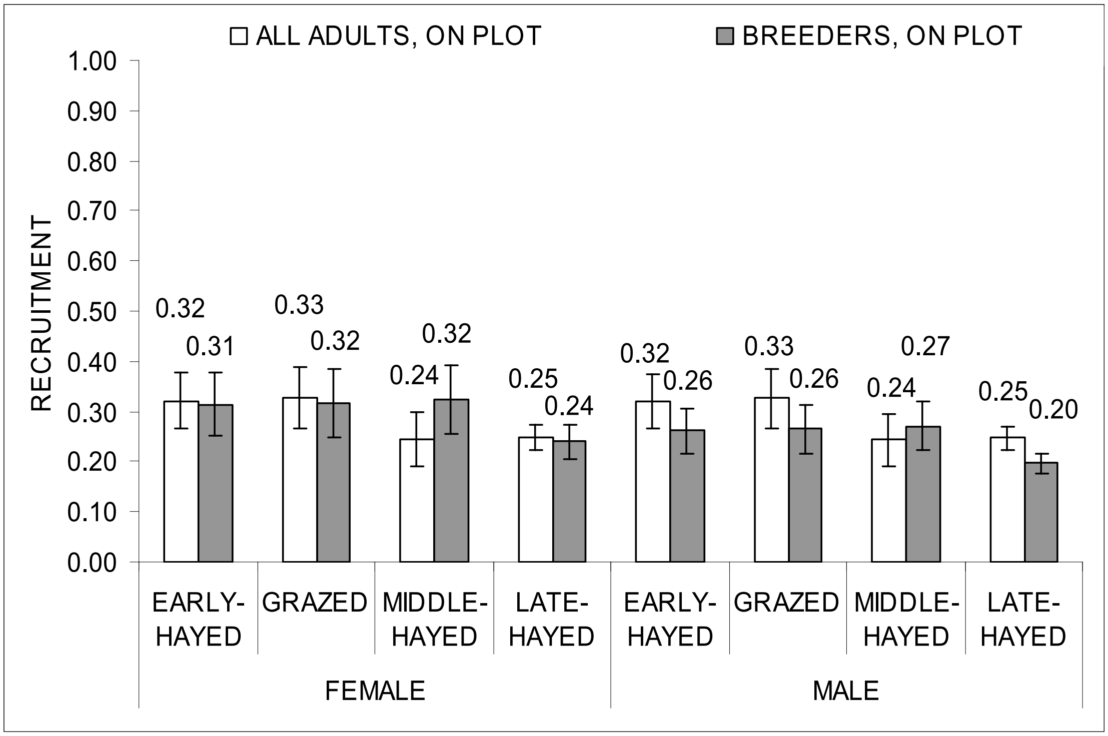
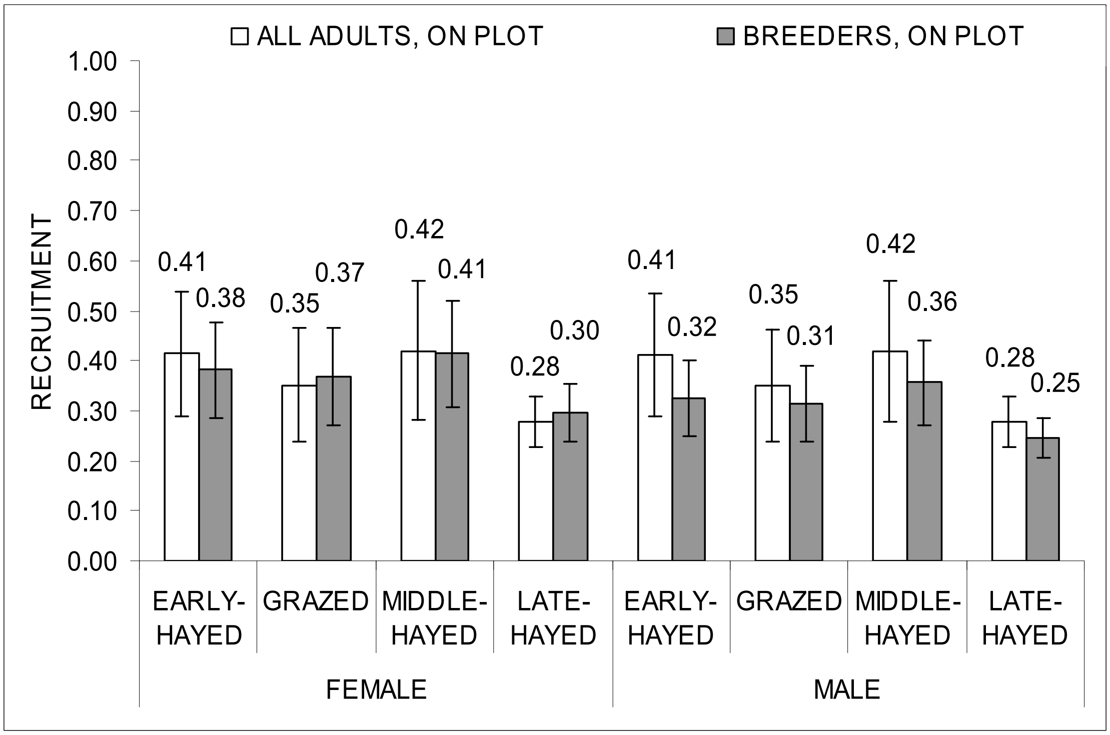


Figure 2A-B: Savannah Sparrow (A) and Bobolink (B) recruitment (*f*) increased with intensified grassland management. The four treatments are ordered by management intensity, from highest intensity (early-hayed) to lowest intensity (late-hayed). Each individual included in BREEDERS, ON PLOT had a known breeding history for at least one year on one of nine treatment fields; with 14.6% more capture histories, ALL ADULTS, ON PLOT included all individuals banded on treatment fields, including potential migrants, floaters, adults whose nests failed before we detected their association, or non-breeders. Error bars indicate SE.


☐ ALL ADULTS, ON PLOT
■ BREEDERS, ON PLOT
RECRUITMENT
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0.32
0.31
0.33
0.32
0.24
0.32
0.25
0.24
0.32
0.26
0.33
0.26
0.24
0.27
0.25
0.20
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
FEMALE
MALE

A


☐ ALL ADULTS, ON PLOT
■ BREEDERS, ON PLOT
RECRUITMENT
1.00
0.90
0.80
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0.60
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0.30
0.20
0.10
0.00
0.41
0.38
0.35
0.37
0.42
0.41
0.28
0.30
0.41
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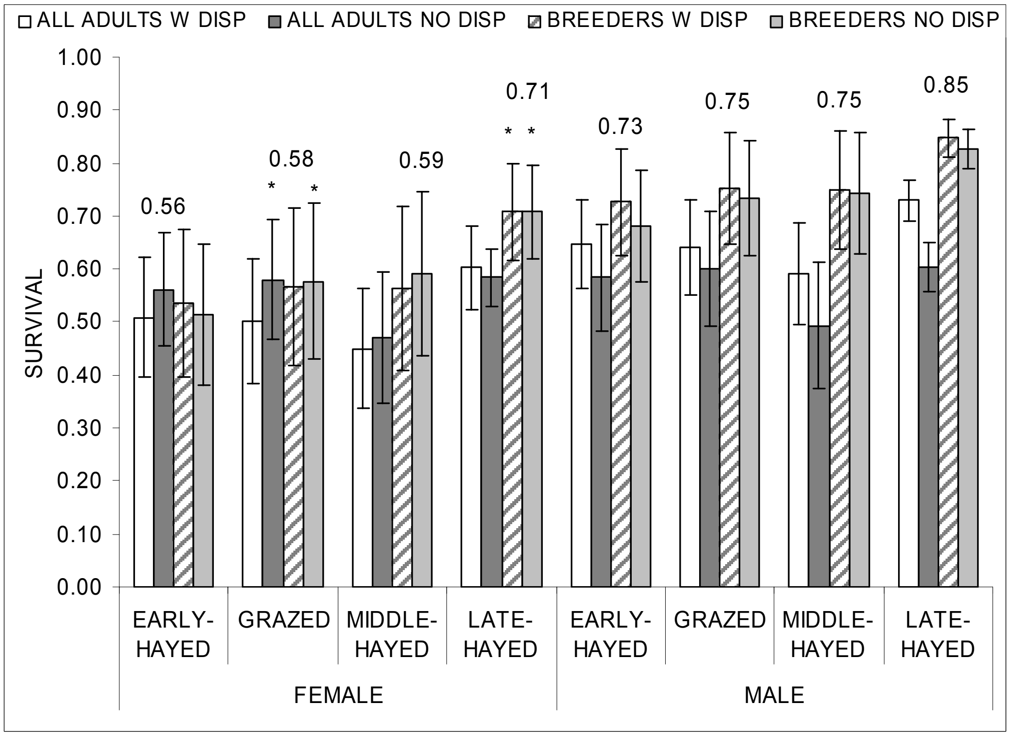
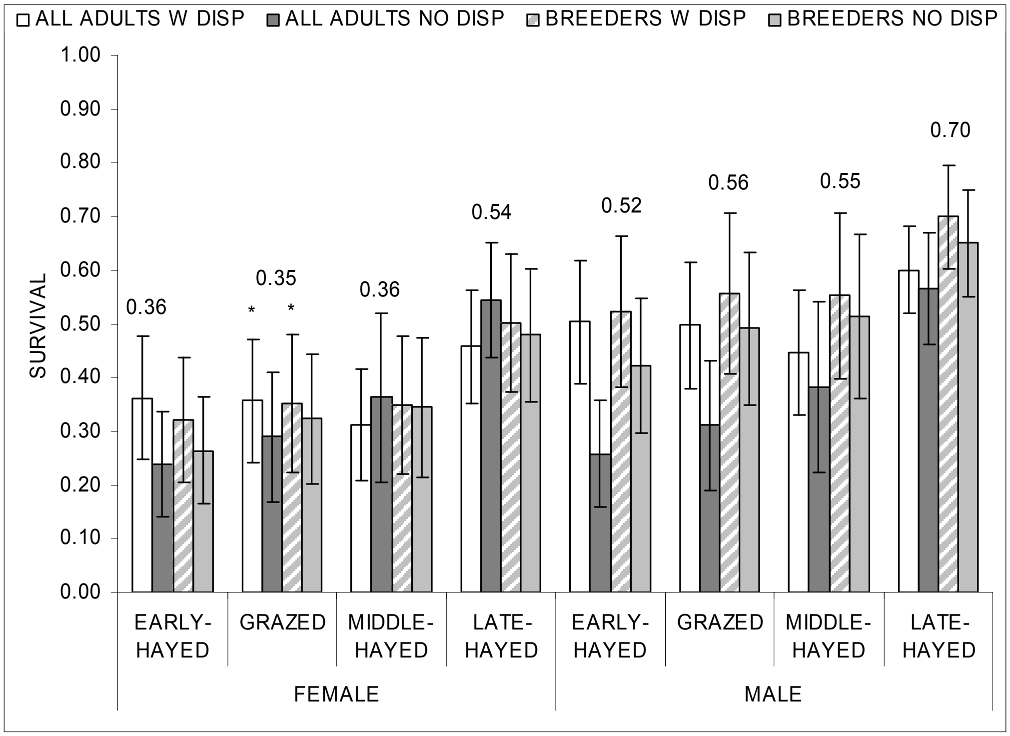
0.35
0.31
0.42
0.36
0.28
0.25
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
FEMALE
MALE

