



Research Papers

Habitat Relationships of Three Grassland Breeding Bird Species: Broad-scale Comparisons and Hayfield Management Implications

Relations entre l'habitat et trois espèces d'oiseaux nicheurs de prairies : comparaisons à grande échelle et implications pour l'aménagement de champs de foin

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ABSTRACT. Generalized recommendations for the conservation of birds in agro-ecosystems have been elusive because studies are often of a local nature, and do not compare source data against those from other regions. In this study, we developed geographically broad habitat relationship models to provide conservation prescriptions for three species that breed in farmed grasslands: Bobolink (*Dolichonyx oryzivorus*), Savannah Sparrow (*Passerculus sandwichensis*), and Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni subvirgatus*). We develop models from our study in Nova Scotia, Canada and confront them with independent data from Wisconsin, USA pastures and Iowa, USA restored prairies. Vegetation that was higher and denser in the prebreeding season was linked to increased occupancy rates and abundance of Bobolinks in each study region. Providing tall spring grass is easily accomplished by not cutting late in the previous year. Savannah Sparrows were instead associated with shorter and sparser spring grass, which highlights the need to simultaneously provide heterogeneous habitat for otherwise ecologically similar species. Nelson's Sharp-tailed Sparrows were more likely to occur, and be numerous, in areas with greater availability of drainage ditches. They and several other species would benefit from provision of ditches with adequate vegetation to promote occupancy. By combining these with other well-established recommendations, such as a delayed first harvest, a greater net conservation benefit can be realized from these working landscapes.

RÉSUMÉ. Les recommandations d'ordre général pour la conservation des oiseaux des écosystèmes agricoles sont difficiles à définir parce que les études n'ont souvent qu'une portée locale et ne comparent pas les données d'origine à celles d'autres régions. Dans cette étude, nous avons développé des modèles de relations avec l'habitat à grande échelle dans le but de fournir des recommandations pour la conservation de trois espèces qui nichent dans les prairies cultivées : le Goglu des prés (*Dolichonyx oryzivorus*), le Bruant des prés (*Passerculus sandwichensis*) et le Bruant de Nelson (*Ammodramus nelsoni subvirgatus*). Nous avons élaboré des modèles à partir de notre étude en Nouvelle-Écosse, au Canada, et nous les avons comparés à des données indépendantes récoltées aux États-Unis, dans des pâturages au Wisconsin et des prairies restaurées en Iowa. La végétation plus haute et plus dense avant la saison de nidification était associée à des taux d'occupation plus élevés et à un plus grand nombre de goglus dans chaque aire d'étude. Il est facile d'obtenir de l'herbe haute au printemps en évitant de couper tardivement l'automne précédent. À l'opposé, les Bruants des prés étaient associés à la présence d'herbes courtes et éparées au printemps, ce qui met en évidence la nécessité de fournir des habitats hétérogènes pour des espèces néanmoins écologiquement similaires. Les Bruants de Nelson fréquentaient davantage et étaient plus nombreux dans les aires où il y avait plus de fossés de drainage. Cette espèce et plusieurs autres profiteraient de la présence de fossés bordés de végétation adéquate. On peut obtenir un bénéfice net de conservation plus important dans ces paysages anthropiques en combinant ces recommandations à d'autres déjà reconnues, comme celle de retarder la première récolte.

Key Words: agriculture; grassland birds; habitat-relationship models; harvest dates; vegetation height-density.

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INTRODUCTION

Many grassland birds breed readily and successfully in natural landscapes, such as tall and shortgrass prairie, but working agricultural landscapes, i.e., agro-ecosystems, are becoming an increasingly important focus for grassland bird conservation (e.g., Vickery et al. 2004). More than half the world's ecologically productive lands are under agricultural production (Badgley 2003), and the sum of conservation efforts in farmlands can therefore provide an enormous net benefit (Petit et al. 1999). Agro-ecosystems are too often treated as "ecological sacrifice areas" (Badgley 2003) in conservation planning.

