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Habitat Use Patterns of Bobolinks and Savannah Sparrows in the Northeastern United States

Utilisation de l’habitat par le Goglu des prés et le Bruant des prés dans le Nord-est des États-Unis

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ABSTRACT. In the northeastern United States, grassland birds regularly use agricultural fields as nesting habitat. However, birds that nest in these fields regularly experience nest failure as a result of agricultural practices, such as mowing and grazing. Therefore, information on both spatial and temporal patterns of habitat use is needed to effectively manage these species. We addressed these complex habitat use patterns by conducting point counts during three time intervals between May 21, 2002 and July 2, 2002 in agricultural fields across the Champlain Valley in Vermont and New York. Early in the breeding season, Bobolinks (*Dolichonyx oryzivorus*) used fields in which the landscape within 2500 m was dominated by open habitats. As mowing began, suitable habitat within 500 m became more important. Savannah Sparrows (*Passerculus sandwichensis*) initially used fields that contained a high proportion of suitable habitat within 500 m. After mowing, features of the field (i.e., size and amount of woody edge) became more important. Each species responded differently to mowing: Savannah Sparrows were equally abundant in mowed and uncut fields, whereas Bobolinks were more abundant in uncut fields. In agricultural areas in the Northeast, large areas (2000 ha) that are mostly nonforested and undeveloped should be targeted for conservation. Within large open areas, smaller patches (80 ha) should be maintained as high-quality, late-cut grassland habitat.

RÉSUMÉ. Dans le Nord-est des États-Unis, les oiseaux de prairie nichent régulièrement dans les champs agricoles. Cependant, la nidification de ces oiseaux échoue souvent en raison des activités agricoles, comme le fauchage et le broutement. Il s’avère donc nécessaire de connaître les caractéristiques spatio-temporelles relatives à l’utilisation de l’habitat pour gérer efficacement ces espèces. Nous avons examiné ces patrons complexes de l’utilisation de l’habitat au moyen de dénombrements par points d’écoute effectués à trois périodes entre le 21 mai et le 2 juillet 2002, dans des champs agricoles de la vallée de Champlain dans les États du Vermont et de New York. Tôt dans la saison de nidification, les Goglus des prés (*Dolichonyx oryzivorus*) ont utilisé des champs situés dans des paysages où les milieux ouverts dominaient dans un rayon de 2 500 m. Lorsque le fauchage a commencé, l’habitat propice dans un rayon de 500 m est devenu plus important. Les Bruants des prés (*Passerculus sandwichensis*) ont utilisé des champs qui offraient un habitat propice dans un rayon de 500 m dès le début de la saison. Une fois le fauchage terminé, les caractéristiques des champs (c.-à-d. la dimension et la quantité de lisières boisées) sont devenues davantage déterminantes. Les deux espèces ont agi différemment face au fauchage : les bruants ont utilisé les champs fauchés et les champs non fauchés de façon égale, tandis que les goglus étaient plus nombreux dans les champs n’ayant pas subi de fauchage. Dans les zones agricoles du Nord-est, les vastes régions (2 000 ha)

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qui ne sont ni boisées ni développées devraient être considérées à des fins de conservation. Dans les grands milieux ouverts, des parcelles plus petites (80 ha) – pour lesquelles le fauchage serait retardé – devraient être conservées en tant que milieux de prairie de qualité supérieure.

Key Words: *Champlain Valley; Dolichonyx oryzivorus; grassland birds; habitat use; hayfields; Passerculus sandwichensis*

INTRODUCTION

Significant declines in grassland bird populations have occurred over the past several decades (Samson and Knopf 1994, Herkert 1995, Peterjohn and Sauer 1999). In many areas, declines have been attributed to changes in the timing and frequency of hay harvest on agricultural fields (Frawley 1989, Warner and Etter 1989, Bollinger et al. 1990, Askins 1993, Giuliano and Daves 2002). In the past, hayfields may have been a suitable surrogate for natural grasslands by providing high-quality nesting habitat for grassland birds (Graber and Graber 1963, Laughlin and Kibbe 1985). However, hay harvest is now conducted earlier and more frequently in the nesting season than even 10 years ago (Troy et al. 2005). Haying destroys nearly all nests and greatly reduces fledgling survival (Frawley 1989, Bollinger et al. 1990, Perlut et al. 2006).

In New England, hayfields are relatively abundant and the amount of natural and undisturbed grasslands is limited. Thus, in most parts of this region, human-modified habitats provide the majority of nesting habitat for grassland birds. Because hayfields undergo regular disturbance by mowing and the nests in those fields are subsequently destroyed, it is important to understand what features attract birds to nest in particular hayfields, both at the time of initial settlement in the spring and after mowing. A bird that initially nests in a hayfield and whose nest is subsequently destroyed has not necessarily failed in reproduction for the season. Many birds will attempt to renest after a failed attempt (Perlut et al. 2006). However, birds that nest in fields that are mowed are confronted with habitat conditions that are dramatically different in vegetation structure (Frawley and Best 1991). If birds attempt another nest, they may either stay in the mowed field or select a different field for renesting. This habitat selection process may or may not be influenced by the same factors used in the initial selection process. Thus, in this temporally dynamic landscape, cues used for habitat selection may change throughout the nesting season and may have important implications for management and conservation. In this study, our objectives were to (1) determine the relative importance of local and landscape factors in influencing the distribution of Bobolinks (*Dolichonyx oryzivorus*) and Savannah Sparrows (*Passerculus sandwichensis*), (2) determine whether the influence of these factors remained constant over the nesting season, and (3) investigate the response of these species to mowing. Specific hypotheses and predictions are stated in *Methods: Model set*.

METHODS

Study area

Field work was conducted in the Champlain Valley of Vermont and New York (US). The Champlain Valley is a relatively flat region surrounding Lake Champlain and is bounded on the east by the Green Mountains (VT) and on the west by the Adirondack Mountains (NY). The study was confined to Addison, Chittenden, Franklin, and Grand Isle counties of Vermont, and Essex and Clinton counties in New York.

This area was historically forested, but most of the forested habitat was cleared for agriculture following Euroamerican settlement in the 1700s and 1800s (Albers 2000). Today there are about 146,000 ha in managed grasslands in the Champlain Valley (National Agricultural Statistics Service, http://www.nass.usda.gov/census/). The primary use of these grasslands is for forage production for the dairy industry and to a lesser degree for beef cows, horses, and sheep. Most fields are actively managed at varying degrees of intensity; hayfields are mowed one to four times per year, and various stocking rates are practiced on pastures.