B

Figure 3A-B: Male Savannah Sparrow (A) and Bobolink (B) survival estimates (ϕ) and precision increased with dispersal searches of < 1.5 km from study fields; female estimates, though, responded only within certain grassland treatments, and this response varied between species. The four treatments are ordered by management intensity, from highest intensity (early-hayed) to lowest intensity (late-hayed). Displayed values are the highest survival estimate; stars indicate equal value between two estimates; error bars indicate SE.


□ ALL ADULTS W DISP
■ ALL ADULTS NO DISP
▨ BREEDERS W DISP
■ BREEDERS NO DISP
SURVIVAL
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0.56
0.58
* *
0.59
0.71
* *
0.73
0.75
0.75
0.85
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
FEMALE
MALE

A


□ ALL ADULTS W DISP
■ ALL ADULTS NO DISP
▨ BREEDERS W DISP
■ BREEDERS NO DISP
SURVIVAL
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0.36
0.35
* *
0.36
0.54
0.52
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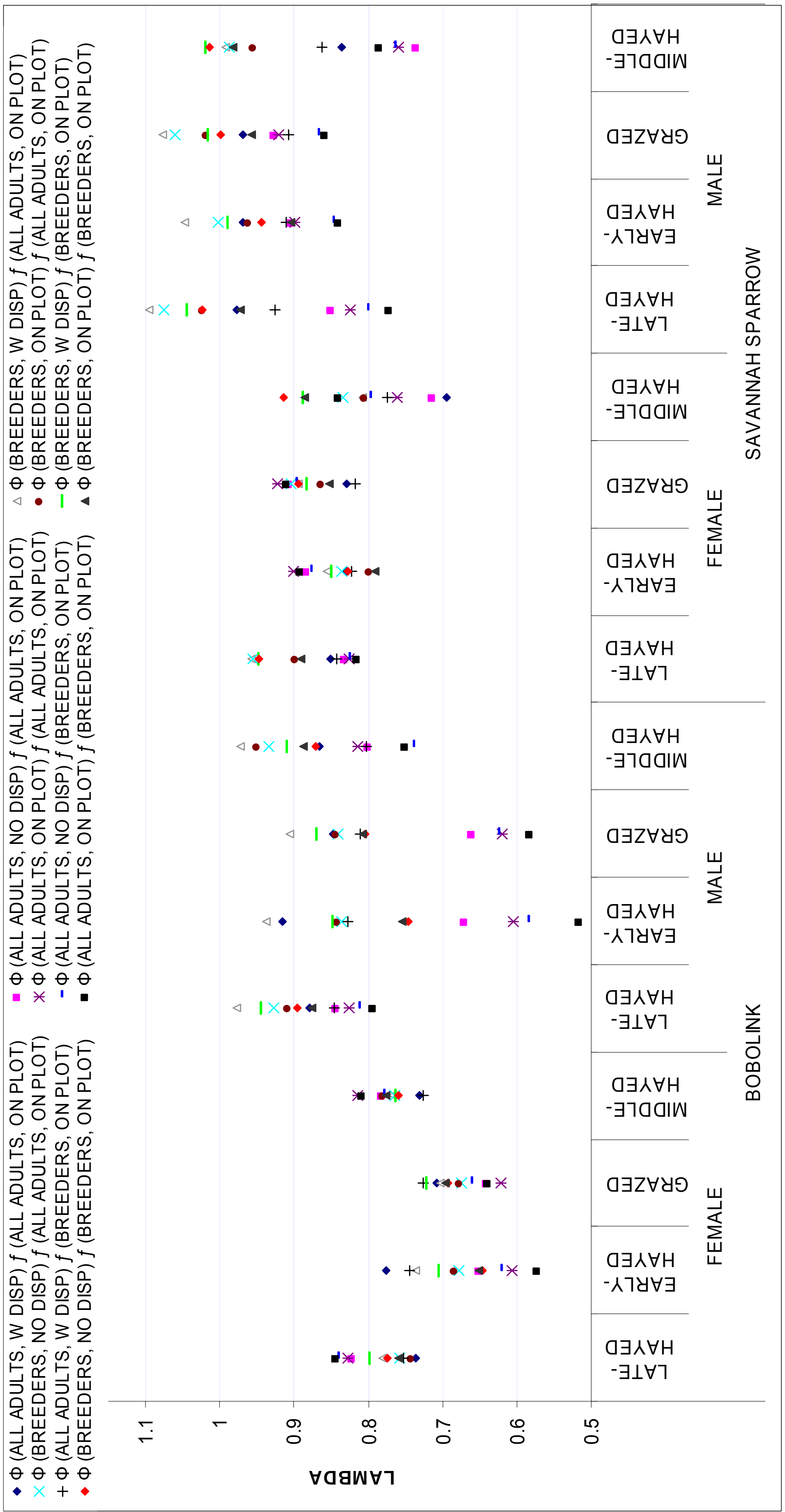
0.55
0.70
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
FEMALE
MALE

B

Figure 4**:** Variation in realized lambda ($\lambda = \phi + f$) estimates for Savannah Sparrows and Bobolinks breeding in four grassland treatment types of the Champlain Valley, Vermont and New York, USA. Variation spans 12 estimates comprised of all combinations of two recruitment estimates and six survival estimates from Objectives 1-3.


◆ Φ (ALL ADULTS, W DISP) ƒ (ALL ADULTS, ON PLOT)
× Φ (BREEDERS, NO DISP) ƒ (ALL ADULTS, ON PLOT)
+ Φ (ALL ADULTS, W DISP) ƒ (BREEDERS, ON PLOT)
◆ Φ (BREEDERS, NO DISP) ƒ (BREEDERS, ON PLOT)
■ Φ (ALL ADULTS, NO DISP) ƒ (ALL ADULTS, ON PLOT)
✳ Φ (ALL ADULTS, ON PLOT) ƒ (ALL ADULTS, ON PLOT)
- Φ (ALL ADULTS, NO DISP) ƒ (BREEDERS, ON PLOT)
■ Φ (ALL ADULTS, ON PLOT) ƒ (BREEDERS, ON PLOT)
△ Φ (BREEDERS, W DISP) ƒ (ALL ADULTS, ON PLOT)
● Φ (BREEDERS, ON PLOT) ƒ (ALL ADULTS, ON PLOT)
- Φ (BREEDERS, W DISP) ƒ (BREEDERS, ON PLOT)
◀ Φ (BREEDERS, ON PLOT) ƒ (BREEDERS, ON PLOT)
LAMBDA
1.1
1
0.9
0.8
0.7
0.6
0.5
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
LATE-HAYED
EARLY-HAYED
GRAZED
MIDDLE-HAYED
FEMALE
MALE
FEMALE
MALE
BOBOLINK
SAVANNAH SPARROW

Chapter 4

Grassland songbird population viability in an agricultural landscape

ABSTRACT

Although North America's grassland songbird population decline is well-documented, it is unclear how local-scale processes affect landscape-scale population persistence. To determine grassland songbird population viability in an agricultural landscape, the Champlain Valley of Vermont and New York, USA, we assessed Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*) annual productivity, adult survival, habitat selection (via recruitment), and density on four grassland treatments: 1) *early-hayed* fields cut before 11 June and again in early- to mid-July; 2) *middle-hayed* fields cut once between 21 June and 10 July; 3) *late-hayed* fields cut after 1 August; and 4) *rotationally-grazed pastures*. We applied these data to a female-based, stochastic, pre-breeding, closed population model to examine whether current grassland management practices can sustain viable populations of breeding songbirds. Additionally, we evaluated six conservation strategies to determine which would most effectively increase population trends.

Given baseline conditions, simulations showed declining populations for both Savannah Sparrows (10 years: $\lambda = 0.99$) and Bobolinks (10 years: $\lambda = 0.75$). Savannah Sparrow populations increased with increases in all demographic parameters, particularly adult survival. However for Bobolinks, increasing adult survival, juvenile survival, or preference for late-hayed fields only slightly decreased the rate of population decline. For both species, increasing the amount of high quality habitat marginally slowed

population declines; increasing the amount of low quality habitat marginally increased population declines. Both species were most sensitive to low productivity and survival on early-hayed fields which comprised 18% of the grass-based landscape. Although conservation efforts have focused on incentives to delaying hay-harvests, this is not viable for most farmers. We instead propose that 1) demography on early-hayed fields can be increased by advancing the initial harvest in late-May, and delaying the second harvest for 65 days; 2) increase preference for late-hayed fields by removing grass at the end of each season.

INTRODUCTION

Over the last 40 years, grassland bird populations have declined more rapidly than any other North American bird guild (Knopf 1994; Peterjohn & Sauer 1999; Murphy 2003; Sauer et al. 2005). Although this trend is regularly cited, it is unclear how local-scale processes (occurring within an agricultural field) affect landscape-scale population persistence. For example, in agricultural regions of the northeastern United States, population declines generally have been attributed to two divergent processes. First, the abandonment of farmland and subsequent forest succession, and second, modernized grassland management, which involves cutting and harvesting hay throughout the growing season, as well as varying grazing intensities. Within an agricultural landscape, individual fields vary in management intensity, increasing variation in demographic rates among fields (Bollinger et al. 1989; Perlut et al. 2006). However, it is unclear how these various management-defined habitats affect landscape-level population persistence.

