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Regional population viability of grassland songbirds: Effects of agricultural management

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ABSTRACT

Although population declines of grassland songbirds in North America and Europe are well-documented, the effect of local processes on regional population persistence is unclear. To assess population viability of grassland songbirds at a regional scale (~150,000 ha), we quantified Savannah Sparrow *Passerculus sandwichensis* and Bobolink *Dolichonyx oryzivorus* annual productivity, adult apparent survival, habitat selection, and density in the four most (regionally) common grassland treatments. We applied these data to a female-based, stochastic, pre-breeding 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, over 10 years, simulations showed a slightly declining or stable Savannah Sparrow population (mean bootstrap $\lambda = 0.99$; 95% CI = 1.00–0.989) and severely declining Bobolink population (mean bootstrap $\lambda = 0.75$; 95% CI = 0.753–0.747). Savannah Sparrow populations were sensitive to increases in all demographic parameters, particularly adult survival. However for Bobolinks, increasing adult apparent survival, juvenile apparent survival, or preference by changing habitat selection cues for late-hayed fields (highest quality) only slightly decreased the rate of decline. For both species, increasing the amount of high-quality habitat (late- and middle-hayed) marginally slowed population declines; increasing the amount of low-quality habitat (early-hayed and grazed) marginally increased population declines. Both species were most sensitive to low productivity and survival on early-hayed fields, despite the fact that this habitat comprised only 18% of the landscape. Management plans for all agricultural regions should increase quality on both low- and high-quality fields by balancing habitat needs, nesting phenology, and species' response to management.

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1. Introduction

Over the last 40 years, grassland bird populations have declined more rapidly than any other North American bird guild (Bollinger and Gavin, 1992; Knopf, 1994; Peterjohn and Sauer, 1999; Sauer et al., 2005); similar declines have been observed in Europe (Chamberlain et al., 2000; Donald et al., 2001, 2006). Although these trends are regularly cited, it is unclear how local processes occurring within an agricultural field affect regional population persistence. For example, in agricultural regions of the northeastern United States, population declines generally have been attributed to two divergent processes: the abandonment of farmland and subsequent forest succession; and, modernized grassland management, which involves cutting and harvesting hay throughout the growing season, as well as rotational grazing at varying intensities. Within an agricultural landscape, individual fields vary in management intensity, increasing variation in demographic rates among fields (Bollinger and Gavin, 1989; Perlut et al., 2006). However, it is unclear how variation in the composition of the landscape with respect to management-defined habitats affects regional population persistence.

Grassland management has changed dramatically over the last 40 years, including earlier first harvest dates and more frequent harvests in North America (Bollinger et al., 1990; Troy et al., 2005) and Europe (Vickery et al., 2001). In the northeastern United States, an increasing proportion of dairy farmers have advanced their initial cutting date from ~1 July to late-May or early-June – a vulnerable time in the breeding cycle, when most birds are in the later part of the incubation or early nestling stage (Perlut et al., 2006). Eggs and nestlings of ground-nesting birds 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, recent increases in harvesting frequency (Troy et al., 2005) result in a shorter window of opportunity (~35 days) for birds to renest in between haying events. 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 (Perlut et al., 2008). Birds breeding in intensively managed fields have ~25% lower apparent survival than those in less-intensively managed fields (Perlut et al., 2008). Modern hayfield management clearly presents a variety of threats to grassland bird populations.

Quantifying these events and how they occur across a region (>150,000 ha) is critical in maintaining or restoring grassland bird populations. More 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 in North America (Rodenhouse et al., 1995) and Europe (e.g. Freemark and Kirk, 2001; Wilson et al., 2005). 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 surprisingly 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 regions, 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 survival within each habitat. Moreover, to reverse declining population trends, optimal conservation strategies need to be identified, evaluated, and implemented. Potential strategies include increasing the total amount of grassland habitat within the breeding landscape, increasing habitat quality without decreasing 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 (*D. oryzivorus*) and Savannah Sparrows (*P. sandwichensis*), obligate grassland species breeding in the Champlain Valley of Vermont and New York, USA. We applied these data to a female-based, stochastic, pre-breeding, 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. A key assumption of the model is that birds could disperse among fields within the region, but the region itself was demographically closed. The research objectives were to: (1) model population growth for Bobolinks and Savannah Sparrows breeding in the Champlain Valley, and (2) assess six alternative landscape-level conservation strategies, targeted at different phases of the annual cycle and breeding ground habitat management, in terms of their efficacy in reversing or dampening population declines.