We randomly located approximately 250 points on a GIS layer of the study area. Nearest to each random location, we located a field that met two criteria: perennial herbaceous cover and current or recent use for agricultural purposes. Nearly all fields were on private property. Ultimately we used 142 fields that met our criteria and for which permission to collect data was granted from landowners. All study fields were at least 2 km apart. Fields were visited three times between May 21 and July 2, 2002.

Bird sampling

Three experienced observers conducted point counts at one permanent survey station at each field. We chose to use point counts in order to maximize the regional coverage of the area sampled. The survey station was located at a random distance into the field from the midpoint of the road side of the field, and a GPS reading was recorded to relocate each point. We visited fields at approximately 2-wk intervals and rotated observers among visits. Visit 1 approximately corresponded to arrival and incubation, and visit 2 to incubation and early fledging. By the end of visit 3, approximately 50% of nests had fledged on an uncut field within the study area (Perlut et al. 2006). At each point and for each visit, an observer conducted one 10-min point count divided into five 2-min intervals. Birds were assigned to an interval based on when they were first detected. Most point counts were conducted between sunrise and 09:00 EST in favorable weather conditions (light to no winds, light to no rain, and negligible fog). We recorded all male and female grassland birds detected. We specifically noted if each bird was within 50 m of the sampling point or beyond the 50 m but still within the field being sampled.

Detection probability

We used a removal method (Farnsworth et al. 2002) to test for differences in bird detection probabilities (p) within 50 m of the sampling station based on environmental or researcher variation. We compared 12 single covariate models, one intercept-only model, and a global model including all 12 covariates. Each model evaluated the effect of a single covariate (continuous or categorical) or multiple covariates (global model) on p. Nine covariates were thought to influence bird abundance and distribution (HABITAT$_{\text{SAVS/BOBO}}$, PROPOPEN500, WOODEDEDGEDENSITY500, PROPOPEN2500, WOODEDEDGEDENSITY2500, AREA, CUT, VEGHEIGHT, and FIELDPERIMETER; see below and Table 1 for summary of variable descriptions). These covariates were included because our primary interest was to document habitat use and we needed to control for potential differences in p among habitats. Three covariates were thought to influence bird singing behavior or observer effects (time of day, date, and observer). We used Huggin's closed capture removal models in program MARK (White and Burnham 1999) to estimate $\hat{p}$ and model fit for each of the 14 candidate models. Using this procedure, we obtained a model averaged $\hat{p}$ for each point count (Burnham and Anderson 2002). Male Bobolinks had $\hat{p} > 0.99$ for all site-date combinations; male Savannah Sparrows had an averaged $\hat{p}$ of 0.945. Importantly, we found little evidence that detection probabilities changed over the course of the breeding season for either species. Thus, the lack of change in detection probability over the course of the breeding season, overall high detection probabilities for both species, and the fact that our model fitting was restricted to male birds within 50 m of the count location led us to conclude that the unadjusted counts of males within 50 m of the sampling station were sufficiently accurate for our modeling analyses. Other authors have reached similar conclusions for point counts of grassland songbirds (Rotella et al. 1999).

Vegetation sampling

At each survey station and during each visit, we sampled vegetation at three locations, each 3 m from the point count location and separated by 120°. A 20 × 60-cm Daubenmire (1959) frame was placed in the vegetation. We estimated percent cover (adding to 100%) in grass (*Poaceae* family), alfalfa (*Medicago sativa* L.), and birdsfoot trefoil (*Lotus corniculatus* L.), clover (*Trifolium* spp.), dandelion (*Taraxacum officinale*), forb, woody vegetation, litter, bare ground, and water. At each of the four corners of the frame, we measured litter depth and the maximum vegetation height. The three (percent cover) or 12 (litter depth, vegetation height) measurements per field were averaged for each visit. Because all fields were actively or recently managed, vegetation characteristics appeared fairly uniform. The apparent uniformity of the fields combined with logistical constraints led us to circumvent more in-depth vegetation measurements. On each visit, the observer noted whether the field had been mowed since the previous visit, and based on vegetation regrowth, estimated number of days since the field was cut (CUT, DAYSSINCECUT; Table 1). We also noted if the field was being actively grazed. However, because we had relatively few pastures and livestock grazing was not managed consistently among pastures or over time during our sampling period, we did not evaluate effects of grazing per se. We assumed that any effects of grazing would be manifested in the vegetation differences.

Landscape data

We obtained landscape data from two data sources. First, we ground-truthed and digitized the area within 500 m of each survey station into a GIS using 23 cover types. We used Digital Orthophoto Quadangles (DOQs; 1:5000) as templates. We converted the digitized data to raster data with 1-m grid cells, matching the grid cell size of the DOQs used for digitizing. We used Fragstats (McGarigal et al. 2002) to derive the proportion of the landscape in each cover type and the edge density of wooded cover types within 500 m (WOODEDEDGEDENSITY500; Table 1).

We used the digitized layer to calculate two field-level variables for each field: field area in hectares (AREA) and the proportion of the field that was bordered by woody vegetation (WOODEDPERIMETER; Table 1). We defined AREA by using a narrow interpretation of the definition from Bakker et al. (2002) as "the grassland area contiguous with the survey area that was of the same cover type and condition as the survey area." For example, all roads were considered to divide a field. Fields divided by fence lines or shrub lines were only considered separate if they were managed differently. This definition may fail to match the birds' perception, but it is useful from a management perspective.

To address the landscape at a greater distance (2500 m), we used a second landscape data source: the Vermont Land Cover/Land Use (LCLU) data available from the Vermont Center for Geographic Information (http://www.vcgi.org). These data were derived from LANDSAT Thematic Mapper Imagery obtained between 1991 and 1993 and have a resolution (grid cell size) of 25 m. We reclassified the LCLU cover types as agricultural, forested, developed, residential, transportation/utilities, and water. From this reclassified layer, we used Fragstats to derive the proportion of the landscape not forested and not developed (PROPOPEN2500) and the forest edge density (WOODEDEDGEDENSITY2500) within 2500 m of each survey point (Table 1).

Analysis

We used two approaches to assess temporal changes in habitat associations with Savannah Sparrow and Bobolink abundances. For our first approach, we used an information theoretic approach to construct and compare models describing hypotheses that relate the abundance of Bobolinks and Savannah Sparrows to predictor variables. We used this approach so we could compare both single-process and multiple-process variables in relation to a null model for each visit and thus assess the relative support for each hypothesis considered. We modeled Bobolinks and Savannah Sparrows separately. Our response variable was the number of males within 50 m of the sampling point. All models with multiple variables were additive models (indicated by + between variable names). Hypotheses are indicated in *italics*. Variable names are indicated in CAPS.