The processes of grassland management in the Northeast have changed dramatically over the last 40 years, including earlier first harvest dates and more frequent harvests (Bollinger et al. 1990; Troy et al. 2005). An increasing proportion of hay farmers have advanced their initial cutting date from mid-summer to late-May or early-June—a vulnerable time in the breeding cycle, when most birds are in the later part of the incubation stage or early nestling stage (Perlut et al. 2006). As ground-nesters, eggs and nestlings are vulnerable to being crushed by the harvest machinery, and nests that survive hay-harvest are likely to be depredated (Bollinger et al. 1990; Perlut et al. 2006). Additionally, a greater harvesting frequency results in a shorter window of opportunity (~35 days) to renest in between haying events (Troy et al. 2005). Along with decreased reproductive success, intensive management causes significant, deleterious effects on adult apparent survival, ϕ, defined as the joint probability that a bird survives and returns to a particular area (Chapter 3). Birds breeding in intensively managed fields have ~25% lower apparent survival than less-intensively managed fields. Modern hayfield management clearly possesses a variety of risks to grassland bird populations.

Quantifying these events and how they occur across a landscape is critical in maintaining or restoring grassland bird populations. Greater than 70% of the world's temperate grasslands are devoted to agriculture or other human uses (Hannah et al. 1995), which leaves agricultural habitats as the primary breeding habitat for many species (Bollinger et al. 1990). This pattern is particularly evident in the northeastern United States, where agricultural regions maintain large, but steadily declining populations of grassland birds. Although the need for conservation is clear, we know surprising little about the sensitivity of population persistence to key life-history parameters or the distribution of management activities across a landscape (but see Bollinger et al. 1990; Wells 1997; Fletcher et al. 2006).

To determine population viability across dynamic agricultural landscapes, conservation biologists must identify how individual fields within the landscape are managed, identify how birds select among management-defined habitat types (density and recruitment), and finally, determine annual productivity and annual survival within each habitat. Moreover, to reverse declining population trends, optimal conservation strategies need to be identified, evaluated, and implemented. These strategies include increasing the total amount of grassland habitat within the breeding landscape, converting low-quality habitat to higher-quality habitat without changes in total breeding habitat, increasing the “attractiveness” of high-quality fields for new breeders, and increasing overwinter survival through improvements in non-breeding habitat quality.

During the 2002-2006 breeding seasons, we collected landscape management data and estimated demographic parameters of Bobolinks (*Dolichonyx oryzivorus*) and Savannah Sparrows (*Passerculus sandwichensis*), grassland obligate species breeding in the Champlain Valley of Vermont and New York, USA. We applied these data to a female-based, stochastic, pre-breeding, closed population model (sensu Donovan and Thompson 2001) to examine whether current grassland management practices throughout the Champlain Valley can sustain viable populations of breeding songbirds. The research objectives were to (1) model population growth for Bobolinks and Savannah Sparrows breeding in the Champlain Valley, and (2) to assess six alternative landscape level conservation strategies, targeted at different phases of the life cycle and breeding ground habitat management, in terms of reversing or dampening population declines.

METHODS

Study area and experimental design

The Champlain Valley is a significant dairy farming region in the northeastern U.S. (Fig. 1), and is surrounded by Green Mountains in to the east and the Adirondack Mountains to the west. The Champlain Valley contains 146,000 ha of managed grassland (NASS 1999), which can be grouped into four general treatment-types:

1. *early-hayed* (EH): hayed in 27 May and 11 June and generally again in early- to mid-July;
2. *middle*-hayed (MH): hayed between 21 June and 10 July;
3. *late-hayed* (LH): hayed after 1 August;

4. *rotationally-grazed pastures* (RG): fields in which cows were rotated through a matrix of paddocks and moved after all of the grass in a paddock was grazed to a farm-specific height. Each paddock is thereby given a multiple week "rest" between grazing events.

Champlain Valley Agricultural Management Trends

To assess the relative proportion of each of the four treatment-defined habitat types within the Champlain Valley, we conducted agricultural land-use surveys from late-May to mid-July. In these surveys, we also measured the relative proportion of grass-based agriculture (hayfield and pasture) to row-crop agriculture (corn). In 2002, we visited 69 randomly selected hayfields (560 ha) and 10 pastures (77 ha) (Shustack 2004) every 10-14 days to determine the land use (row crop, pasture, hayfield), cutting interval, grazing intensity. In 2003-2006 we expanded the survey to include the original 79 fields as well as all fields visible from the road survey point (2002-2005 cutting data published in Perlut et al. 2006). The 2003-2006 total survey included 347-424 hayfields (1364-1579 ha), 98-166 pastures (958-1142 ha), and 74-119 corn fields (856-1279 ha). We assumed that management activities on these fields were representative of the Champlain Valley as a whole.

Distribution of birds across habitats

To evaluate the distribution of Savannah Sparrows and Bobolinks across the four treatment-defined habitats, in 2004-2005 we conducted point counts on twenty 25 km^2, randomly selected agricultural blocks within the Champlain Valley (Fig 1). Blocks were stratified by the total percentage of area (ha) devoted to agriculture. Each year, we conducted three 10-minute point counts for every field located within the center 4 km^2

section of each 25 km^2 block (*n* = 217 fields). During each point count, trained observers recorded the time in which individual Savannah Sparrow and Bobolink were first detected, as well as sex. Only birds within the given count field were recorded. We used Huggins closed capture removal models (Huggins 1989) within program MARK (White and Burnham 1999) with 2 minute intervals to determine detection probability (Shustack 2004). We then estimated density for each of the four treatment-defined habitats. These raw survey data did not require adjusting, as the detection probability (p) was > 0.93.

Demographic parameters

We assesed annual productivity, survivorship, and recruitment on the four treatment-defined habitat types in three study areas: (1) Shelburne, Vermont (2002-2006 EH, LH, RG), (2) Hinesburg, Vermont (2003-2006 EH, LH, MH, RG), and (3) Cumberland Head, New York (2002-2005 LH; 2003-2005 MH; Figure 1). Each treatment field was a minimum of 10.5 ha, and study areas were > 8 km apart. Fields were composed of a mixture of cool season grasses and forbs (see Perlut et al. 2006 for details on vegetation and management).

Annual productivity, adult survival, and recruitment data were collected during the 2002-2006 breeding seasons. Beginning on 8 May, we captured birds with mist-nets, and placed unique combinations of three color bands and a single metal U.S. Fish and Wildlife Service band on the legs of all adults of both species. Color-banded birds were continuously resighted throughout the breeding season. In mid-May we began intensive, season-long nest searching and nest monitoring (*n* = 733 Savannah Sparrow, 447 Bobolink nests). After locating a nest, we immediately identified the associated female and male. If either adult was unbanded, we captured and banded those individuals near the nest location. A nest was visited every one to two days until it either failed or the nestlings fledged. Nestlings of all known nests were banded with a single metal U.S. Fish and Wildlife band on day six or seven.

Annual productivity was estimated as the number of female offspring produced in a breeding season by a single adult female (Table 1). This model assumes a balanced nestling sex ratio (Wheelwright & Seabury 2003).

Apparent survival (ϕ) and recruitment (f) estimates were obtained with the Pradel survival and recruitment (Pradel 1996) model option in Program MARK (White & Burnham 1999). Apparent survival is the probability that an individual bird survives *and* returns to an area of interest, whereas recruitment is the probability that an adult present in an area of interest is a newly recruited member of the breeding population through birth or emigration. Apparent survival estimates for Bobolinks and Savannah Sparrows are sensitive to both the presence of non-breeders in the population as well as to local (< 1.5 km from treatment fields) between-year dispersal (Chapter 3). In general, the inclusion of non-breeders in the analysis lowers apparent survival estimates, while the inclusion of observations of marked individuals that dispersed off site increased apparent survival estimates (Pradel et al. 1997; Cilimburg et al. 2002). These methodological factors caused within-treatment apparent survival estimates to vary by 0.09-0.14 for female Savannah Sparrows and 0.08-0.17 for female Bobolinks (Table 1). From these rates, we selected treatment- and species-specific survival estimates to use as baseline survival estimates in the population model. For Savannah Sparrows, the baseline survival rate was the set of survival estimates that produced population trends that most closely matched the Breeding Bird Survey trend for Vermont (annual declines: Bobolinks: -

3.18%; Savannah Sparrow: -0.20%; Sauer et al. 2005). For Bobolinks, the baseline survival rate was the highest survival rate estimated within each treatment. For both species, and especially Bobolinks, the baseline rates in the population model were biased low because despite dedicated search efforts, birds could disperse off of study areas and not be detected. Nonetheless, this bias does not affect the relative ranking of the different conservation strategies we assessed.

Our data did not allow estimation of juvenile survival because most fledglings do not return to the same field in which they were born (Greenwood and Harvey 1982). Given successful fledging, there is no reason to expect that juvenile survival varies with the grassland treatment-type from which they fledged. Therefore, juvenile survival was modeled as 50% of adult survival from the late-hayed habitat (Vierling 2000).

Model description

We used the field data (amounts of each of the four-treatment defined habitats in the Champlain Valley, and their corresponding density estimates, annual productivity, apparent survival, and recruitment) to parameterize a landscape-level population viability analysis for Savannah Sparrows and Bobolinks in the Champlain Valley. This female-based, pre-breeding, population model simulated 25 years, with 1,000 replications of each stochastic trial. The model was closed with respect to immigration into the Champlain Valley. The model assumed two age classes, second year (first-year breeders) and after second year (older breeders). The age classes differ only with respect to survival and gaining a territory in a habitat (see below), but not with respect to breeding success. Population census occurred at the beginning of the breeding season, whereby each surviving individual has migrated from the breeding grounds, overwintered, and migrated back to the breeding grounds when it is censused.

Population parameters, particularly annual productivity, showed high annual variability within a treatment; therefore, species and treatment-specific productivity, adult survival, and juvenile survival were treated as stochastic parameters (Table 1). For productivity, the model randomly selected treatment-specific annual estimates from a normal distribution, based on the mean and standard deviation. Because survival estimates are probabilities ranging between zero and one, the model randomly selected annual estimates from a beta distribution between stated bounds. The shape of the beta distribution was controlled by two parameters, α and β, which were estimated from the mean and standard deviation of annual survivorship.