It has been consistently difficult to recommend broad-scale conservation actions for grassland birds in working landscapes partly as a result of two factors: (1) most information is collected at a local extent and assumed to apply across a species' distribution, and (2) vegetation characteristics, although important, are often the only set of explanatory variables considered. For example, invertebrates are the primary prey of many grassland bird species and show correlations with abundance (Söderström et al. 2001), but very few studies of grassland birds have addressed such variables (c.f., Wittenberger 1980, Clere and Bretagnolle 2001). This is likely because it is easier to discuss management options with producers regarding vegetation than it is invertebrate prey availability; nonetheless, examining such variables is essential to refining conservation approaches for grassland birds.

Appropriate conservation recommendations should come from examination of more than one correlate of fitness, such as where the species is found (presence/absence), how many are there, i.e., abundance, and whether they are breeding, i.e., reproductive activity. Many studies examine only one of these parameters at a time. These results may be misleading, for instance, because reproductive rates and abundance may not be correlated (Winter and Faaborg 1999, Fletcher and Koford 2002) and can provide very different indications of habitat quality and population persistence from which to direct conservation efforts (Van Horne 1983). Effective management in agro-ecosystems requires understanding the broadscale importance of explanatory variables biologically relevant to more than one population response. The predictive accuracy of models should also be tested both within

the generating dataset and against independent datasets from other areas (e.g., Betts et al. 2006).

In this study, we sought to determine which, if any, variables were consistently associated with indirect measures of fitness components for several bird species residing in agricultural grasslands. We selected three grassland bird species to study: Bobolink (*Dolichonyx oryzivorus*), Savannah Sparrow (*Passerculus sandwichensis*), and Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni subvirgatus* – Acadian race). The Acadian race of Nelson's Sharp-tailed Sparrow, hereafter "Nelson's Sparrow", primarily breeds in saltmarsh, but commonly shows facultative breeding in wetter areas of agricultural land (Nocera et al. 2007), similar to the midwestern subspecies (*A. n. nelsoni*; Murray 1969, Greenlaw and Rising 1994). We chose these species because they breed in different grassland types, e.g., hayfields, pastures, prairie, and have broad geographic ranges, except for Nelson's Sparrow, which has a very restricted range and offers a basis for comparison. We model their occurrence, abundance, and reproductive activity with predictive variables describing vegetation structure, management activity, physiography, and prey abundance. The models are developed from field data collected from hayfields in Nova Scotia, Canada, and tested against models generated using independent data, made available to us from extensive studies in different environments, i.e., prairie, restored grasslands, and pasture, elsewhere in Iowa and Wisconsin, USA. Ultimately, if certain variables retain their importance across such a geographic distance as Nova Scotia to Iowa and Wisconsin, and across the range of agro-ecosystem land uses we examine here, then we can make a case for model generality and more confidently identify appropriate conservation actions at a broad scale.

METHODS

Study sites

From May to August 2002–2004, we conducted breeding bird and habitat surveys across sites in the western Annapolis Valley, Nova Scotia, Canada, centered on 44°45'N, 65°31'W): Belleisle (210 ha), Upper Belleisle (116 ha), Queen Anne (180 ha), and Pea Round (142 ha). These sites are dyked and drained for agriculture. Fields at Queen Anne, Belleisle and Upper Belleisle are mixtures of timothy (*Phleum pratense*), meadow fox-tail

(*Alopecurus pratensis*), various bluegrass species (*Poa* spp.), and reed canary grass (*Phalaris arundinacea*). The same mixtures of grasses are planted at Pea Round, with the addition of several homogenous alfalfa swards (*Medicago sativa*).

Study fields were not grazed or planted in nonforage crops, and did not receive any pesticide applications during the study. Date of first hay harvest at Queen Anne, Upper Belleisle, and Belleisle takes place after 1 July, which is later than the typical for the region, except for a small field cut early for silage at Queen Anne. Harvest dates were staggered within these three sites, i.e., 1 July–15 August. Conversely, Pea Round is cultivated solely for dairy operations and most harvest is for silage; first-cut begins before 15 June.