Following our model ranking, we further investigated patterns in our data by determining Spearman rank correlations between each habitat variable and bird abundance for each visit. We expected strength and statistical strength of the correlation coefficients to vary over each visit if habitat associations and thus bird preferences changed over the course of the breeding season. We report nominal *P*-values throughout. This approach allowed us to examine each variable individually over each visit.

Model set

Available Habitat (H1): $\text{HABITAT}_{\text{SAVS/BOBO}}$. This hypothesis follows from the argument of Andrén (1994), who suggested that landscape composition of potential habitat is generally more important than configuration. Specifically, this model focused on nonforested habitats that Savannah Sparrows or Bobolinks might use for breeding.

Near Landscape Openness (H2): PROPOPEN500 + WOODEDEDGEDENSITY500. This hypothesis follows from the assertion by Walk and Warner

Table 1. Derivations of variables used in Poisson regression models, correlation analysis, and detection probability modeling of male Savannah Sparrow and male Bobolink abundance. Point counts were conducted from May 21 to July 2, 2002 in agricultural fields in the Champlain Valley of Vermont and New York.

HABITAT$_{SAVS}$: the sum of the proportions of the landscape within 500 m of the survey stations in each of the following grassland types: pastures, alfalfa, grass and mixed grass/alfalfa hayfields, fallow fields, and old fields.

HABITAT$_{BOBO}$: the sum of the proportions of the landscape within 500 m of the point count stations in each of the following grassland types: pastures, grass and mixed grass/alfalfa hayfields, and old fields.

PROPOPEN500: the sum of the proportions of the landscape within 500 m that is not forested or developed based on digitized maps.

WOODEDEDGEDENSITY500: edge density of forest cover within 500 m, serving as an indication of the "brokenness" of the landscape based on digitized maps.

PROPOPEN2500: the sum of the proportions of the landscape within 2500 m that is not forested or developed, based on the LCLU data set.

WOODEDEDGEDENSITY2500: edge density of forest cover within 2500 m, serving as an indication of the "brokenness" of the landscape, based on LCLU data set.

LEGUME: the percent cover of the alfalfa, trefoil, and clover.

FORB: the percent cover of forbs, including dandelions (excluding legumes).

LITTERDEPTH: vertical depth of litter.

AREA: the size of the field in hectares (see text for field size definition).

WOODEDPERIMETER: the proportion of AREA that is bordered by trees (see text for details).

DAYSSINCECUT: the number of days since the field was mowed, or the number of days since May 1, 2002 if the field was uncut.

NUMBERCUTS: the number of cuts performed on the field during the study period; serves as an indicator of management intensity on the field.

CUT: a categorical variable describing whether a field had been cut in the previous 2 weeks; used in removal analyses.

VEGHEIGHT: mean height of vegetation in the survey area on a given count; used in removal analyses.

FIELDPERIMETER: the perimeter of the field in which the survey point was located (meters); used in removal analyses.

(1999): "because these avian species evolved in an ecosystem with characteristic open space and often fail to recognize small habitat patches...", areas that are not necessarily suitable habitat (e.g., cornfields or water) still contribute to the openness of the landscape.

Distant Landscape Openness (H3): PROPOPEN2500 + WOODEDEDGEDENSITY2500. Because birds are highly mobile and both species are migratory, the distance that they evaluate the landscape may be greater than 500 m. Therefore, this hypothesis is similar to the *Near Landscape Openness* hypothesis (H2), but reflects landscape openness at a 2500-m spatial scale.

Field Vegetation (H4): LEGUME + FORB + LITTERDEPTH. This hypothesis predicts that local field vegetation is critical to determining habitat use by Bobolinks and Savannah Sparrows. Previous studies have shown that Bobolinks occur in higher densities in fields with relatively low amounts of total vegetative cover, low amounts of alfalfa, high amounts of litter cover, and higher grass-to-legume ratios (Bollinger and Gavin 1992). For Savannah Sparrows, previous studies have suggested that litter depth and dense ground vegetation are important in habitat selection (Wheelright and Rising 1993, Herkert 1994, Vickery et al. 1994).

Mowing (H5): NUMBERCUTS + DAYSSINCECUT. When a field is cut, nest failure is expected along with dramatic changes to the vegetation. We expected that cutting would decrease abundances and as the number of days since cutting increased, vegetation would regrow and more birds would move back into the field.

Field Characteristics (H6): AREA + WOODEDPERIMETER. Previous studies have suggested that field size (Herkert 1994, Vickery et al. 1994, Bollinger 1995) and the amount of woody edge around the field (Bakker et al. 2002) are important for habitat selection in Savannah Sparrows and Bobolinks.

Combination Models. Habitat selection is likely influenced by many factors (Hilden 1965). Therefore, we considered four combination models that included multiple selection criteria from the first six hypotheses in an additive framework: H7 = *Field Vegetation* (H4) + *Mowing* (H5); H8 = *Field Vegetation* (H4) + *Mowing* (H5) + *Field Characteristics* (H6); H9 = *Near Landscape Openness* (H2) + *Field Vegetation* (H4) + *Mowing* (H5) + *Field Characteristics* (H6); H10 = *Distant Landscape Openness* (H3) + *Field Vegetation* (H4) + *Mowing* (H5) + *Field Characteristics* (H6).

We used Poisson regression to fit the observed bird counts for each candidate model. Models were parameterized by specifying a Poisson distribution using Proc GENMOD (SAS Institute 2004). For each visit and for both species, we assessed goodness of fit of the full model by finding the differences between the deviance of the full model and deviance of the null model (a model that included only the intercept).

We ranked the candidate models for each species and for each visit by using Akaike's Information Criterion for small sample sizes and overdispersed data ($QAIC_c$). We used the goodness-of-fit chi-square statistic from the global model divided by the degrees of freedom to estimate the variance inflation factor in order to make the quasi-likelihood adjustments separately for each species and visit combination. The model with the lowest $QAIC_c$ was considered the best supported model. From the $QAIC_c$ scores, we calculated the Akaike weights (w_i) and the $\Delta QAIC_c$ values. Because we had few models, we report the models in the 90% confidence sets and parameter estimates for variables in those models (Burnham and Anderson 2002). By fitting each model for each visit, we could determine whether the order of rankings of the models changed over visits, reflecting seasonal changes in habitat use patterns. We examined the coefficients for each parameter in each model to determine whether 95% confidence intervals excluded zero.