2. Materials and methods

2.1. Study area and experimental design

The Champlain Valley is a significant dairy farming region in the northeastern US (Fig. 1), and is surrounded by the Green Mountains to the east and the Adirondack Mountains to the west. The Champlain Valley contains 146,000 ha of managed grassland (US Department of Agriculture, 2007), which can be grouped into four general treatment-types:

1. *early-hayed* (*EH*): hayed between 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, typically after most birds have ended their reproductive season;
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.

2.2. Champlain valley agricultural management trends

To assess the relative proportion of each of the four treatment-defined habitat types within the Champlain Valley, we
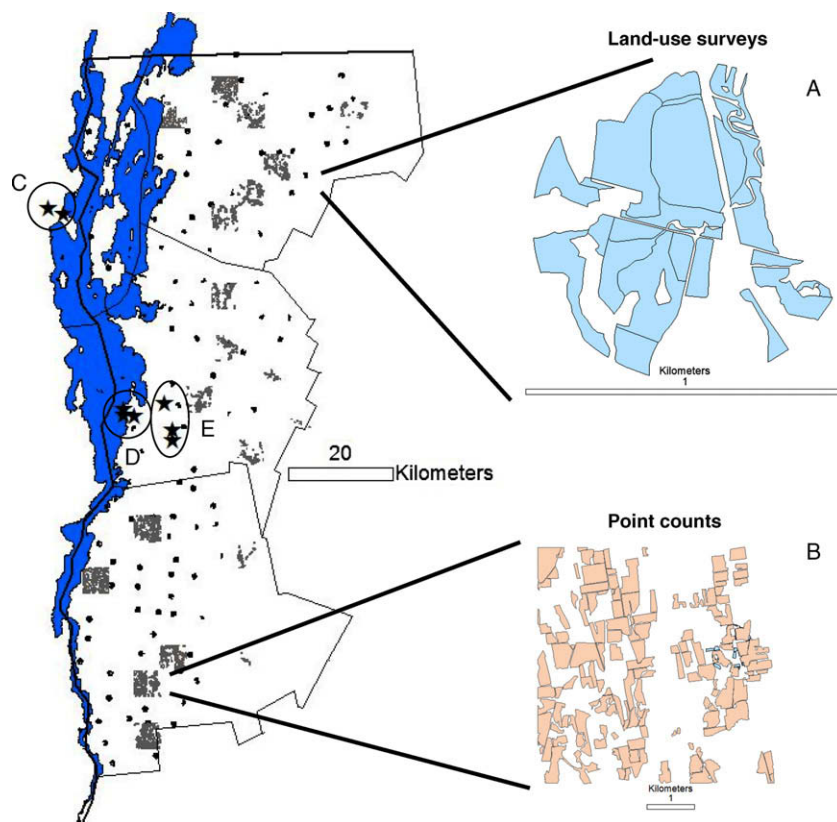
Fig. 1 – The Champlain Valley of Vermont and New York, USA, contains 146,000 ha of managed grasslands (US Department of Agriculture, 2007). Study areas include: agricultural land-use surveys (A); point counts within the center 4 km² section of each of the twenty 25 km² blocks (B); demographic study in (C) Cumberland Head, NY, (D) Shelburne, VT, and (E) Hinesburg, VT.

conducted agricultural land-use surveys from late-May to mid-July (Fig. 1A). 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, and grazing intensity (stocking rate). In 2003–2006 we expanded the survey to include the original 79 hayfields and pastures as well as all fields visible from the original road survey point (2002–2005 cutting data published in Perlut et al., 2006). The 2003–2006 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.

2.3. 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 km², randomly selected agricultural blocks within the Champlain Valley (Fig 1B). Blocks were stratified by the total percentage of area (ha) devoted to agriculture (range: 0.8–59%). Each year, between 17–19 May and 25–30 June, we conducted three fixed-radius (field boundary) 10-min point counts in every field located within the center 4 km² section of each 25 km² block

($n = 217$ fields; mean size: 6.1 ha, min: 0.9 ha, max: 42 ha; $n = 61$ early-hayed (388 ha), 67 middle-hayed (531 ha), 71 late-hayed (330 ha), 18 grazed (76 ha) fields). During each point count, between 05:00 am and 10:00, standing in the center of a given field, trained observers recorded the time at which individual Savannah Sparrow and Bobolink were first detected, as well as their sex (if known). 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 min intervals to determine detection probability. We then estimated density for each of the four treatment-defined habitats based on detections of 410 Bobolinks and 355 Savannah Sparrows. These raw survey data did not require adjusting, as the detection probability (p) was >0.93 and did not vary by treatment-type.