Breeding bird sampling

Bobolinks, Savannah Sparrows, and Nelson's Sparrows were surveyed at 52 point-count stations distributed among a total of 18 fields, i.e., 52 stations x 3 yr each, visited 8–12 times/yr [mean = 10 counts per stations]. To avoid double-counting birds, point-count station centres were placed >175 m apart. This distance is greater than the typical territory size of Bobolinks (Martin and Gavin 1995), which have the largest territories among the species we studied. Five-minute point-count surveys (50 m radii; Hutto et al. 1986) were conducted between 30 min after sunrise and 1000 AST, i.e., weather permitting: wind <25kph, no precipitation. We chose a 50 m radius for point-counts because Nelson's Sparrow can be difficult to detect reliably beyond this distance (Nocera, *unpublished data*). Because most fields at our study sites were under a delayed hay harvest regimen, we conducted point-count surveys throughout the breeding season. However, in five instances at Pea Round, where fields were cut early, we ceased counts at stations in those fields after cutting.

All point-count data were summarized by mean abundance per season, to reduce the inflationary effect of floaters and non-residents on overall analyses (Betts et al. 2005). We modeled mean abundance for each study species with the sexes combined and also constructed sex-specific models for Bobolinks, as they are sexually dichromatic. Mean density per station for all years and sexes combined was 0.91 for Bobolink, 1.25 for Savannah Sparrow, and 0.19 for Nelson's Sparrow.

We chose to intensively sample our 52 stations, i.e., 10 times each, to calculate indirect estimates of reproductive activity. Reproductive activity was indexed by monitoring breeding phenology and behavior of birds whose territories included the point-count station (sensu Vickery et al. 1992; Christoferson and Morrison 2001; Betts et al. 2005). Based on these behavioral observations, each station was ascribed an ordinal reproductive activity index, for each species, for the season. Following Vickery et al. (1992), we attributed an index score of 0 when no, or few, birds were present; 1 for male presence only (> three weeks); 2 for male and female presence only (> 3 wk); 3 for a confirmed pair present, seen with nesting material, or exhibiting other signs of breeding; 4 for adults seen carrying food to presumed nestlings; and 5 for evidence of fledging success. Our observations of food carrying are unlikely to have been biased by mate feeding, as no species we studied delivers food to incubating mates (Wheelwright and Rising, 1993, Greenlaw and Rising 1994, Martin and Gavin 1995). However, we cannot rule out possible observations of self-feeding, although this bias is likely to be small because invertebrates, easily observed in the bill, are the sole food fed to nestlings of each study species, whereas adults supplement up to 50% of their diet with small seeds that are eaten whole (Martin and Gavin 1995). To determine if a bird was a resident, we use 3 wk from the date of first observation at a station as a cut-off to help ensure that fewer nonterritorial floaters are counted accidentally. This reproductive activity index has been shown to underestimate true reproductive success (Rivers et al. 2003), but the estimates are consistent and allow for statistical comparisons across many landscape types and study designs (Betts et al. 2005).

Predictive variable sampling

We included 27 variables from four broad categories: vegetation, prey, management, and physiography as predictors of breeding bird demographics (Table 1).

Vegetation was measured in 100 m wide plots, centered on each point-count station. Vegetation measurements were made twice per season, first during territory establishment in late May, and again in late June. The mean of four vegetation measurements, one taken in each cardinal direction, for each plot was used as the predictive variable.

Table 1. Predictive variables used in modeling, acronyms, and data summaries. Sample point mean and range for each study area are shown as years combined. Abundance of insect orders is expressed as catch-per-unit-effort; all other variables show units in parentheses. No artificial mean is derived for ordinal and binary variables, shown as "na." Variables not measured in Iowa and Wisconsin study areas are denoted by --.