Occupancy patterns

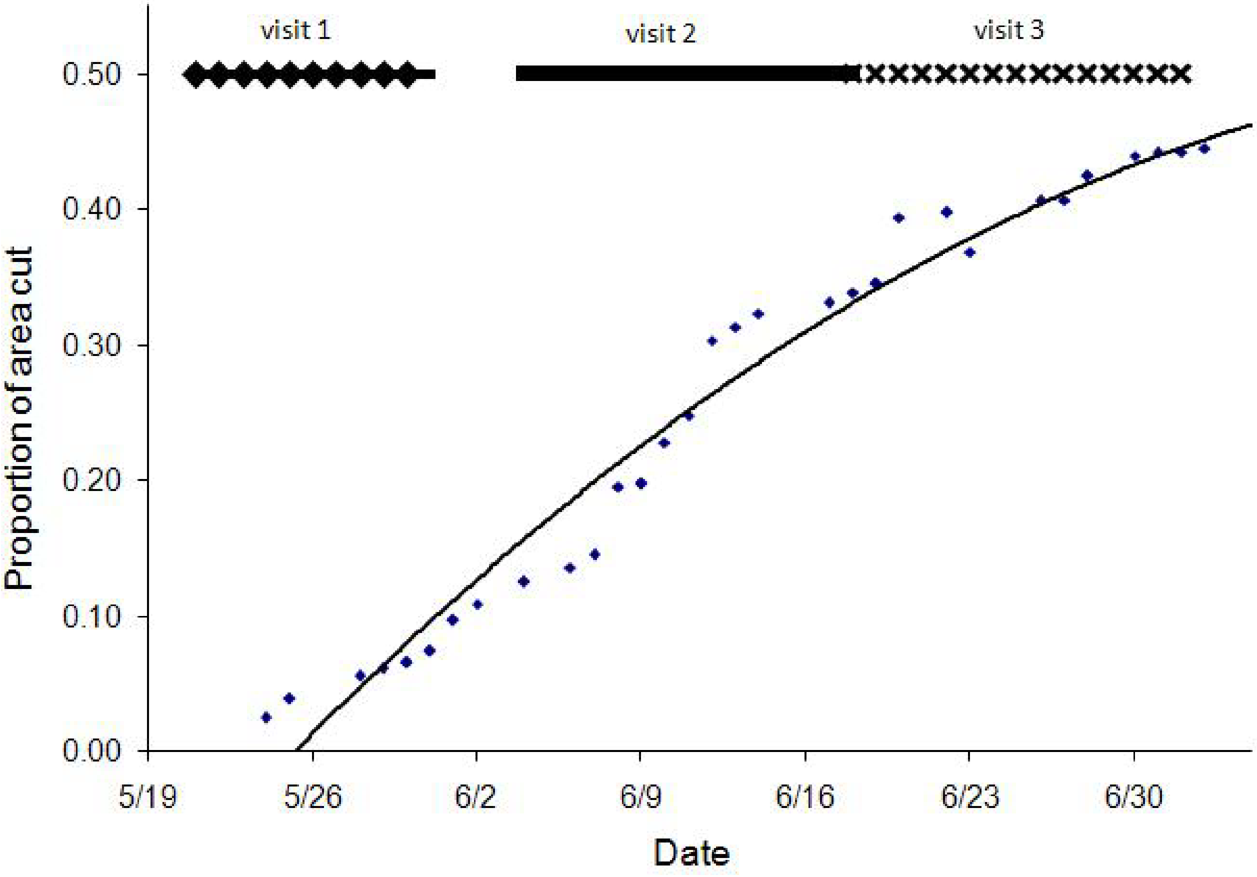
In order to examine the effects of mowing on occupancy patterns, we treated each pair of consecutive field visits (e.g., visits 1 and 2 and visits 2 and 3) as an opportunity for a change in bird occupancy. A field could be occupied on both visits, occupied on neither visit, go from occupied to unoccupied, which we call local extinction, or go from unoccupied to occupied, which we call local colonization. In addition, each field might also change mowing condition between sequential visits. Each field had three possible mowing histories over the three visits: never mowed (uncut-uncut-uncut), mowed between visits 1 and 2 and left to regrow (uncut-cut-regrowth), or mowed between visits 2 and 3 (uncut-uncut-cut). We tabulated the occupancy patterns for each type of paired field status (uncut-uncut, uncut-cut, and cut-regrowth) separately in order to infer effects of mowing.

For this analysis we used the presence or absence of a male in a field (e.g., not restricted to within 50 m of the sampling station). We chose to use bird presence/absence data from the whole field because we were primarily concerned with inferring management effects that covered the whole field and we were not specifically interested in density. We excluded the five miscellaneous fields (see below) from this analysis.

RESULTS

The 142 fields used in analysis included 87 grass-dominated hayfields, 22 alfalfa-dominated hayfields, 17 pastures, 11 mixed alfalfa and grass hayfields, and 5 miscellaneous fields. Of these 142 fields, 30 were cut by visit 2 and 17 more were cut by visit 3, comprising 45% of the total area sampled (Fig. 1). The avifauna was dominated by Bobolinks and Savannah Sparrows (Table 2). We detected between

Fig. 1. The proportion of the agricultural field area cut from May 21 to July 2, 2002 in the Champlain Valley of Vermont and New York. Proportions represent proportion of area (not proportion of fields, n = 142) that contained the bird and vegetation sampling stations. Data points represent mowed fields. The trend line suggests a slowing of cutting in late June and July.



one and five individuals of Grasshopper Sparrows (*Ammodramus savannarum*), Northern Harriers (*Circus cyaneus*), and Upland Sandpipers (*Bartramia longicauda*). Eastern Meadowlarks (*Sturnella magna*) were detected at approximately one-third of survey stations, but rarely within the 50-m radius sampling area.

Bobolinks

Bobolink abundance was correlated with multiple habitat variables over all visits, but several patterns are apparent. On all three visits, variables reflecting the amount of habitat at three spatial scales (AREA, PROPOPEN500, and PROPOPEN2500) were consistently the variables with some of the strongest correlations. When cutting began after visit 1, the variables reflecting mowing intensity on the field became more important, as reflected by the stronger correlations and smaller P-values on visits 2 and 3 (Table 3).

For visit 1, there was strong support for the Distant Landscape Openness Hypothesis (H3; $w_i = 0.79$). The model ranked second was the combination model, Hypothesis 10 (Table 4). There was little support for any other models in visit 1. The only

Table 2. Total number of occupied fields, total number of occupied 50-m sampling stations, and abundance of birds within occupied 50-m sampling stations by male Savannah Sparrows (SAVS) and male Bobolinks (BOBO) on point counts conducted in the Champlain Valley, May 21 to July 2, 2002. The columns for Mean and SD refer to the number of birds per count within 50 m of the sampling station on counts that contained at least one Savannah Sparrow or Bobolink. Notice that the density of SAVS and BOBO in occupied sites increases on each successive visit.