The model began by populating the four habitat treatments in year t (Fig. 2A). The initial population size was the product of the total area (ha) of each treatment and its corresponding female density (Table 1). The initial population then bred at the habitat specific productivity rate (Fig. 2B), producing juveniles from each habitat type (Fig. 2C)

After the breeding season, adults migrated to non-breeding areas, and returned to the breeding grounds at treatment-specific survival rates (Table 1; Fig. 2D and 2F). The four treatments were then populated with all females who survived from to year t to year t_{t+1}. In the Champlain Valley, 87-91% of resighted or recaptured female Bobolinks and Savannah Sparrows returned to the field in which they previously bred, regardless of previous years' nesting success, treatment-type, or the available habitat within 1.5 km radius (Fajardo unpubl. data). Therefore, this model assumed that surviving adults always returned to the same treatment-defined habitat type.

After the breeding season, juveniles migrated to non-breeding areas (Fig. 2E), and returned to the breeding grounds at a rate of 0.5 * adult survivorship for the late-hayed treatment (Fig. 2F). Surviving individuals (called the second-year pool) then attempted to secure a breeding location in one of the four treatment types in year *t+1*. The second-year pool was distributed among the four habitats by a selection coefficient, *f*, which assumes that an order of habitat preference exists and available habitats are ranked relative to this preference (Fig. 2G). Thus, with a second-year pool of 10 and selection coefficients of 0.5, 0.2, 0.2, and 0.1, five individuals would settle in habitat one, two in habitat two, two in habitat three, and one in habitat four. Selection preference is likely determined by both structural cues (Perlut et al. 2006) and 'public information' (Nocera et al. 2005), though final second-year settlement densities are also affected by territory availability. Because both species have mixed-mating strategies, with high rates of polygynous associations (Wheelwright and Rising 1993; Martin and Gavin 1995), we assumed that female-female despotic interaction had little influence in habitat selection. Species and treatment-specific selection coefficients were obtained through Pradel recruitment models sister to the survival models described above, where *f* is the probability that an adult is a newly recruited member of the breeding population through birth or emigration. Thus, fields with small *f* indicated that the proportion of second-year recruits is comparatively low (low habitat preference), while fields with comparatively high *f*'s indicated that the proportion of second-year recruits is high (high habitat preference). The four recruitment estimates were scaled such that their sum was 1.0, proportionally distributing each year's surviving juvenile class according to preference (Table 1; for models and values see Chapter 3).

The second-year pool was distributed into respective treatments by the selection coefficients. These second-year females either gained territories in the habitat, or were forced to leave because the carrying capacity, K, had been reached for that habitat. K was (arbitrarily) set at five-times the initial treatment-specific population size. A habitat absorbed recruits until the total number of surviving adults and second-year recruits who obtain territories equaled K. When a treatment reached K, individuals who did not gain a territory were forced to seek less preferred habitat, and moved to the habitat with the next greatest selection coefficient that still had vacant territories. If all four habitats were full, the excluded floaters did not breed as a result of either death or emigration from the Champlain Valley.

This model was parameterized for Savannah Sparrows and Bobolinks separately. However, the Bobolink model included one additional, quasi spatially-explicit step. Female Savannah Sparrows remained on early-hayed fields and immediately renest post-harvest (Perlut et al. 2006). However, from nesting and point count-density data, we determined that only 40% of the original, pre-harvest Bobolink population size attempted to breed on early-hayed fields following a cut. The remaining 60% of the original females in early-hayed fields dispersed throughout the Champlain Valley and settled in fields that had not yet been hayed (Strong unpubl. data). As a result, the model redistributed 60% of the initial, early-hayed Bobolink population throughout the remaining three treatment-types according to the selection coefficients. These birds bred in the treatment to which they moved.

The final breeding population for each treatment included the number of surviving adults and second-year recruits, and any additional recruits that entered a treatment because their preferred habitat was at K. Finally, females within each treatment bred, the juveniles from all four populations were pooled, and the simulation continued to the next year, again incorporating survival, selection, and productivity.

Conservation Strategies

With all demographic parameters held at baseline values, we evaluated six conservation strategies, targeted at different life-history or management options that could be implemented to dampen or reverse population declines. Strategy 1 tested population sensitivity to changes in adult and juvenile survival by raising treatment-specific values by increments of 5%, 10%, and 25%. These simulations were intended to reveal the effect of potential management activities on the non-breeding grounds that would increase survivorship for all birds, regardless of the treatment in which they breed.

Strategies 2 and 3 focused on increasing the total amount of habitat that can be used by grassland birds, such as converting corn to grassland habitat. In strategy 2, we simulated an increase in high-quality habitat (middle- and late-hayed) by 5%, 10%, and 25%. These scenarios reflected potential changes in land management through several federal and state conservation initiatives, such as the Wildlife Habitat Incentives Program and Environmental Quality Incentives Program. In strategy 3, we returned high-quality habitats to their base size and increased the amount of low-quality habitats (early-hayed and grazed) by 5%, 10%, and 25%. These scenarios reflect the current trends in agricultural management within the Champlain Valley (Troy et al. 2005).

Strategies 4 and 5 focused on decreasing the proportion of early-hayed fields while keeping the total acreage available for grassland birds constant. Here, parameter values for middle-hayed, late-hayed, and grazed fields were held constant. In strategy 4, early-hayed parameters for productivity and survival changed to those of grazed fields, thereby slightly increasing survival and productivity on early-hayed fields, while retaining the structural components that would affect habitat selection. In strategy 5, early-hayed parameters for productivity and survival were changed to that of middle-hayed fields, further increasing survival and productivity on early-hayed fields while retaining structural components. Thus, these later two simulations addressed potential changes in management practices on early-hayed fields.

Finally, in strategy 6 we used management to increase the attractiveness (*f*) of late-hayed fields. Late hayed fields often contain significant amounts of thatch which delays spring regrowth, and may therefore act a deterrent in habitat selection; but thatch can be removed by farmers late in the season, increasing attractiveness (Perlut unpubl. data). Here, *f* on late-hayed fields increased by 5%, 10%, and 25%, and *f* in each of the other three treatments decreased by an equal value among the three such that the total parameter values could be scaled to sum 1.0.

RESULTS

Champlain Valley Agricultural Management Trends

Grass-based agriculture, hayfields and pastures, comprised 80% of the total agricultural landscape (Fig. 3A). Corn comprised the remaining 20%, and this area is thus available to be converted to grass-based agriculture (conservation strategies 2 and 3). Although there was annual variation, the majority of hayfields in the Champlain Valley were cut annually during the breeding season; early-hayed, middle-hayed, and late-hayed fields comprised 18%, 25%, and 35% of the grass-based landscape (Table 1; Fig. 3B).

Distribution of birds across habitats

Female Savannah Sparrow density was similar across early-hayed and late-hayed fields (0.30 females/ha and 0.29 females/ha), as well as across grazed and middle-hayed fields (0.25 females/ha and 0.23 females/ha; Table 1). Female Bobolink density showed greater variation among treatments, and was highest in late-hayed fields (0.36 females/ha) and lowest in grazed fields (0.20 females/ha; Table 1).

Demographic parameters

For both species, annual productivity was closely associated with management intensity. Savannah Sparrow productivity was greatest on middle-hayed, followed by late-hayed, grazed, and early-hayed fields. For Bobolinks, productivity was greatest on late-hayed, followed by middle-hayed, grazed, and early-hayed fields (Table 1). Thus, early-hayed fields had the lowest annual productivity for both species.

Adult apparent survival was also associated with management intensity for both species. Apparent survival, was highest on late-hayed fields, followed by middle-hayed, grazed, and early-hayed fields, respectively (Table 1).

Recruitment, and therefore the selection coefficient f, of second-year females was lowest on late-hayed fields, and nearly consistent for early-hayed, grazed, and middle-hayed fields for both species (Table 1).

Baseline model results

Baseline simulations showed declining populations of both Savannah Sparrows and Bobolinks, though the rate of decline was significantly greater for Bobolinks (Table 2; Fig. 4). Here, over ten years, Savannah Sparrow and Bobolink populations declined by

8% and 94% respectively (Table 2). Comparatively, BBS data would show a 2% Savannah Sparrow and 28% Bobolink population declines over ten years.

Conservation Strategies

Strategy 1. For both species, model results suggest that conservation strategies outside the breeding period important in population persistence. Given the baseline survivorship, density, productivity, recruitment, and habitat estimates, Savannah Sparrows responded positively to increases in annual survival (Table 2; Fig. 4); the strongest positive response occurred through increasing adult survival. Increases in juvenile survival also positively influenced population growth. For Bobolinks, increasing adult or juvenile survival decreased the rate of population decline, though the effects were notably weaker than for Savannah Sparrows (Table 2; Fig. 4).

Strategies 2 and 3. Interestingly, in strategy 2, for both species, increasing the amount of high-quality habitat by 5%, 10% and 25% only slightly increased population growth (Table 2; Fig. 4). Strategy 3 identified that increasing low-quality habitat by 5%, 10%, and 25% only slightly decreased population growth (Table 2; Fig. 4). These results are due to two causes: density was a function of survival and selection and not a function of habitat area, so the number of adults per unit area did not necessarily respond to increased habitat amount; and the habitat selection coefficient (recruitment) remained constant, such that individuals still selected low quality habitats even though high-quality habitats were more available.

Strategies 4 and 5. The strongest effect, causing Savannah Sparrow populations to grow and dampening Bobolink declines, occurred when we simulated changes in management practices. Here, in analyses 4 and 5, productivity and survival on early-hayed fields was increased to the grazed or middle-hayed rates (Table 2; Fig. 4), essentially converting early-hayed fields to middle-hayed or grazed fields. In these models, quality of the poor habitats increased while their selection coefficient remained constant. The total number of birds in these habitats increased because survivorship increased, resulting in greater annual productivity. Although the selection coefficient stayed the same, the result was that proportionally more birds selected these "improved" habitats. Shifting to grazed habitats' rates of survival and productivity caused Savannah Sparrow population growth to increase by 42% and Bobolink population declines slowed by 8% over ten years, as compared to baseline declines. Substituting middle-hayed values for early-hayed rates showed even greater effects on population growth—over ten years, Savannah Sparrow populations increased by 124% and slowed Bobolink population decline by 11%, as compared to baseline declines (Fig. 4).