2.4. Demographic parameters

We assessed annual productivity, apparent survivorship, and recruitment on the four treatment-defined habitat types in three replicate 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; Fig. 1A–C). Each treatment field was a minimum of 10.5 ha (range: 13.2–38.3 ha; mean: 21.1 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 each year, we captured birds with mist-nets both passively and with play-back recordings, and placed unique combinations of three color bands and a single metal US Fish and Wildlife Service band on the legs of all adults of both species. Color-banded birds were resighted weekly throughout the breeding season. In mid-May we began intensive, season-long nest searching and nest monitoring (n = 733 Savannah Sparrow, 447 Bobolink nests). Nests were located by behavioral observations and by flushing incubating birds with bamboo sticks. 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 1–2 days until it either failed or the nestlings fledged. Nestlings of all known nests were banded with a single metal US Fish and Wildlife band on day 6 or 7. One week after fledging or failing, we relocated color-banded adult females to monitor renesting.

Annual productivity was estimated as the number of female offspring produced in a breeding season by a single adult female; productivity was evaluated for a minimum of 41 females in each treatment for both species (Table 1). This model assumes a balanced nestling sex ratio (Wheelwright and Seabury, 2003).

Apparent survival (φ) and recruitment (f) were estimated with the Pradel (1996) survival and recruitment model option in MARK (White and Burnham, 1999). Apparent survival is the probability that an individual bird survives and returns to an area of interest (treatment field), 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 immigration. 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 (Perlut et al., 2008). 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 (Perlut et al., 2008; Table 1). However, increased search efforts beyond the local scale evaluated by Perlut et al., 2008 (>1.5 km) are expected to result in marginal increases in apparent survival because 87–91% of Savannah Sparrows and Bobolinks select breeding sites within 300 m of previous breeding locations (Fajardo et al., unpublished data). From these rates, we selected treatment- and species-specific survival estimates to use as baseline survival estimates in the population model. For Savannah Sparrows, we used estimates for breeders with resighting observations limited to the study site; these estimates had highest value in three of the four treatments and also had the lowest standard errors (Perlut et al., 2008). 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, remain in the Champlain Valley, and not be detected.

Our data did not allow estimation of juvenile (post-parental care) survival because most fledglings do not return to the

Table 1 – Demographic and landscape values used to parameterize model				
	Early-hayed	Rotationally-grazed	Middle-hayed	Late-hayed
Amount of habitat (ha)	26,192	32,120	36,442	51,246
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 (# female young/female/year)	0.65 ± 0.07 (n = 289)	1.06 ± 0.11 (n = 141)	1.65 ± 0.26 (n = 63)	1.40 ± 0.18 (n = 152)
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 (*f*)	0.32 ± 0.06	0.33 ± 0.06	0.24 ± 0.05	0.25 ± 0.02
Scaled selection coefficient	0.263	0.265	0.272	0.201
Bobolink				
Female density (per ha)	0.25	0.20	0.33	0.36
Annual productivity (# female young female/year)	0.02 ± 0.02 (n = 41)	0.88 ± 0.15 (n = 60)	1.12 ± 0.11 (n = 98)	1.40 ± 0.11 (n = 162)
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 (*f*)	0.38 ± 0.10	0.30 ± 0.06	0.41 ± 0.11	0.37 ± 0.10
Scaled selection coefficient	0.261	0.253	0.284	0.202

Variance estimates may overestimate true annual variability in model parameters because they include both process and sampling variation. Juvenile survival is assumed to be 50% of the highest adult survival estimate. Error values indicate standard error.

same field in which they were born (Greenwood and Harvey, 1982; Fajardo, unpublished data). For simplicity, we assumed that juvenile survival did not vary with the grassland treatment-type from which they fledged (but see Lloyd and Martin 2005). Therefore, juvenile survival was modeled as 50% of highest adult survival from the late-hayed habitat (Vierling, 2000).