Acronym	Variable description	Nova Scotia		Iowa		Wisconsin	
		Mean	Range	Mean	Range	Mean	Range
<u>Invertebrate Abundance</u>							
<i>ARA</i>	Aranea in pitfalls	10.5	0.6-38.1	--	--	--	--
<i>CHI</i>	Chilopoda in pitfalls	0.1	0-0.9	--	--	--	--
<i>COLS</i>	Coleoptera in sweeps [†]	5.4	0-113.0	--	--	--	--
<i>COLP</i>	Coleoptera in pitfalls [†]	10.6	1.0-110.6	--	--	--	--
<i>DIP</i>	Diptera in sweeps	7.1	0-39.6	--	--	--	--
<i>DIPL</i>	Diplopoda in pitfalls	0.1	0-1.5	--	--	--	--
<i>HEMI</i>	Hemiptera in sweeps	13.6	0-74.3	--	--	--	--
<i>HYM</i>	adult Hymenoptera in sweeps	1.0	0-7.0	--	--	--	--
<i>ISO</i>	Isopoda collected in pitfalls	3.4	0-189.7	--	--	--	--
<i>LEP</i>	adult Lepidoptera in sweeps	1.2	0-8.3	--	--	--	--
<i>LHL</i>	<i>LEP</i> and <i>HYM</i> larvae in sweeps	2.2	0-11.0	--	--	--	--
<i>LUM</i>	Lumbricina in pitfalls	0.2	0-2.4	--	--	--	--
<i>ODO</i>	Odonata in sweeps	0.5	0-4.4	--	--	--	--
<i>OPIL</i>	Opiliones in pitfalls	0.2	0-1.1	--	--	--	--
<i>ORTH</i>	Orthoptera in sweeps	0.5	0-6.5	--	--	--	--
<i>STY</i>	Abundance of Styломmatophora in pitfalls	0.3	0-7.0	--	--	--	--
<u>Vegetation</u>							
<i>ALF</i>	Presence/absence of Alfalfa	na	na	--	--	--	--
<i>COV</i>	Live vegetative cover in a frame (%)	69.7	24.5-100	84.0	55.1-99.5	69.8	28.8-100
<i>FORB</i>	Forb cover in a frame (%)	23.4	0-96.3	26.3	0-8.5	29.5	0-81.3
<i>GR</i>	Grass cover in a frame (%)	76.6	3.8-100	52.2	8.2-81.1	70.5	18.8-100

(con'd)

<i>HD</i>	Height/density (dm) of May vegetation	3.0	1.0-7.5	4.7	1.2-12.2	0.9	0-3.1
<i>SPT</i>	Presence/absence of <i>Spartina</i> spp. (cordgrass)	na	na	--	--	--	--
Other							
<i>DIT</i>	Length of ditch (m) in point-count plot	2.8	0-11.5	--	--	--	--
<i>HARV</i>	Harvest date in the current year	6 Jul	6 Jun-15 Aug	--	--	--	--
<i>HPY</i>	Harvest date in the preceding year	5 Jul	6 Jun-15 Aug	--	--	--	--
P_c^{bobo}	Conditional detection probability for Bobolink	0.44	0.42-0.45	--	--	--	--
P_c^{savs}	Conditional detection probability for Savannah Sparrow	0.41	0.4-0.45	--	--	--	--
P_c^{nsts}	Conditional detection probability for Nelson's Sparrow	0.40	0.35-0.42	--	--	--	--
<i>YR</i>	2002, 2003, or 2004	na	na	--	--	--	--

† *COLS* and *COLP* represent prey abundance estimates from the same taxonomic order, but were considered as separate variables because they reliably sampled different families (Elateridae (click beetles) by sweeps, and Carabidae (ground beetles and tiger beetles) by pitfalls).

Grass height and density, hereafter “*HD*” (Table 1) were measured simultaneously in each plot using a visual obstruction “Robel pole” (Robel et al. 1970) placed ~5 m from the plot center. Live vegetative cover (%), and the percent of that cover that was grass or forbs, were determined within plots using Daubenmire frames (Daubenmire 1959) thrown (> 5 m) in each cardinal direction from the plot center. Litter depth was measured within the frame with a ruler against a profile cut from the soil. The presence/absence of alfalfa, a known negative correlate of Bobolink abundance (Bollinger 1988; Bollinger et al. 1990), and slough cordgrass (*Spartina pectinata*), a putative positive correlate of Nelson's Sparrow occurrence (Murray 1969) was also determined for each plot.