Strategy 6. Bobolinks and Savannah Sparrows responded differently to changes in second-year bird's strength of habitat selection (*f*) for late-hayed fields. For Savannah Sparrows, a 25% increase in preference in late-hayed fields resulted in positive population growth; for Bobolinks, the effect was similar to increases in adult or juvenile survival, where population declines slowed by only 3-4% as compared to baseline conditions (Table 2).

DISCUSSION

Given current land-use patterns, and no immigration from other regions, these results strongly suggest that grassland songbird populations are currently not viable in the Champlain Valley. These results are consistent with the Breeding Bird Survey results (Sauer et al. 2005), and elucidate the mechanisms by which populations are declining.

Early-hayed and grazed fields, with low annual survival, low productivity, and high attractiveness, accounted for 40% of the grass-based agricultural landscape. The deleterious demographic effects associated with these treatments overshadowed the population sources, middle- and late-hayed habitats, which composed 60% of the available grass-based habitat.

Although our results are consistent with the BBS declines, they suggested the decline is much more severe than the BBS reveals. The discrepancy could be due to two factors. First, our model assumes a closed population. The Champlain Valley is likely closed to immigration from eastern and western populations by significant mountain ranges (Adirondack Mountains, New York, and Green Mountains, Vermont). However, the Valley may be open to movements between the northern St. Lawrence plain, Canada, and southern agricultural regions of Massachusetts and New York, USA. These areas may provide a source of immigrants that rescue the Champlain Valley population in ways not accounted for in the model. Nonetheless, agricultural practices in both northern and southern regions are such that management likely has similar effects on at least a portion of these populations.

Second, it is likely that baseline survival rates used in the population model were too low, especially for Bobolinks. Apparent survival is the probability that an individual survives and returns to an area of interest (White and Burnham 1999). Following nest failure, population nesting (field-level) failure, and habitat destruction, female Bobolinks may become nomadic, both within and between years, searching for males whose territories hold appropriate resources (Greenwood 1980). This potential to disperse likely biases apparent survival rates downward

Another consideration centers on the four treatment study design. Cutting occurs constantly throughout the Champlain Valley, such that at least one additional treatment type should potentially be included in the study design, depicting the effects of haying from 12-20 June, when 7-16% of hayland was cut (Fig. 3B). Although inclusion of this habitat type may more closely approximate the study system, its demography is likely similar to that observed on grazed fields; therefore, we doubt its effects would be large enough to alter the population declines documented (Fig. 4). Nevertheless, it is important to recognize that land-use in agricultural landscapes is dynamic and that ecological questions must take into account the factors that influence within-year and between-year change, namely weather, and agricultural trends.

Conservation Strategies

Although these assumptions are important considerations, our models nonetheless justify immediate conservation planning in agricultural landscapes, both in breeding and non-breeding regions. Planning should consider how to improve demography in the current landscape composition, particularly in early-hayed fields, as well as future changes to the type and amount of habitat. Below, we discuss four land-use change scenarios that may characterize the Champlain Valley in the future. The first three scenarios could result in a net increase in current grass-based agriculture; the fourth could result in a decline in grassland habitat, though maintains an important landscape cue, potentially benefiting songbirds.

In the first scenario, the current strong movement in Vermont agriculture towards grass-based, pasturing, and/or organic dairy farming continues. Here, some portion of corn is converted to pasture. However, in the Champlain Valley, the term 'pasture' is ambiguous because farmers vary their methods based on a number of variables including the size of the herd, available habitat for grazing, available time for management, and type of forage provided. Ignoring these factors, this study pooled all pastures into a single, strictly defined rotationally grazed category. It is currently unclear if the local demography of grassland birds on rotationally grazed pastures is different than those in other pasture management styles. Since pastures comprise 18% of the entire agricultural landscape and 22% of the grass-based landscape, this information may be critical for land managers and conservation funding, particularly if pasturing-based dairying increases in the landscape. Nonetheless, given current demographic levels in pastures, increasing acreage alone will not alleviate or hasten population declines (Fig. 4).

Second, the Champlain Valley may see an increase in rural single family homes built on large (formerly agricultural) parcels. This trend favors grass-based rather than corn-based management, where landowners tend to manage their lands opportunistically, having a local farmer cut, and at times, collect the hay. As a result, farmers prioritize higher quality fields that require the minimum amount of transportation to their barn or silo, and therefore commonly cut these fields in the middle-haying period. This pattern may result in an increased amount of high-quality (middle- and late-hayed) habitat. However, it comes with a trend towards fragmentation and succession into shrubs and forest—both negative influences on population viability. Increased high-quality habitat alone will not stabilize populations (Fig. 4). If this trend results in conversion of early- to middle- or late-hayed fields, populations will benefit.

Third, if technology to convert cellulose to ethanol becomes a major national funding priority, and successfully develops into a viable fuel source, grass may replace a notable portion of corn plantings. This economy would increase the amount of land devoted to late-hayed habitats, as farmers would manage for increased biomass. Shifting from corn to switchgrass (*Panicum virgatum*), a common biofuel grown the Midwest, can have positive effects on songbird abundance (Murray et al. 2003), and no negative effects on reproduction (Murray and Best 2003). Switchgrass is not currently sown in Vermont, though, conservation plans incorporating monoculture agriculture should proceed cautiously, as reed canarygrass (*Phalaris arundinacea* L.) monocultures have low songbird densities (Strong pers. obs.). Although increasing the amount of middle- and late-hayed habitat slightly increased population viability, even a 25% increase in land area did not stabilize populations (Fig. 4). However, as in the previous scenario, if early-hayed fields are converted to late-hayed fields, populations will respond. Additionally, this type of farming results in the grass and stubble being collected after harvest—a characteristic that increases the attractiveness of late-hayed fields. Here, we have shown that alone, habitat selection by second-year birds had little effect on population growth. Therefore, increased attractiveness of late-hayed fields will affect population growth only in conjunction with other conservation measures.

The fourth scenario projects dairy herds in the Champlain Valley to continue increasing in size. Here the amount of corn habitat increases, as the percentage of corn silage in larger farm diets continues to increase. This trend could result in both a conversion of idle grassland to corn, as well as a rotation (~6-8 year) with alfalfa, both unsuitable, low quality breeding habitat. Although this scenario results in an increase of non-breeding habitats, on a local scale, the presence of agricultural lands increases grassland songbird density (Shustack 2004); thus, well sited corn fields, within matrixes of middle- and late-hayed fields, may help increase densities within these source habitats.

Recent grassland bird conservation programs have uniformly called for expansion of delayed mowing (Massachusetts Audubon Society 2003, Natural Resources Conservation Service 2005), creating more late-hayed habitat from early- or middle-hayed fields. These programs result in fields with higher productivity. We suggest that their value can be further enhanced by increasing the attractiveness (to recruits) of late-hayed fields. In Perlut et al. (2006), both Bobolinks and Savannah Sparrows initiated nesting activities significantly earlier on early- and middle-hayed fields than late-hayed fields. Assuming this trend at least partially represents habitat preference, late-hayed fields may be initially less attractive because previous years remaining grass suppresses early growth. Therefore, managers may increase attractiveness of late-hayed fields by removing the previous year's thatch. Again, these fields economic value may sharply increase if grass-based ethanol becomes a viable product.

While the benefits of these source habitats are obvious, these programs are not viable for active farms, as managers are unable to convert their productive early-hayed fields to late-hayed fields. This inability is important, as these models clearly show that population decline is driven by early-hayed fields. Hay farmers aggressively aim for late-May or early-June harvest because forage protein levels are higher early in the growing season (Cherney et al. 1993); high protein forage in turn increases milk production by lactating dairy cows (Bosworth and Stringer 1985). Nonetheless, stabilizing populations, particularly for Bobolinks, is dependent on increased productivity and survival in early-hayed fields (Fig. 4). Therefore, conservation plans involving early-hayed fields must fulfill both farmer's harvest and bird's demographic needs.

Early-hayed fields can potentially be managed for high-quality agricultural yields and moderate- to high-quality songbird habitat. In Perlut et al. (2006), and again here, we propose the following plan to improve songbird demography on early-hayed fields. First, the entire harvest process, including cutting, collecting, and removing hay, as well as nutrient management, must be completed prior to 2 June. The earliest possible May harvest date is encouraged, as earlier harvest will lessen the parental care investment adults make before certain, haying-mediated nest failure, and will increase the probability and density of Bobolinks repopulating hayed fields. Second, a cutting interval of 65 days may be sufficient to support both species reproductive needs. In this plan farmers get a moderate volume, high protein first-crop, and a high volume, comparatively lower protein second-crop. Meanwhile, Savannah Sparrow first nesting-attempts fail, however, renesting efforts would not be influenced by the second harvest. Bobolink first nesting-attempts also fail, however, females have a sufficient window of opportunity within which to repopulate fields 15-days post-harvest, renest, and care for fledglings. A 3-year pilot project based around this plan is current being tested in Vermont by the National Resource Conservation Service (NRCS 2007). The program is aimed at active, high-quality hayfields, > 20 acres of continuous, well configured hayland, composed of at least 50-70% grass. Farmers and landowners can sign three year contracts where in return for bird-friendly management they receive $100 per acre per year. While farmer's interest in such a plan is unknown, it represents an important paradigm shift in grassland bird conservation—acknowledging and acting on a management plan for agricultural landscapes that can benefit both farmer's and bird's needs.

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LITERATURE CITED

Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping of eastern populations of the Bobolink. Wildlife Society Bulletin **18**:143-150.

Bollinger, E. K., and T. A. Gavin. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk **106**: 584-594.

Bosworth, S.C., and W. C. Stringer. 1985. Cutting management of alfalfa, red clover, and birdsfoot trefoil. Agronomy Facts 7, The Pennsylvania State University, State College, Pennsylvania, USA.

Cherney, D. J. R., J. H. Cherney, and R. F. Lucey. 1993. In vitro digestion kinetics and quality of perennial grasses as influenced by forage maturity. Journal of Dairy Science **76**:790-797.

Cilimburg, A. B., M. S. Linderberg, J. J. Tewksbury, and S. J. Hejl. 2002. Effects of dispersal on survival probabilities of adult Yellow Warblers (*Dendroica Petechia*). Auk **119**:778-789.

Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications **11**:871-882.

Fletcher, R. J., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. Journal of Wildlife Management **70**:145-157.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics. **13**:1–21.

Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation **4**:128-155.

Huggins, H. M. 1989. On the statistical analysis of capture experiments. Biometrika **76**:133-140.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology **15**:247-257.