2.5. 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 1000 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 differed only with respect to survival and gaining a territory in a habitat (see below), but not with respect to breeding success. Population censuses 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 estimated across years. Because survival estimates are probabilities ranging between 0 and 1, 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 was initiated 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–F). The four treatments were then populated with all females who survived from 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, unpublished 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
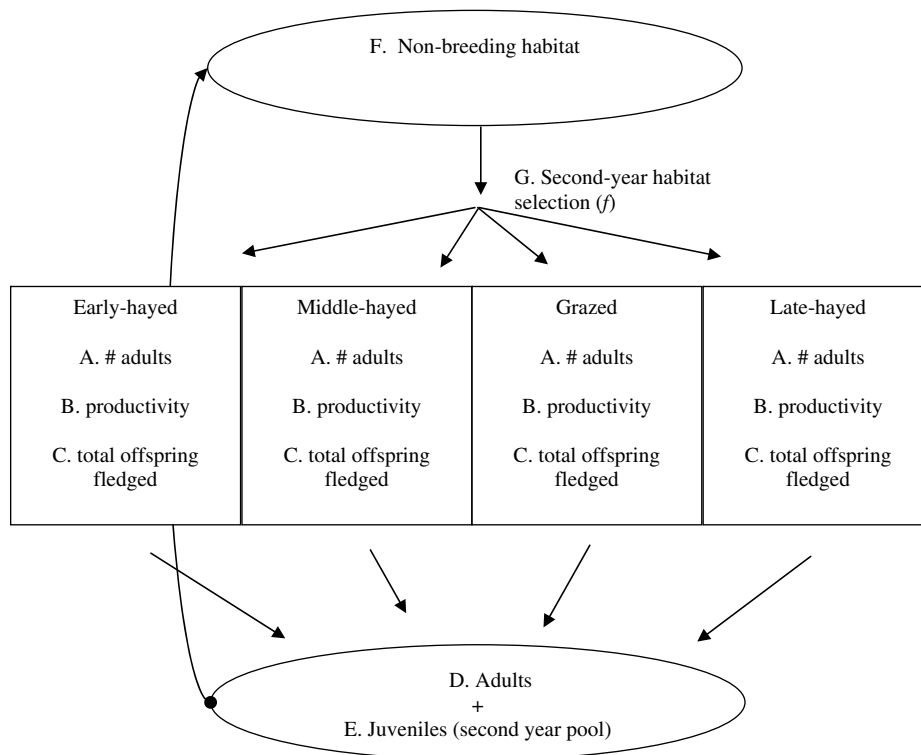

Fig. 2 – Schematic for this female-specific, stochastic, landscape-level, population model.

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 assumed 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 1, two in habitat 2, two in habitat 3, and one in habitat 4. Selection preference is likely determined by both structural cues (Perlut et al., 2006) and 'social 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 related 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 immigration. Thus, a small f indicated that the proportion of second-year recruits is comparatively low (low habitat preference), while a high f indicated that the proportion of second-year recruits is high (high habitat preference). We acknowledge that habitat preference is difficult to determine (Robertson and Hutto 2006) and that the recruitment parameter of the Pradel model is not synonymous with a coefficient of habitat preference; it is more of an indicator of realized selection. Because neither of these species shows age-specific plumage, we further acknowledge that not all individuals that are recruited into a breeding population are second-year recruits. For instance, bobolinks may disperse to new fields after haying. However, because we banded the vast majority of adults on each treatment field, we are confident that new birds are recruits and not previous breeders to that field that were not detected. 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 Perlut et al. (2008)).

After the second-year pool was distributed into respective treatments by the selection coefficients, these 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 level that did not constrain population growth. 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 (which did not occur).

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 renested post-harvest (Perlut et al., 2006). How-

ever, 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, unpublished data). As a result, the model redistributed 60% of the initial, early-hayed Bobolink population throughout the remaining three treatment-types within the same breeding season, according to the selection coefficients. These birds bred in the treatment to which they moved.

The final breeding population for each treatment was the sum of the number of surviving adults and second-year recruits, including 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.

2.6. Conservation strategies

After running simulations with all demographic parameters held at baseline values, we evaluated six conservation strategies targeted at different life history stages or management options that could alter population trends. 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; productivity and survival were high) 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 (both early-hayed and grazed; productivity and survival were low) 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 re-growth, and may therefore act as a deterrent in habitat selection to these species; but thatch can be removed by farmers late in the season, increasing attractiveness (Perlut, unpublished data). Attractiveness affects density, where an increase in *f* correspondingly increased density. 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 to 1.0.