		Number occupied		Bird abundance		
	Visit	Field	50 m	50 m	Mean	SD
SAVS	1	62	22	26	1.18	0.50
	2	65	33	45	1.36	0.60
	3	64	28	45	1.61	0.92
BOBO	1	77	32	69	2.16	1.23
	2	63	31	81	2.61	1.82
	3	48	26	74	2.85	2.58

parameter estimates in Hypotheses 3 and 10 that did not include zero in the 95% confidence interval was PROPOPEN2500 (positive coefficient, Table 5), suggesting more birds occurred on fields where open habitats dominated the landscape.

For visit 2, the Available Habitat Hypothesis (H1) was selected as the best model ($w_i = 0.62$, Table 4). Distant Landscape Openness (H3; $w_i = 0.08$), Mowing Hypothesis (H5; $w_i = 0.08$), Near Landscape Openness (H2; $w_i = 0.05$), and Combination Models 9 ($w_i = 0.04$) and 7($w_i = 0.04$) completed the 90% confidence set and were all within $\Delta QAIC_c < 5.71$. Parameter estimates among the models in the 90% confidence sets included two parameters with confidence intervals not overlapping zero: $HABITAT_{BOBO}$ (positive coefficient) and PROPOPEN2500 (positive coefficient, Table 5). Thus, the amount of potential nesting habitat within 500 m became important during the second visit.

For visit 3, Hypothesis 10: Combination Model 3+4+5+6, was overwhelmingly selected ($w_i = 0.98$, Table 4). The only parameter estimate without zero in the 95% confidence interval for Combination Model Hypothesis 10 was PROPOPEN2500 (positive coefficient, Table 5). Thus, the amount of open landscape within 2500 m was important in all visits, but available habitat within 500 m was important in visit 2. Field Vegetation (H4), Field Characteristics (H6), and Combination Models 7 and 8 were always ranked low and had little support. Near Landscape Openness (H2) and Mowing (H5) generally had little support and low rankings.

Although Bobolinks were present on many hayfields prior to mowing, they were generally absent after the fields were cut. We detected only one Bobolink in a recently cut field that had been unoccupied on a previous visit and in only seven of 47 cases did Bobolinks remain or colonize fields that had been recently cut (e.g., uncut-cut). In only three of 29 cases were fields that exhibited regrowth (i.e., cut-regrowth) occupied by Bobolinks. Most local colonization (12 of 14 cases) occurred in fields that were not cut during the season (Table 6).

Savannah Sparrows

As with Bobolinks, Savannah Sparrow abundances were consistently positively correlated with AREA, PROPOPEN500, and PROPOPEN2500. In addition, Savannah Sparrow abundance was positively correlated with habitat in the 500-m

Table 3. Spearman correlation coefficients (ρ) for male Savannah Sparrow and male Bobolink abundance on agricultural fields and habitat variables from the Champlain Valley of Vermont and New York over three sampling occasions (visits).

	Bobolink						Savannah Sparrow					
	Visit 1		Visit 2		Visit 3		Visit 1		Visit 2		Visit 3	
	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*
$\text{HABITAT}_{\text{BOBO/SAVS}}$	0.143	0.089	0.270	0.001	0.196	0.020	0.232	0.006	0.214	0.010	0.263	0.002
PROPOPEN500	0.209	0.013	0.193	0.021	0.191	0.024	0.227	0.006	0.222	0.008	0.246	0.003
WOODEDEDGEDENSITY500	–0.072	0.397	–0.110	0.194	–0.121	0.152	–0.184	0.028	–0.037	0.662	–0.163	0.054
PROPOPEN2500	0.339	0.000	0.259	0.002	0.243	0.004	0.211	0.012	0.178	0.034	0.233	0.005
WOODEDEDGEDENSITY 2500	0.081	0.339	–0.021	0.807	–0.043	0.612	–0.040	0.639	–0.173	0.040	–0.093	0.274
LEGUME	0.186	0.027	0.171	0.042	–0.043	0.609	0.195	0.020	–0.008	0.929	0.105	0.213
FORB	0.075	0.375	0.138	0.102	0.142	0.094	0.058	0.494	0.099	0.242	–0.026	0.756
LITTERDEPTH	–0.099	0.240	–0.037	0.664	0.161	0.057	–0.088	0.295	–0.121	0.152	–0.105	0.217
AREA	0.275	0.001	0.258	0.002	0.214	0.011	0.276	0.001	0.179	0.033	0.216	0.010
WOODEDPERIMETER	–0.067	0.431	–0.096	0.255	–0.128	0.132	–0.202	0.016	–0.238	0.004	–0.338	0.000
DAYSSINCECUT	0.036	0.670	0.052	0.542	0.166	0.050	–0.130	0.124	–0.098	0.246	–0.239	0.004
NUMBERCUTS	–0.052	0.540	–0.184	0.029	–0.258	0.002	0.084	0.318	0.125	0.138	0.167	0.047
CUT	N/A	N/A	0.217	0.009	0.175	0.038	N/A	N/A	–0.174	0.039	–0.141	0.096
VEGHEIGHT	0.129	0.127	0.161	0.055	0.289	0.001	–0.049	0.565	–0.114	0.176	–0.255	0.002

landscapes ($\text{HABITAT500}_{\text{SAVS}}$). In contrast to the Bobolinks, the woody perimeter (WOODEDPERIMETER) was consistently negatively correlated to Savannah Sparrow abundance. For visit 3, the variables reflecting cutting suggest that Savannah Sparrows have an affinity toward cut fields: Savannah Sparrows were negatively correlated with the time since cutting (DAYSSINCECUT), positively correlated with fields that were cut more (NUMBERCUTS), and negatively correlated with fields with taller vegetation (VEGHEIGHT, Table 3).

For visit 1, three models, Available Habitat (H1), Near Landscape Openness (H2), and Field Characteristics (H6), were included in the 90% confidence set with Akaike weights of 0.71, 0.13, and 0.09, respectively (Table 7). Among the supported models, the parameter estimates lacking zero in their 95% confidence intervals were $\text{HABITAT}_{\text{SAVS}}$ (positive coefficient), PROPOPEN500 (positive coefficient), and AREA (positive coefficient, Table 5).