Martin, S. G., and T. A. Gavin. 1995. Bobolink (*Dolichonyx* oryzivorus). Birds of North America **176**:1-24.

Massachusetts Audubon Society. 2003. http://www.massaudubon.org/Birds_and_Beyond/grassland/large.php#conservation.

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

Murray, J. D., and L. B. Best. 2003. Short-term bird response to harvesting switchgrass for biomass in Iowa. Journal of Wildlife Management **67**:611-621.

Murray, L. D., L. B. Best, T. J. Jacobsen, and M. L. Braster. 2003. Potential effects on grassland birds of converting marginal cropland to switchgrass biomass production. Biomass & Bioenergy **25**:167-175.

National Agricultural Statistics Service (NASS). 1999. USDA. http://www.nass.usda.gov/census/.

Natural Resources Conservation Service (NRCS). 2005. Conservation Practice Standards. http://www.nrcs.usda.gov/technical/efotg/.

Natural Resources Conservation Service (NRCS). 2007. EQIP incentives for grassland bird conservation. http://www.vt.nrcs.usda.gov/programs/EQIP/EQIP_2007/Index.html

Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2005. Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society B **273**:349-355.

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.

Pradel, R. 1996. Utilization of mark-recapture for the study of recruitment and population growth. Biometrics **52**:703-709.

Pradel, R., J. E. Hines, J. D. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. Biometrics **53**:60-72.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2005. Version 6.2.2006.* USGS Patuxent Wildlife Research Center*, Laurel, MD*

Shustack, D. P. 2004. Bobolink and Savannah Sparrow habitat selection in the Champlain Valley. Thesis. University of Vermont, Burlington, Vermont, USA.

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

Vierling, K. T. 2000. Source and sink habitats of Red-winged Blackbirds in a rural/suburban landscape. Ecological Applications **10**:1211-1218.

Wells, J. V. 1997. Population viability analysis for Maine Grasshopper Sparrows. Pages 153-169 in P. Vickery and P. Dunnwiddie, editors. Grasslands of Northeastern North America: Ecology and Conservation of Native and Agricultural Landscapes. Massachusetts Audubon Society, Lincoln, MA.

Wheelwright, N. T., and J. D. Rising. 1993. Savannah Sparrow. Birds of North America **45**:1-28.

Wheelwright, N. T., and R. E. Seabury. 2003. Fifty:fifty offspring sex rations in Savannah Sparrows (*Passerculus sandwichensis*). Auk **120**:171-179.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**:S120-S139.

Table 1. Demographic and landscape values used to parameterize model. Adult apparent survival estimates show range used to establish baseline survival values.

		early-hayed	grazed	middle-hayed	late-hayed
	Amount of habitat (ha)	26192	32120	36442	51246
	Proportion of habitat	0.18	0.22	0.25	0.35
Savannah Sparrow	Female density (per ha)	0.30	0.25	0.23	0.29
	Annual productivity	0.65 ± 0.07	1.06 ± 0.11	1.65 ± 0.26	1.40 ± 0.18
	Adult survival	0.48±0.11 to 0.58±0.09	0.50±0.12 to 0.59±0.10	0.45±0.11 to 0.59±0.16	0.58±0.04 to 0.71±0.09
	Baseline survival	0.51 ± 0.13	0.58 ± 0.15	0.59 ± 0.16	0.71 ± 0.09
	Juvenile survival	0.29±0.02 to 0.35±0.04	0.29±0.02 to 0.35±0.04	0.29±0.02 to 0.35±0.04	0.29±0.02 to 0.35±0.04
	Recruitment	0.32	0.33	0.24	0.25
	Scaled selection coefficient	0.263	0.265	0.272	0.201

Bobolink	Female density (per ha)	0.25	0.2	0.33	0.36
	Annual productivity	0.02 ± 0.02	0.88 ± 0.15	1.12 ± 0.11	1.40 ± 0.11
	Adult survival	0.19±0.08 to 0.36±0.11	0.27±0.11 to 0.36±0.11	0.31±0.10 to 0.40±0.16	0.46±0.11 to 0.55±0.09
	Baseline survival	0.36 ± 0.11	0.36 ± 0.11	0.40 ± 0.16	0.55 ± 0.09
	Juvenile survival	0.23±0.05 to 0.27±0.04	0.23±0.05 to 0.27±0.04	0.23±0.05 to 0.27±0.04	0.23±0.05 to 0.27±0.04
	Recruitment	0.38	0.30	0.41	0.37
	Scaled selection coefficient	0.261	0.253	0.284	0.202

Table 2. Population viability with respect to conservation strategies. The first row illustrates the baseline population growth, with which to compare all other analyses.

conservation strategy			Savannah Sparrow		Bobolink	
			10 years	25 years	10 years	25 years
		baseline	-7.8%	-13.1%	-94.2%	-99.9%
strategy 1	Δ adult survival	5%	52.6%	174.4%	-87.7%	-99.7%
		10%	143.4%	287.2%	-81.2%	-99.0%
		25%	302.3%	302.7%	-41.5%	-78.6%
	Δ juvenile survival	5%	9.8%	37.5%	-90.6%	-99.8%
		10%	29.3%	97.6%	-89.0%	-99.8%
		25%	112.7%	282.2%	-81.9%	-99.1%
strategy 2	Δ high quality grass habitat	5%	-6.7%	-9.1%	-92.2%	-99.9%
		10%	-4.5%	-9.1%	-92.0%	-99.9%
		25%	-2.7%	-9.2%	-91.9%	-99.9%
strategy 3	Δ low quality grass habitat	5%	-7.3%	-13.9%	-92.0%	-99.9%
		10%	-7.6%	-13.6%	-92.1%	-99.9%
		25%	-10.3%	-14.6%	-92.3%	-99.9%
strategy 4	EH=G	ϕ + productivity	33.9%	118.0%	-86.6%	-99.6%
strategy 5	EH=MH	ϕ + productivity	116.1%	282.1%	-83.0%	-99.2%
strategy 6	Δ selection for late-hayed fields	5%	-5.3%	-6.2%	-91.6%	-99.9%
		10%	-1.6%	1.5%	-91.3%	-99.9%
		25%	5.9%	23.2%	-90.7%	-99.8%

Figure 1. The Champlain Valley of Vermont and New York, USA, contains 146,000 ha of managed grasslands (NASS 1999). Stars indicate study areas for demographic study.

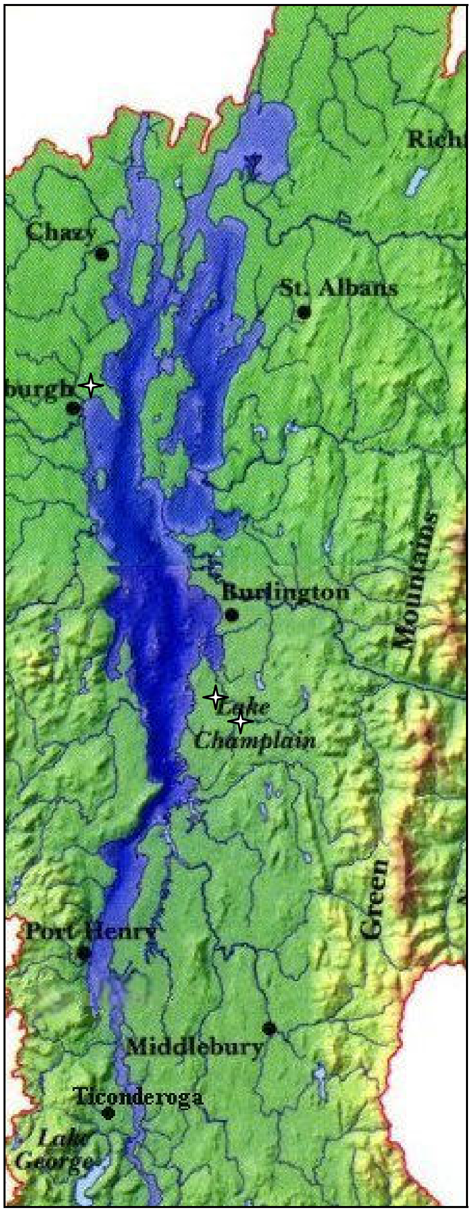


Figure 2. Schematic for this female-specific, stochastic, landscape-level, closed population model.