3. Results

3.1. *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).
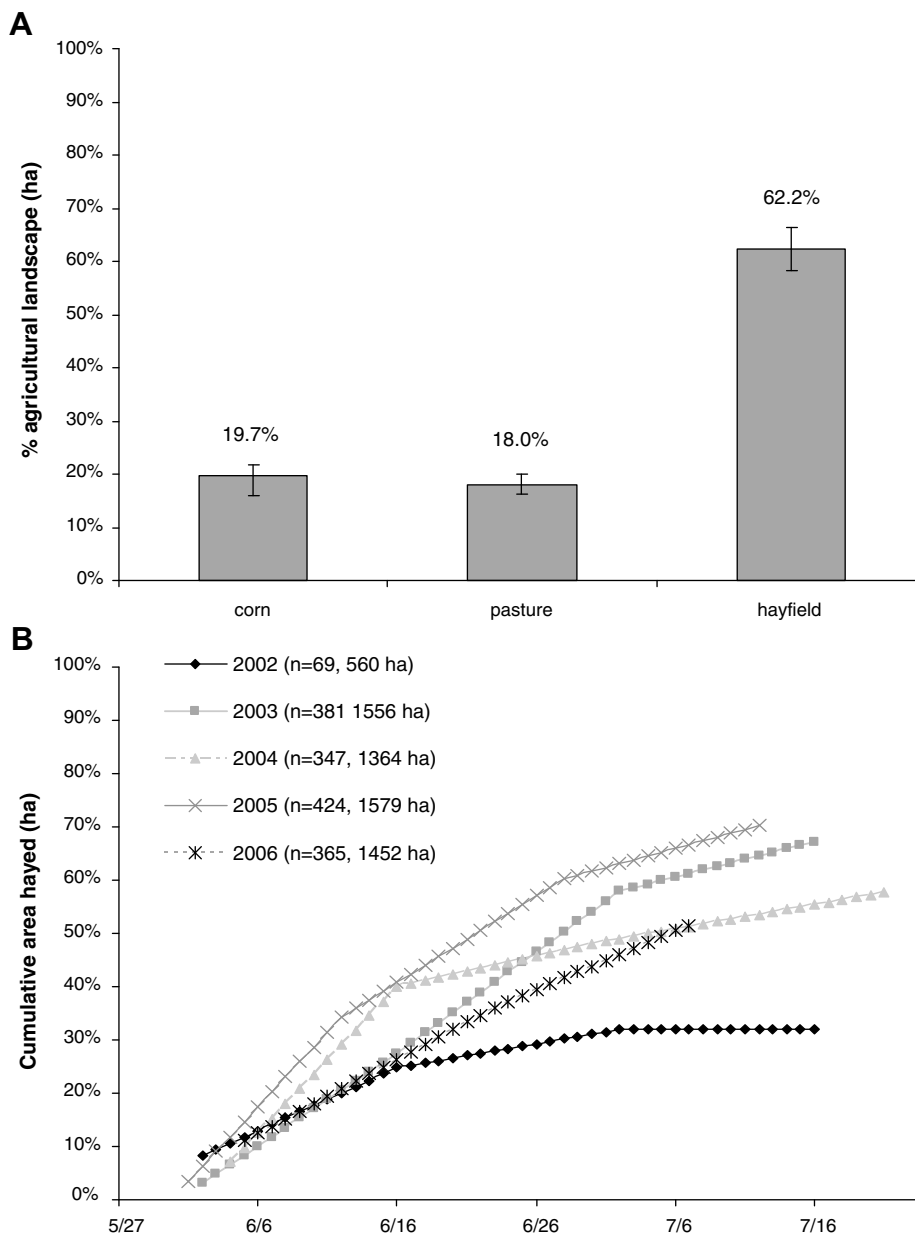

Fig. 3 – Agricultural land-use survey (A) of the Champlain Valley of Vermont and New York, USA, 2003–2006 (2186–2521 ha/year), showed a dominance of grass-based farming. Cumulative area hayed (B), Champlain Valley, 2002–2006.

3.2.   Distribution of birds across habitats

Female Savannah Sparrow density was similar across early-hayed and late-hayed fields, as well as across grazed and middle-hayed fields (Table 1). Female Bobolink density showed greater variation among treatments, and was highest in late-hayed fields and lowest in grazed fields (Table 1).

3.3.   Demographic parameters

For both species, annual productivity was closely associated with management intensity and similar between species. 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).

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, for recruited females was lowest on late-hayed fields, and nearly consistent for early-hayed, grazed, and middle-hayed fields for both species (Table 1).