In visit 2, the best-approximating model was Field Characteristics (H6), which had an Akaike weight of 0.78 (Table 7). The Available Habitat Hypothesis (H1) was ranked second (w_i = 0.11), and Combination Model Hypothesis 8 was ranked third and completed the 90% confidence set (w_i = 0.04, Table 5). In the supported models for visit 2, $\text{HABITAT}_{\text{SAVS}}$ (positive coefficient), AREA (positive coefficient), and WOODEDPERIMETER (negative coefficients) did not include zero in the confidence interval (Table 5).

Abundance patterns in visit 3 were best supported by Field Characteristics (H6; w_i = 0.86, Table 7).

Table 4. $QAIC_c$ rankings, number of parameters (K), log likelihoods, $QAIC_c$, $\Delta QAIC_c$, and Akaike weights (w_i) for Poisson regression models reflecting hypotheses of habitat use for point count data on male Bobolink abundance conducted between May 21 and July 2, 2002 in the Champlain Valley of Vermont and New York. Only models included in the 90% confidence set are shown.

	Model	Model description	K	log likelihood	$QAIC_c$	$\Delta QAIC_c$	w_i
Visit 1	3	Distant Land Open	4	–99.1	102.59	0.00	0.79
	10	3+4+5+6	10	–87.82	105.24	2.65	0.21
Visit 2	1	Habitat	3	–113.49	99.57	0.00	0.62
	3	Distant Land Open	4	–115.87	103.64	4.07	0.08
	5	Mowing	4	–115.9	103.67	4.10	0.08
	2	Near Land Open	4	–117.06	104.63	5.05	0.05
	9	2+4+5+6	11	–98.32	104.94	5.37	0.04
	7	4+5	7	–109.9	105.28	5.71	0.04
Visit 3	10	3+4+5+6	11	–67.38	86.06	0.00	0.98

One other model, Available Habitat (H1), was included in the 90% confidence set ($w_i = 0.06$) but had $\Delta QAIC_c = 5.28$, suggesting only weak support for this model. $HABITAT_{SAVS}$ (positive coefficient) and WOODEDPERIMETER (negative coefficient) both had confidence intervals that excluded zero (Table 5).

There are several patterns in the model ranking over the three visits. In visit 1, hypotheses reflecting the landscape at 500 m were most important. The spatial scale of important models decreased to the field level on visits 2 and 3, where Available Habitat (H1) and Field Characteristics (H6) were within the 90% confidence interval for each visit. Distant Open Land (H3), Vegetation (H4), Mowing (H5), and Combination Models 7, 9, and 10 were never included in the 90% confidence intervals for any visit. Highly parameterized models received little support for Savannah Sparrows.

Occupancy patterns revealed that Savannah Sparrows did not appear to abandon cut fields but rather remained in and colonized cut fields (31 of 47 cases). In another 20 cases, Savannah Sparrows stayed in fields that had been recently cut (uncut-cut). In 23 of 29 cases, fields exhibiting regrowth (i.e., cut-regrowth) were occupied by Savannah Sparrows. Occupancy patterns of Savannah Sparrows in uncut fields were somewhat different than Bobolinks with greater rates of local extinction and colonization, more unoccupied fields, and fewer fields that remained unoccupied (Table 6).

DISCUSSION

Most studies of habitat use emphasize spatial distribution patterns with an implicit or explicit assumption that habitat quality is constant over time. For grassland birds in agricultural landscapes, this assumption is inherently false, and changes in habitat quality likely occur at more rapid rates than these birds experienced historically. Thus, for this suite of birds, it is important to understand habitat use patterns at the time of initial settlement, as well as how these patterns change as agricultural management proceeds throughout the nesting season.

At initial settlement (visit 1), both Bobolinks and Savannah Sparrows showed patterns of habitat use

Table 5. Model parameter estimates for supported (contained in 90% confidence set) Poisson regression models reflecting habitat usage hypotheses for male Bobolinks and male Savannah Sparrows based on point count data from May 21 to July 2, 2002 from the Champlain Valley of Vermont and New York.

	Bobolink				Savannah Sparrow			
Visit	Model	Parameter	Estimate	SE	Model	Parameter	Estimate	SE
1	3	INTERCEPT	−4.384	1.195*	1	INTERCEPT	−3.589	0.652*
		PROPOPEN2500	0.041	0.011*		$\text{HABITAT}_{\text{SAVS}}$	0.044	0.013*
		WOODEDEDGEDENSITY2500	0.014	0.008	2	INTERCEPT	−2.49	1.186*
	10	INTERCEPT	−4.839	1.351*		PROPOPEN500	0.025	0.012*
		PROPOPEN2500	0.054	0.013*		WOODEDEDGEDENSITY500	−0.008	0.008
		WOODEDEDGEDENSITY2500	0.015	0.008	6	INTERCEPT	−1.585	0.512*
		LEGUME	−0.006	0.009		AREA	0.065	0.028*
		FORB	−0.004	0.013		WOODEDPERIMETER	−1.438	0.756
		LITTERDEPTH	−0.218	0.11				
		NUMBERCUTS	−0.72	0.436				
		AREA	−0.017	0.034				
		WOODEDPERIMETER	1.179	0.679				
2	1	INTERCEPT	−1.839	0.471*	1	INTERCEPT	−2.375	0.480*
		$\text{HABITAT}_{\text{BOBO}}$	0.035	0.011*		$\text{HABITAT}_{\text{SAVS}}$	0.03	0.010*
	2	INTERCEPT	−1.171	0.956	6	INTERCEPT	−0.904	0.410*
		PROPOPEN500	0.018	0.009		AREA	0.057	0.023*
		WOODEDEDGEDENSITY500	−0.005	0.006		WOODEDPERIMETER	−1.556	0.617*
	3	INTERCEPT	−2.014	1.008	8	INTERCEPT	−1.171	0.84
		PROPOPEN2500	0.026	0.009*		LEGUME	−0.01	0.01
		WOODEDEDGEDENSITY2500	0	0.008		DAND_FORB	0.015	0.009
	5	INTERCEPT	−0.976	0.955		LITTERDEPTH	−0.038	0.094
		NUMBERCUTS	−0.788	0.499		NUMBERCUTS	0.382	0.408
		DAYSSINCECUT	0.019	0.023		DAYSSINCECUT	0	0.017
	7	INTERCEPT	−1.046	1.004		AREA	0.056	0.025*
		LEGUME	0.014	0.009		WOODEDPERIMETER	−1.417	0.638*
		FORB	0.016	0.01				

(con'd)