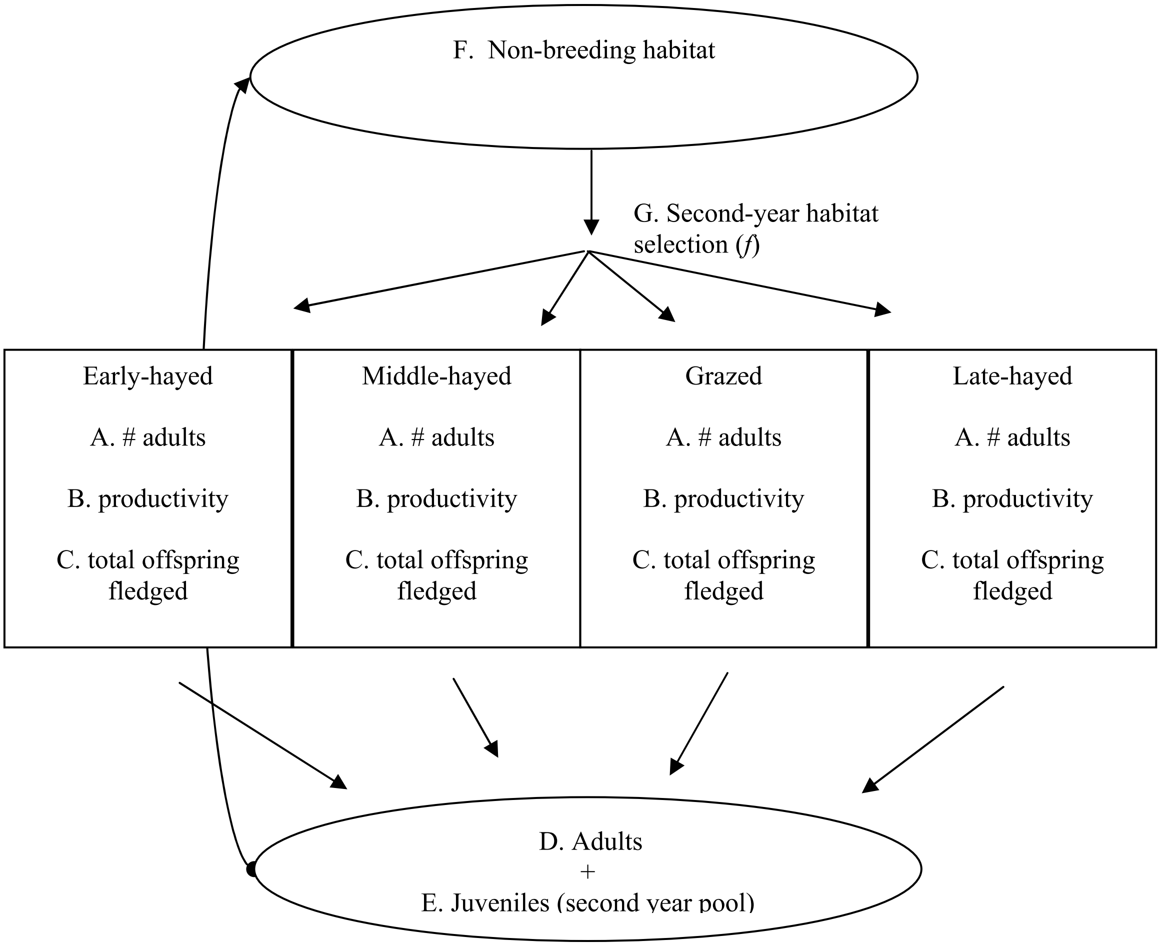
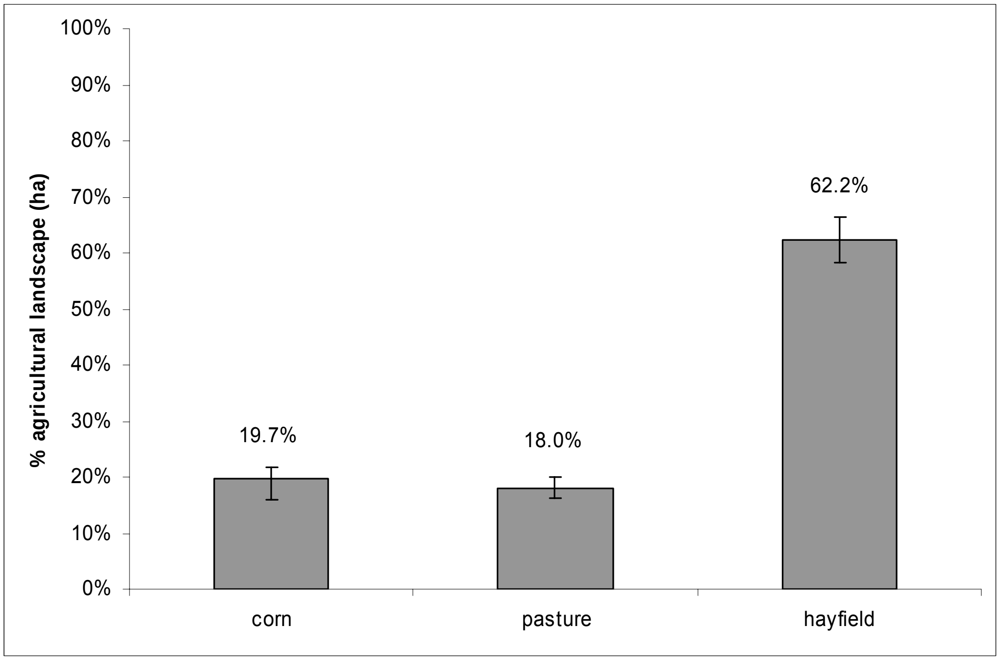


Figure 3A-B. Agricultural land-use survey (A) of the Champlain Valley of Vermont and New York, USA, 2003-2006 (2186-2521 ha/ year), showed a dominance of grass-based farming. Cumulative area hayed (B), Champlain Valley, 2002-2006.



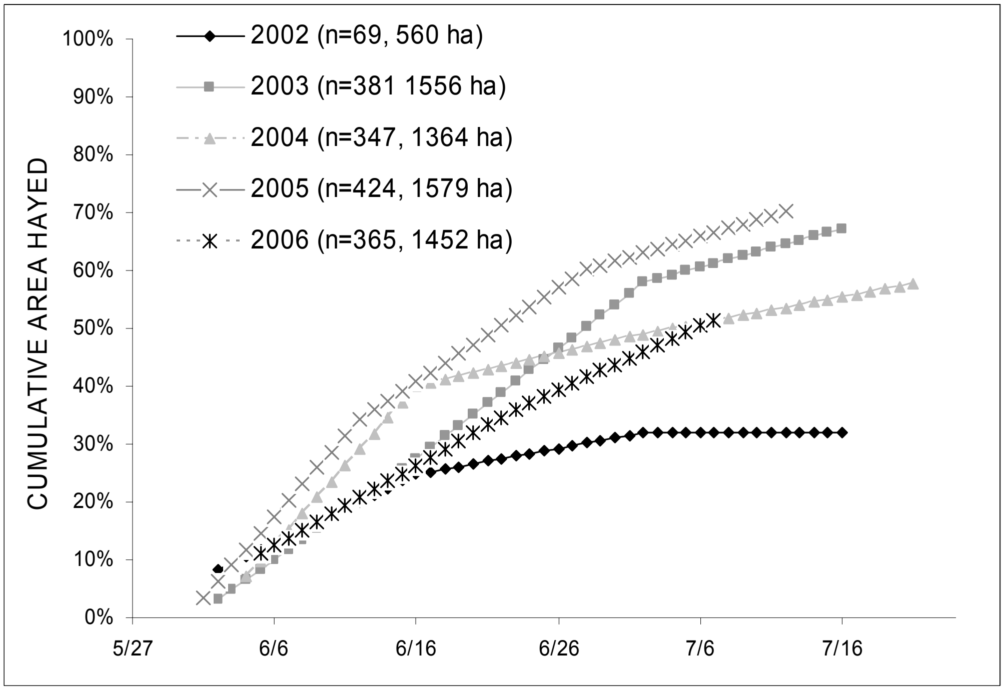
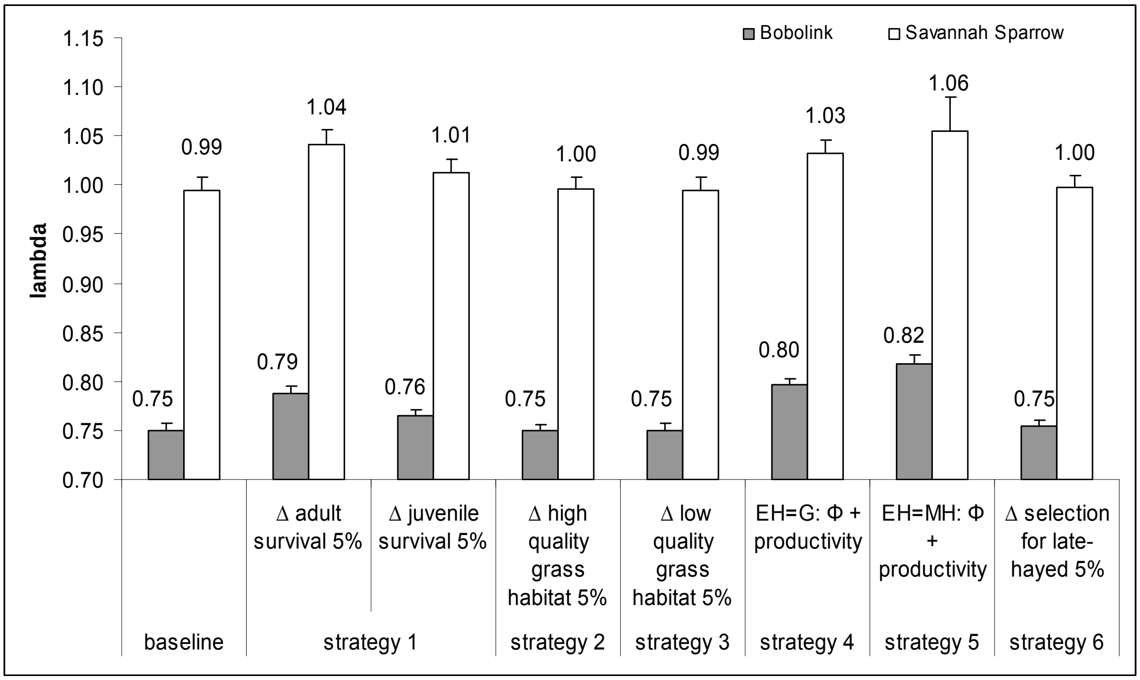


Figure 4. Mean lambda (N_{t+1}/N_t) values for 25 years of simulations. Lambda values of 1 indicate stable populations, while values < 1 indicate declining populations, and values > 1 indicate growing populations. Error bars indicate standard deviation.



Postscript: The next ten summers

This dissertation contributes some answers to longstanding ecological, evolutionary, and conservation questions. These chapters, however, present as many questions as they do answers. Without a doubt, I could spend the next ten years studying these same Champlain Valley hayfields and pastures. The Valley is an ideal, and idyllic, study system for many reasons: it offers a landscape in which it is relatively easy to collect meaningful amounts of data in a short period of time; contains (at least currently) abundant species that are easy to observe and tolerant to research activities; provides good species' comparisons between Bobolinks and Savannah Sparrows, which share ecological constraints but differ in life-history strategies; provides insight and understanding into the ecology of declining species; is readily accessible from Burlington, Vermont; its habitats are safe and easy to move about freely; it is highly accessible to students new to field biology to gain practical field experience; requires relatively few research materials; has a strong social and cultural relationship to Vermont's landscape; and, finally, is a beautiful place to live and work.