3.4.   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). Over 10 years, Savannah Sparrow and Bobolink populations declined by 7.8% (95% CI = 2.9–12.7%) and 94% (95% CI = 48.2–140.2%), respectively (Table 2). Comparatively, BBS data would show a 2% Savannah Sparrow and 28% Bobolink population decline over 10 years. Thus the model rates of decline are between 3.3 and 3.9 times more severe than the BBS trends indicate; these differences are due, in part, to using apparent survival in the models instead of true survival and because the model simulated a closed system and did not account for immigration into the Champlain Valley, as the BBS data would detect (see Section 4).

3.5.   Conservation strategies

3.5.1.   Strategy 1
For both species, model results suggest that conservation strategies outside the breeding period are important in population persistence. Given the baseline values for demographic parameters and management practices, 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, though not as dramatically. For Bobolinks, increasing adult or juvenile survival decreased the rate of population decline; the effects were only slightly weaker for Savannah Sparrows (Table 2; Fig. 4).

3.5.2.   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. First, density (total number of females per ha) was not a function of habitat area, so the number of adults per unit area did not necessarily respond to increased habitat amount. Second, the habitat selection coefficient (recruitment) remained constant, such that individuals still selected low-quality habitats even though high-quality habitats were more available.

3.5.3.   Strategies 4 and 5
The strongest effect, causing Savannah Sparrow populations to grow and dampening Bobolink declines, occurred when we kept total grassland habitat the same but 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 the Savannah Sparrow population to increase by 42% and Bobolink population declines slowed by 8% over 10 years, as compared to baseline declines. Substituting middle-hayed values for early-hayed rates showed even greater effects on population growth—over 10 years, Savannah Sparrow populations increased by 124% and slowed Bobolink population decline by 11%, as compared to baseline declines (Fig. 4).

3.5.4.   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).

4.   Discussion

Given current land-use patterns and no immigration from other regions, these results strongly suggest that grassland songbird populations, especially Bobolinks, are currently not viable in the Champlain Valley. These results are consistent with the Breeding Bird Survey trends (Sauer et al., 2005) and elucidate the mechanisms by which populations are declining. Early-hayed and rotationally-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 effects of population sources, middle- and late-hayed habitats, which composed 60% of the available grass-based habitat.

| | Savannah Sparrow | | | | | | Bobolink | | | | | |
| Conservation strategies | 10 years | | | 25 years | | | 10 years | | | 25 years | | |
	Mean (%)	95% Upper (%)	95% Lower (%)	Mean (%)	95% Upper (%)	95% Lower (%)	Mean (%)	95% Upper (%)	95% Lower (%)	Mean (%)	95% Upper (%)	95% Lower (%)
Baseline	−7.8	−2.9	−12.7	−13.1	−5.3	−20.9	−94.2	−48.2	−140.2	−99.9	−25.5	−174.3
Strategy 1												
Δ Adult survival												
5%	52.6	18.4	86.8	174.4	75.1	273.6	−87.7	−46.0	−129.5	−99.7	−28.4	−171.0
10%	143.4	53.5	233.4	287.2	74.5	499.9	−81.2	−44.5	−117.8	−99.0	−31.9	−166.1
25%	302.3	52.2	552.5	302.7	14.7	590.6	−41.5	−25.8	−57.2	−78.6	−38.8	−118.4
Δ Juvenile survival												
5%	9.8	4.0	15.7	37.5	17.4	57.7	−90.6	−46.1	−135.1	−99.8	−26.5	−173.2
10%	29.3	10.3	48.2	97.6	43.8	151.5	−89.0	−46.1	−131.9	−99.8	−27.6	−171.9
25%	112.7	40.9	184.5	282.2	91.8	472.7	−81.9	−44.9	−118.8	−99.1	−31.7	−166.5
Strategy 2												
Δ High quality grass habitat												
5%	−6.7	−3.0	−10.5	−9.1	−3.4	−14.8	−92.2	−46.2	−138.2	−99.9	−25.5	−174.3
10%	−4.5	−2.1	−6.9	−9.1	−4.6	−13.5	−92.0	−46.3	−137.8	−99.9	−25.7	−174.1
25%	−2.7	−1.4	−4.1	−9.2	−5.9	−12.5	−91.9	−46.8	−136.9	−99.9	−26.1	−173.7
Strategy 3												
Δ Low quality grass habitat												
5%	−7.3	−2.5	−12.0	−13.9	−6.2	−21.6	−92.0	−45.8	−138.2	−99.9	−25.4	−174.4
10%	−7.6	−2.9	−12.4	−13.6	−5.9	−21.3	−92.1	−45.5	−138.7	−99.9	−25.2	−174.6
25%	−10.3	−4.0	−16.7	−14.6	−5.2	−23.9	−92.3	−45.3	−139.3	−99.9	−25.0	−174.8
Strategy 4												
SWITCH: EH = G												
ƒ + productivity	33.9	11.7	56.2	118.0	52.5	183.5	−86.6	−45.2	−128.0	−99.6	−28.7	−170.5
Strategy 5												
SWITCH: EH = MH												
ƒ + productivity	116.1	43.1	189.0	282.1	89.8	474.3	−83.0	−43.7	−122.3	−99.2	−30.2	−168.1
Strategy 6												
Δ Selection for late-hayed												
5%	−5.3	−1.9	−8.6	−6.2	−1.7	−10.7	−91.6	−45.7	−137.5	−99.9	−25.7	−174.1
10%	−1.6	0.0	−3.3	1.5	1.8	1.3	−91.3	−45.6	−137.1	−99.9	−25.8	−174.0
25%	5.9	3.3	8.4	23.2	11.3	35.0	−90.7	−45.4	−136.0	−99.8	−26.1	−173.6