		LITTERDEPTH	–0.031	0.098				
		NUMBERCUTS	–0.965	0.547				
		DAYSSINCECUT	0.009	0.025				
	9	INTERCEPT	–2.852	1.673				
		PROPOPEN500	0.025	0.012				
		WOODEDEDGEDENSITY500	–0.004	0.006				
		LEGUME	0.008	0.009				
		FORB	0.015	0.01				
		LITTERDEPTH	–0.011	0.097				
		NUMBERCUTS	–0.852	0.532				
		DAYSSINCECUT	0.02	0.026				
		AREA	0.013	0.031				
		WOODEDPERIMETER	0.605	0.851				
3	10	INTERCEPT	–4.348	2.021*	1	INTERCEPT	–2.688	0.612*
		PROPOPEN2500	0.047	0.012*		HABITAT$_{SAVS}$	0.037	0.012*
		WOODEDEDGEDENSITY2500	0.002	0.009	6	INTERCEPT	–0.314	0.454
		LEGUME	–0.015	0.017		AREA	0.039	0.029
		FORB	0.003	0.011		WOODEDPERIMETER	–2.675	0.796*
		LITTERDEPTH	–0.205	0.135				
		NUMBERCUTS	–1.476	0.865				
		DAYSSINCECUT	0.023	0.026				
		AREA	0.035	0.026				
		WOODEDPERIMETER	0.541	0.673				

*95% confidence interval for parameter excludes zero.

that were strongly influenced by features outside the immediate grassland patch. However, the scale at which these species assessed the habitat differed. Bobolinks were most influenced by landscape features within a 2500-m radius of the field, whereas Savannah Sparrows were most influenced by landscape features within 500 m. Although there is some consistency in the importance of various habitat features over the course of the breeding season, the scale at which habitat selection decisions were made (for both species) narrowed from visit 1 to visit 2. The spatial scale of the best supported model for Bobolinks changed from 2500 m (e.g., Distant Landscape Openness, H3) in visit 1 to 500 m (Available Habitat, H1) in visit 2. By contrast, for Savannah Sparrows, the spatial scale of the best supported model decreased from 500 m (Available Habitat, H1) in visit 1 to the field level (Field Characteristics, H6) in visit 2. These results support general hierarchical habitat selection models proposed by Hilden (1965) and Hutto (1985) during initial habitat selection.

Table 6. Occupancy patterns of male Bobolinks and male Savannah Sparrows between visits based on changes in field conditions on agricultural fields in the Champlain Valley of Vermont and New York, May 21 to July 2, 2002. Each heading reflects a possible mowing history between successive sampling visits: never mowed (uncut-uncut), mowed between visits (uncut-cut) or allowed to regrow following earlier mowing (cut-regrowth). Counts reflect number of fields. Each field in the study is represented twice because each field had two opportunities to undergo change in mowing (i.e., between visits 1 and 2 and between visits 2 and 3).

Field condition	Bobolink	Savannah Sparrow
Uncut-uncut		
Never recorded	77	97
Always recorded	87	53
Local colonization	12	19
Local extinction	21	28
Uncut-cut		
Never recorded	20	14
Always recorded	6	20
Local colonization	1	11
Local extinction	20	2
Cut-regrowth		
Never recorded	23	4
Always recorded	2	20
Local colonization	1	3
Local extinction	3	2

Mowing resulted in different responses by Bobolinks and Savannah Sparrows. In fields that were cut, occupancy patterns revealed only 13% of sampling intervals retained or gained (local colonization) Bobolinks; this value was 71% for Savannah Sparrows. These different behavioral responses led to different patterns of habitat use as hay harvest progressed during the growing season. Without banded birds it was impossible to determine whether birds actually moved among fields over the course of the breeding season. However, high detection probabilities, which were consistent across the study period, suggest that birds were not simply becoming less detectable across the three visits. Further, studies of color-banded birds in the Champlain Valley (Perlut et al. 2006) and radio telemetry results (Strong, *unpublished data*) support these temporal changes in habitat use patterns at smaller spatial scales. We discuss these patterns of habitat use in more detail, provide possible reasons for the patterns, and suggest possible applications for management of these species.

Table 7. QAIC$_c$ rankings, number of parameters (K), log likelihoods, QAIC$_c$, ΔQAIC$_c$, and Akaike weights (w_i) for Poisson regression models reflecting habitat usage hypotheses for point count data on male Savannah Sparrow abundance conducted between May 21 and July 2, 2002 in the Champlain Valley of Vermont and New York. Only models included in the 90% confidence set are shown.

	Model	Model description	K	log likelihood	QAIC$_c$	ΔQAIC$_c$	w_i
Visit 1	1	Habitat	3	–63.44	127.34	0.00	0.71
	2	Near Land Open	4	–64.14	130.79	3.45	0.13
	6	Field Characteristics	4	–64.48	131.43	4.08	0.09
Visit 2	6	Field Characteristics	4	–87.56	153.32	0.00	0.78
	1	Habitat	3	–91.22	157.25	3.94	0.11
	8	4+5+6	9	–84.37	159.1	5.79	0.04
Visit 3	6	Field Characteristics	4	–81.67	100.73	0.00	0.86
	1	Habitat	3	–88.21	106.01	5.28	0.06

Bobolinks

Although patterns of habitat selection by Bobolinks were strongly affected by mowing, there was some consistency in the model ranks for the fields that had or retained Bobolinks. Landscape features consistently ranked high for Bobolinks, a result that has been found in other studies (Ribic and Sample 2001, Thogmartin et al. 2006). Yet the scale, magnitude of importance, and relative importance changed with successive visits. Across all visits, habitat use was influenced by the larger landscape (e.g., Distant Landscape Openness, H3). Even in visit 3, where Combination Model Hypothesis 10 (Distant Landscape Openness, Field Vegetation, Mowing, and Field Characteristics) was ranked higher than the Distant Landscape Openness Hypothesis (H3), the Distant Landscape Openness Hypothesis likely provided most of the explanatory power of Hypothesis 10. In visit 2, after some Bobolinks had been displaced by mowing, areas with more grassland (within 500 m) were important habitats, as indicated by the Available Habitat Hypothesis (H1) receiving the greatest support. This narrower scale (500 m) of field use may reflect the cues Bobolinks use to prospect for new fields after being displaced. Landscapes with a high proportion of open habitat (i.e., 2500 m radius) may tend to be managed more intensively due to their greater agricultural productivity relative to farms in more wooded landscapes (Strong, *unpublished data*). Thus, Bobolinks may search for the "next best" landscape (i.e., 500 m) when displaced as a result of cutting. Specifically it was the more distant amount of nonforested and undeveloped area of the landscape (i.e., at 2500 m and not 500 m) that was most influential for initial field use, but after mowing, more local factors (visit 2) were important.