These qualities combine to present a study system that is open for exploring a wide range of ecological and evolutionary questions. All questions, however, arise from the collection of long-term demographic data, centered around banding, resighting, and nest-monitoring on at least a portion of the study fields. These basic demographic data will enable us to better understand ecological processes in dynamic, anthropogenic environments. I do not know of another avian ecology monitoring program using comparable human-mediated habitats, although perhaps a similar forestry-related study system exists. Some of the following projects could be explored in one to two summers, making them ideal undergraduate thesis or Masters research. Expanding from the baseline demographic work future projects could include:

- identify the habitat selection cues Bobolinks use during haying-mediated dispersal from early-hayed fields
- identify if, how, and why management causes nestling and fledgling sex ratios of both species to differ from unity
- examine the relationship between songbird nest predation and small mammal community dynamics in early-, middle-, and late-hayed fields
- explore how trait selection changes with shifts in the social and genetic mating systems pre- and post-harvest on early-hayed fields, and compared to behavior on the late-hayed field
- evaluate the demographic benefits, particularly for Bobolinks, of the early-haying plan proposed in Chapters 1 and 4
- evaluate the use of and demographic benefits of fields enrolled in the Wildlife Habitat Incentives Program (WHIP), which pays for delayed mowing
- explore the Bobolink social mating system, genetic mating system, and male-male interactions within and between clusters of synchronous nests (2-4) found throughout middle- and late-hayed fields

Two additional projects, with related taxa and habitat, though not on the current study fields include:

- establishing a long-term, citizen science nest monitoring project with the Green Mountain and Otter Creek Audubon chapters: trained biologists, with or without the help of volunteers, find a nest(s), band at least the associated female, and the volunteer monitors the fate of the nest(s)
- explore the habitat selection and demographic success of the few remaining populations of other obligate grassland songbirds, including Grasshopper Sparrow (*Ammodramus savannarum*), Vesper Sparrow (*Pooecetes gramineus*), and Horned Lark (*Eremophila alpestris*), particularly at Camp Johnson, Colchester, VT, and the Franklin County Airport, Highgate, VT

This is a diverse, though certainly not exhaustive, list of research ideas. The success of each will depend on the researcher, landowner or agency motivation, and of course, funding source. Hopefully during at least part of my career I can help answer some of these questions, as well as many other questions yet unasked.

Appendices

Chapter 1

Appendix 1: Coefficient estimates from Logistic-exposure nest success model set (Table 1) for Savannah Sparrow and Bobolink nests in the Champlain Valley (NY, VT) 2002-2005.

	Para		TREATMENT				SPECIES		YEAR				TREATMENT*SPECIES							
	L1		EARLY	GRAZED	LATE	MIDDLE	BOBO	SAVS	2002	2003	2004	2005	EARLY		GRAZED		LATE		MIDDLE	
MODEL	L2	INT											BOBO	SAVS	BOBO	SAVS	BOBO	SAVS	BOBO	SAVS
	Est	3.62	-1.39	-0.70	-0.41	0.00	-0.63	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.38	0.00	0.96	0.00	0.00	0.00
treatment * species interaction	SE	0.20	0.21	0.24	0.24	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.33	0.00	0.30	0.00	0.00	0.00
$\omega_i = 0.57$	LCL	3.23	-1.80	-1.17	-0.88	0.00	-1.10	0.00	0.00	0.00	0.00	0.00	-0.24	0.00	-0.26	0.00	0.36	0.00	0.00	0.00
	UCL	4.01	-0.97	-0.24	0.05	0.00	-0.16	0.00	0.00	0.00	0.00	0.00	0.95	0.00	1.01	0.00	1.56	0.00	0.00	0.00
	Est	3.64	-1.75	-0.54	-0.19	0.00	0.00	0.00	-0.20	-0.59	-0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
treatment * year interaction	SE	0.21	0.26	0.32	0.30	0.00	0.00	0.00	0.27	0.27	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\omega_i = 0.27$	LCL	3.23	-2.26	-1.16	-0.78	0.00	0.00	0.00	-0.73	-1.12	-1.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	UCL	4.04	-1.25	0.08	0.41	0.00	0.00	0.00	0.34	-0.05	-0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Est	3.36	-1.06	-0.39	0.16	0.00	-0.17	0.00	0.00	0.05	-0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
treatment + species + year	SE	0.14	0.14	0.16	0.15	0.00	0.10	0.00	0.16	0.13	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\omega_i = 0.05$	LCL	3.08	-1.34	-0.70	-0.14	0.00	-0.37	0.00	-0.32	-0.21	-0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	UCL	3.64	-0.78	-0.09	0.46	0.00	0.03	0.00	0.32	0.31	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Est	3.32	-1.10	-0.44	0.15	0.00	-0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
treatment + species	SE	0.13	0.14	0.16	0.15	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\omega_i = 0.04$	LCL	3.07	-1.37	-0.74	-0.13	0.00	-0.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	UCL	3.56	-0.84	-0.13	0.44	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Est	3.26	-0.99	-0.35	0.16	0.00	0.00	0.00	-0.01	0.06	-0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
treatment + year	SE	0.13	0.13	0.15	0.15	0.00	0.00	0.00	0.16	0.13	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\omega_i = 0.04$	LCL	3.01	-1.25	-0.66	-0.13	0.00	0.00	0.00	-0.33	-0.20	-0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	UCL	3.52	-0.72	-0.05	0.46	0.00	0.00	0.00	0.31	0.32	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Est	3.22	-1.03	-0.39	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
treatment	SE	0.11	0.13	0.15	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\omega_i = 0.03$	LCL	3.01	-1.29	-0.69	-0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	UCL	3.44	-0.78	-0.10	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 1 continued:

	Par								TREATMENT*YEAR								SCALE
	L1	EARLY				GRAZED				LATE				MIDDLE			0.00
MODEL	L2	2002	2003	2004	2005	2002	2003	2004	2005	2002	2003	2004	2005	2003	2004	2005	0.00
treatment * species interaction	Est	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
$\omega_i = 0.57$	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	UCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
treatment * year interaction	Est	0.82	1.28	0.85	0.00	-0.46	0.31	0.34	0.00	0.00	0.66	0.62	0.00	0.00	0.00	0.00	1.00
$\omega_i = 0.27$	SE	0.37	0.35	0.34	0.00	0.64	0.41	0.40	0.00	0.00	0.41	0.40	0.00	0.00	0.00	0.00	0.00
	LCL	0.10	0.59	0.20	0.00	-1.71	-0.50	-0.45	0.00	0.00	-0.15	-0.17	0.00	0.00	0.00	0.00	1.00
	UCL	1.54	1.96	1.51	0.00	0.78	1.11	1.13	0.00	0.00	1.46	1.40	0.00	0.00	0.00	0.00	1.00
treatment + species + year	Est	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
$\omega_i = 0.05$	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	UCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Treatment + species	Est	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
$\omega_i = 0.04$	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	UCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
treatment + year	Est	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
$\omega_i = 0.04$	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	UCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
treatment	Est	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
$\omega_i = 0.03$	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	UCL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00

Appendix 2: Apparent nest success (ANS) was generally noticeably higher than logistic-exposure (L-E) nest success in the Champlain Valley (NY, VT) 2002-2005. The potential number of failed nests missed is the number of nests needed to attain the model nest success results given that the number of fledged nests was the true number of fledged nests.

						ANS		L-E NEST SUCCESS	
SPECIES	TREATMENT	YEAR	FAILED	FLEDGED	TOTAL	ANS	ANS AVG	L-E NS	L-E NS AVG
BOBO	GRAZED	2003	15	8	23	0.35	0.34	0.20	0.21
		2004	16	10	26	0.38		0.19	
		2005	3	4	7	0.57		0.22	
	EARLY	2002	8	0	8	0.00	0.02	0.06	0.05
		2003	10	0	10	0.00		0.06	
		2004	20	0	20	0.00		0.04	
		2005	2	1	3	0.33		0.04	
	MIDDLE	2003	27	2	29	0.07	0.39	0.31	0.32
		2004	16	7	23	0.30		0.29	
		2005	16	25	41	0.61		0.36	
	LATE	2002	32	35	67	0.52	0.64	0.45	0.46
		2003	7	19	26	0.73		0.48	
		2004	12	22	34	0.65		0.45	
		2005	5	22	27	0.81		0.47	
SAVS	GRAZED	2002	4	2	6	0.33	0.46	0.22	0.25
		2003	13	15	28	0.54		0.26	
		2004	29	20	49	0.41		0.24	
		2005	15	16	31	0.52		0.28	
	EARLY	2002	22	18	40	0.45	0.21	0.09	0.08
		2003	33	15	48	0.31		0.10	
		2004	102	10	112	0.09		0.07	
		2005	54	7	61	0.11		0.06	
	MIDDLE	2003	6	21	27	0.78	0.66	0.44	0.45
		2004	11	14	25	0.56		0.41	
		2005	8	12	20	0.60		0.50	
	LATE	2002	9	17	26	0.65	0.55	0.39	0.40
		2003	16	25	41	0.61		0.41	
		2004	20	28	48	0.58		0.39	
		2005	16	6	22	0.27		0.41	

Chapter 3

APPENDIX 1: Sample sizes for survival and recruitment analyses, including individuals banded in 2002-05 (*N*), and resight-recaptured in 2003-2006 (*R*) in the Champlain Valley of Vermont, USA and New York, USA. All WITH DISPERSERS and NO DISPERSERS analyses respectively only included data from Vermont, as off-treatment searches did not occur around the New York treatment fields.

			EARLY-HAYED		MIDDLE-HAYED		LATE-HAYED		GRAZED		TOTAL	TOTAL
SET	SPECIES	SEX	N	R	N	R	N	R	N	R	(N)	(R)
BREEDERS, ON PLOT	BOBOLINK	FEMALE	52	6	78	16	83	39	37	5	250	66
		MALE	38	12	37	18	54	31	10	3	139	64
	SAVANNAH SPARROW	FEMALE	81	40	43	15	65	24	57	26	246	105
		MALE	73	51	48	31	55	41	43	32	219	155
ALL ADULTS, ON PLOT	BOBOLINK	FEMALE	52	6	96	16	97	39	40	5	285	66
		MALE	39	13	53	18	83	30	16	3	191	64
	SAVANNAH SPARROW	FEMALE	105	40	53	15	77	24	67	26	302	105
		MALE	81	50	73	31	82	42	52	32	288	155
BREEDERS, WITH & NO DISPERSERS	BOBOLINK	FEMALE	52	6	60	9	57	27	37	5	206	47
		MALE	38	12	23	14	35	23	10	3	106	52
	SAVANNAH SPARROW	FEMALE	82	41	12	5	37	19	57	26	188	91
		MALE	73	51	14	9	25	21	43	32	155	113
ALL ADULTS, WITH & NO DISPERSERS	BOBOLINK	FEMALE	52	6	66	9	59	27	40	5	217	47
		MALE	39	13	34	14	52	22	16	3	141	52
	SAVANNAH SPARROW	FEMALE	105	40	16	5	42	20	67	26	230	91
		MALE	81	50	23	9	42	22	52	32	198	113