The first row illustrates the baseline population growth, with which to compare all other analyses. Apparent survival is indicated as φ; EH, early-hayed; MH, middle-hayed; G, grazed.

Table 2 – Population viability with respect to conservation strategies
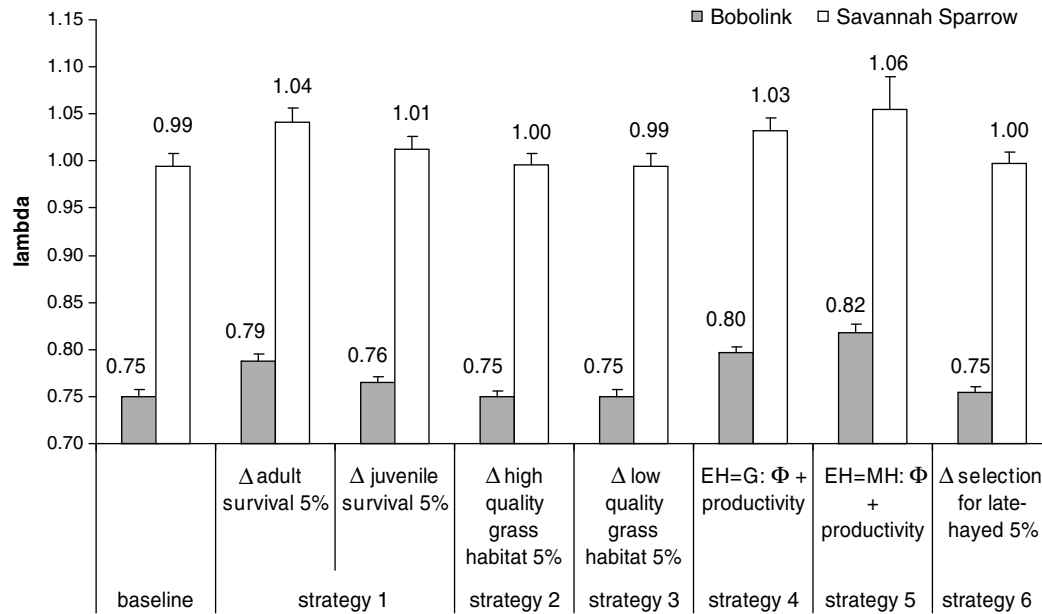
Fig. 4 – Mean lambda (N_{t+1}/N_t) values for 25 years of simulations. Lambda values of 1 indicate stable populations, while values <1 indicate declining populations, and values >1 indicate growing populations. EH, early-hayed; MH, middle-hayed; G, grazed error bars indicate standard deviation. Strategy 1 tested population sensitivity to changes in treatment-specific adult and juvenile survival. Strategy 2 simulated an increase in high-quality habitat (middle- and late-hayed; productivity and survival were high). Strategy 3 returned high-quality habitats to their base size and increased the amount of low-quality habitats (both early-hayed and grazed; productivity and survival were low). 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.