There are several possible explanations for this pattern, many of which are interrelated. An intrinsic desire or biological need for large open areas could drive this pattern. In contrast, the earliest Bobolinks to return may randomly settle in a large open area simply based on greater habitat availability (i.e., the hypothesis of random placement; Coleman et al. 1982). Both of these explanations may interact with social behavior through site fidelity and conspecific attraction (Cody 1981). If early males returning to the Champlain Valley preferentially select fields in open areas, positive feedbacks acting through the attraction of conspecifics may then lead to even greater densities in those fields (but see Nocera et al. 2006).

The two parameters included in Distant Landscape Openness (H3) were PROPOPEN2500 and WOODEDEDGEDENSITY2500. Of the two parameters in this model, PROPOPEN2500 was more important than WOODEDEDGEDENSITY2500, as the confidence intervals for WOODEDEDGEDENSITY2500 always included zero. It is interesting to note that it is not necessarily the amount of available habitat (i.e., Available Habitat, H1) in the landscape but rather the overall "openness" of the landscape that appeared to be more important for creating an attractive landscape for Bobolinks. This pattern suggests that hayfields or pastures in landscapes with high proportions of row crops (e.g., corn) may remain suitable for Bobolinks. The counts of Bobolinks also provide insight into habitat use over the three visits. Mowed fields were unsuitable for Bobolinks. Additionally, the count data suggest substantial movements as we documented both local extinction and colonization of uncut fields after visit 1. Bobolinks also moved into fields that were already occupied, as indicated by the increasing densities on fields that remained uncut and supported by postcutting movements (Martin and Gavin 1995, Perlut et al. 2006; Strong, *unpublished data*). However, following cutting, some Bobolinks may have abandoned their reproductive effort for the season. They may not have found suitable territories or mates, or remaining fields may have been saturated. Further, considering the time requirements for renesting (establishing a territory, finding a mate, and incubation through postfledging care), male Bobolinks may not have had sufficient time for extensive preparations for migration (fat deposition and molt). Bollinger et al. (1990) estimated this cut-off date for female Bobolinks to be June 20, and Perlut et al. (2006) documented that 90% of female Bobolinks in the Champlain Valley have initiated nests by this time. For males, who must reselect fields and re-establish territories, the cut-off date may be even earlier.

Savannah Sparrows

Models describing Savannah Sparrows' habitat use patterns were different than for Bobolinks. Over the three visits, field characteristics and the landscape at 500 m were most important. Landscape variables within 500 m, specifically the amount of available habitat and the openness of the landscape, were consistently important but declined for visits 2 and 3. Conversely, the characteristics of the field were most important in visits 2 and 3. Savannah Sparrows' preference for larger fields with less wooded edges was similar to reports from elsewhere in their range (Wiens 1969, Johnson and Igl 2001, Bakker et al. 2002).

Savannah Sparrows demonstrated a response to mowing that was different from Bobolinks. Instead of avoiding mowed fields, Savannah Sparrows seemed to be attracted to them and may have even immigrated into cut fields. This is indicated by their apparent persistence in fields that had been cut and their colonization of newly cut fields. Similar within-season movement and colonization behavior has also been observed in Grasshopper and Vesper Sparrows (*Pooecetes gramineus*) in mowed fields in Iowa (Frawley and Best 1991) and Grasshopper Sparrows in burned fields in Florida (Shriver et al. 1999).

Our results support Savannah Sparrows' reputation as generalists because they will use hayfields with grass only a few centimeters high and a large proportion of bare ground. The influx to mowed fields may demonstrate a propensity for fields with shorter vegetation, which may not be available later in the growing season. Our study confirmed that Savannah Sparrows were present and singing in mowed fields, but further research is needed to address actual reproduction in cut fields, as point counts are unable to yield this information. Concurrent research on these species has shown that Savannah Sparrows in mowed fields may successfully reproduce as long as there is enough time to fledge offspring before the subsequent mowing (Perlut et al. 2006). However, both birth and survival rates were lower in fields cut by June 11 (Perlut et al. 2006, 2008). In general, Savannah Sparrows may be more inclined than Bobolinks to attempt to renest because they have fewer time constraints given their short-distance migration and later departure dates.

If maintaining grassland bird habitat in the Champlain Valley is a conservation goal, the data from this study suggest three management considerations. First, because species respond to habitat conditions at different spatial scales, and because grassland habitat conditions change throughout the breeding season, multiple temporal and spatial scales warrant consideration. Second, reserves for grassland birds should be concentrated in mostly nonforested and nondeveloped landscapes of 2000 ha (i.e., the area of a 2500-m radius circle). Third, within these large open areas, subsets of smaller areas of 80 ha (i.e., the area of a 500-m radius circle) should contain as much grassland and late-cut hayfields as possible to provide initial nesting areas as well as uncut fields, which provide habitat for displaced Bobolinks.

Although our study reveals several important conservation considerations for bird distributions and habitat use, additional data are needed to fully understand and manage this system. Data on within-season dispersal of marked birds would help us better understand the scale at which bird redistribution occurs following cutting. Data on mating and reproductive success is also needed to accurately relate habitat quality to bird abundance, as this study focused only on bird distributions. The implications for altered fledgling chronologies due to agricultural practices should also be considered as young produced later in the season may be less likely to be recruited into the breeding population (Perrins 1970). Finally, whereas our study focuses on the two most abundant species in our system, data for rare species, such as Grasshopper Sparrow, Upland Sandpiper, and Eastern Meadowlark, are also needed to better evaluate the generality of our results and appropriateness of using one or two species to develop conservation measures for a larger suite of grassland birds.

Because Savannah Sparrows and Bobolinks respond to mowing differently, it is important to consider temporal aspects of mowing in light of species-specific behaviors. Asynchronous cutting over a large geographic area likely leads to decreased nest success, as birds that renest or disperse and renest after cutting are still exposed to the risk of further cutting. Cost-share programs, such as the delayed mowing practice in WHIP, can increase nesting success for grassland birds. However, this practice is unlikely to be implemented by dairy farmers who need high protein forage for milk production. In Vermont, the Natural Resources Conservation Service has incorporated a "grassland bird incentive" into EQIP, such that farmers are paid ($55/ha) for delaying second cuts by 65 days, provided first cuts are completed by June 2 (NRCS 2009). Moving first cut dates earlier and second cuts later allows displaced Bobolinks more time to reselect another field and successfully fledge young.

Responses to this article can be read online at:
http://www.ace-eco.org/vol5/iss2/art11/responses/

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