Although our modeling results are consistent with the BBS declines, they suggest a more severe decline than the BBS reveals. The discrepancy could be due to two factors. First, our model assumed a closed regional 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. 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 or habitat destruction (from land-use change), female Bobolinks may become nomadic, both within and between-years, searching for males whose territories hold appropriate resources (Greenwood, 1980). Although apparent survival estimates accounted for short distance dispersal (<1.5 km; Perlut et al., 2008), the potential to disperse at larger scales biases apparent survival rates downward. This model treats individuals who survived and dispersed >1.5 km as dead. By redistributing birds from early-hayed fields and allowing them to breed, this model accounted for some of the biases associated with decreased survival rates as a result of dispersal. Nonetheless, more rigorous

estimates of direct survival and dispersal distances would enhance the model.

4.1. Conservation strategies

Although consideration of these caveats is important, our models nonetheless justify immediate conservation planning in agricultural landscapes. Planning should evaluate how to improve birth and survival rates in the current landscape composition, particularly in early-hayed fields, as well as the implications of future changes to the type and amount of habitat. Below, we discuss four land-use change scenarios that may characterize grass-based agricultural landscapes in the future.

In the first scenario, the current trend in Vermont agriculture towards grass-based, pasturing, and/or organic dairy farming continues. Here, some portion of corn is converted to pasture. Since pastures comprise 18% of the entire agricultural landscape and 22% of the grass-based landscape, increases in the proportion or total acreage of this habitat type may be critical for land managers and conservation funding, particularly if pasturing-based dairying increases in the landscape. Given current estimates of demographic levels in pastures, increasing acreage alone will neither alleviate nor hasten population declines (Fig. 4). However, 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. Further research on the effects of variation in grazing practices on songbird demography would be useful in population models.

Second, increasing human populations may cause an increase in rural single family homes built on large (formerly agricultural) parcels. In urbanizing landscapes, conversion of grasslands to housing developments will necessarily lead to decreased population size if remaining habitats are no longer suitable. 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 minimize 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 where annual productivity and annual survival is high. 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). However, 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 international 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, can have positive effects on songbird abundance (Murray et al., 2003), including Savannah Sparrows and Bobolinks (Roth et al., 2005), with no negative effects on reproduction (Murray and Best, 2003). Although switchgrass is not currently sown in Vermont for forage, it has local potential as a biofuel (S. Bosworth, pers. comm.); nonetheless, 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 positively. 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 to continue increasing in size. Here the amount of corn habitat increases, as the percentage of corn silage fed to herds on larger farms continues to increase.

This trend could result in both a conversion of idle grassland to corn, as well as a (∼6–8 year) rotation with alfalfa, also, low-quality breeding habitat. Although not specifically modeled, this scenario would likely result in population declines greater than those in simulated in scenario 4 (increase in proportion of low-quality habitat), as corn is rarely used by breeding birds.

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 and survival. 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 less attractive initially because the remaining grass (both stubble and thatch) from the previous year suppresses early growth. Therefore, for Bobolinks and Savannah Sparrows, one possibility for increasing attractiveness of late-hayed fields is to remove the previous year's thatch; it is important to note that grassland species with different habitat needs may not respond similarly. Again, these field's economic values may sharply increase if grass-based ethanol becomes a viable product.

While the benefits of middle- and late-hayed fields as source habitats are obvious, these management options are not viable for active farms, as managers are unable to convert their productive early-hayed fields to late-hayed fields (see Troy et al., 2005). This constraint is important, as these models clearly show that population decline is driven by demographics in early-hayed fields. Dairy farmers aim aggressively 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 should fulfill both farmer's forage requirements and bird's reproductive 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), we suggested a delayed second cut that should be considered to improve songbird demography on early-hayed fields. First, the entire harvest process, including cutting, collecting, and removing hay, as well as nutrient management, should be completed prior to 31 May. The earlier harvest will lessen the energetic investment adults make before haying-mediated nest failure, and will increase the probability of Bobolinks repopulating hayed fields. The earlier harvest followed by a 65 day cutting interval can support songbird reproductive needs. In this plan, farmers get a moderate volume, high protein first-crop, and a high volume, comparatively lower protein second-crop. Savannah Sparrow's 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, select a mate, renest (∼26–29 days), and care for fledglings. A 3 year pilot project based around this

plan is being tested in Vermont in 2007–2009 by the National Resource Conservation Service (NRCS, 2007) aimed at active hayfields, >20 acres (8.1 ha) composed of at least 50–70% grass. Farmers and landowners can sign 3 year contracts where in return for delayed second cuts they receive $100 per acre per year. While farmer interest in such a plan is currently being evaluated, 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. Stabilizing population declines for grassland species is dependent on diverse management and conservation plans, as no single conservation program will conserve species throughout agricultural landscapes (Kleijn et al., 2001; Araújo et al., 2008).

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