Terrestrial invertebrate abundance, quantified as catch-per-unit-effort, was sampled using pitfall traps checked weekly throughout the study season. One pitfall trap was placed 10 m north and south of each plot center. Pitfall traps were 15 cm deep plastic cups, flush to soil surface, with 3–5 cm of a soap and water mixture on the bottom. All captured

specimens were identified to order, or further when possible. Although pitfall traps captured specimens from a large number of taxa, those most represented by this method, and reported here, are Aranea (spiders), Chilopoda (centipedes), Coleoptera (beetles), Diplopoda (millipedes), Isopoda (sowbugs), Lumbricina (earthworms; class Oligochaeta), Stylommatophora (slugs; class Gastropoda), and Opiliones (harvestmen).

To sample a greater proportion of flying insects, we conducted weekly sweep-netting, which involved a series of horizontal sweeps with a sailcloth sweep net through the grass canopy along a 10 m transect east and west of plot centers. All captured specimens were identified to order, or further when possible, and quantified as catch-per-unit-effort. Although sweeps captured specimens from a large number of taxa, this method captured more aerial arthropods than pitfall trapping, and better represented Diptera (flies), Hemiptera (true bugs), Hymenoptera (wasps, bees, ants), Lepidoptera (moths, butterflies), Odonata (primarily damselflies), and Orthoptera (grasshoppers). Both adults and larvae were

represented in Hymenoptera and Lepidoptera, and we use the order name in reference to only adults. Because some larvae of these two orders cannot be separated without labor-intensive techniques, we collapsed larvae data to a composite variable of “Lepidoptera and Hymenoptera larvae” (*LHL*, Table 1) that can be viewed more simply as “caterpillars”. Note that both techniques captured a large number Coleoptera. We separate these in modeling according to capture method (Table 1) because sweeps collected more Elateridae (click beetles) and pitfalls more Carabidae (ground beetles and tiger beetles).

Lastly, we included five variables generally descriptive of physiography and management. For each plot, we converted date of harvest to an annual-Julian date. For modeling, we use date of harvest in the current year and in the previous year. To control for annual effects we included the sample year as a covariate. Because pilot work (Nocera and Milton, *unpublished data*) in 2000-2001 indicated that Nelson’s Sparrows frequented hayfield drainage ditches, we also quantified the amount of ditch contained in each plot and measured from 1:10,000 scale air photos.

Independent data sets

To test the models, we obtained data (Renfrew 2002) from a random subsample of 50 point-count stations conducted each year from 1997-1999 across 74 pastures in six southwestern Wisconsin counties. Point-count surveys of five-minute duration with a fixed 100 m radius were conducted twice per year (once each in May and June) during which all individuals seen or heard were counted. Because a 100 m radius was used in the Wisconsin study, which covers four times more area than counts using 50 m at the other two sites, i.e., Nova Scotia and Iowa, we reduced all abundance data from Wisconsin by a factor of four. This correction requires the realistic, although untested, assumption that the relationship between log-area and log-density is linear. The two species in common with the present study are Savannah Sparrow, which were sampled in comparable densities (0.83 individuals/sample point vs. 1.25 in Nova Scotia), and Bobolink, which occurred in higher densities in Nova Scotia (0.19 vs. 0.91).

Vegetation measurements in Wisconsin were conducted in late May along four transects at right angles to each point-count station. Measurements

in common with our study (as per Table 1) were % live cover, % of live cover that was forbs, and litter depth, which were estimated to the nearest 5% in Daubenmire frames. Visual obstruction measurements were made with a Robel pole (*HD* as per Table 1), modified slightly as readings were made at a height of 1.5 m. Cover measurements were similar to the present study, but because the study was conducted in grazed pastures, both *HD* (mean = 0.87 dm) and litter measurements (mean = 1.02 cm) were below those in Nova Scotia hayfields (mean = 3.0 dm and 3.3 cm, respectively).

The second independent dataset (Fletcher 2003) is a random subsample of 204 point-count stations drawn from a total 279 and 42 transects drawn from a total 60 conducted from 1999–2000 across 30 prairie/restored grassland sites in northern Iowa. Point-count surveys were conducted within a fixed 50 m radius, and counts along 25 m width transects of 100–400 m length, three times per year, generally once in late May, mid-June, and early July, during which all individuals seen or heard were counted. Bobolinks were sampled at higher densities (1.7 individuals/sample unit) to the present study (0.91), however Savannah Sparrows were encountered at lower densities (0.34 vs. 1.25).

Iowa vegetation measurements were conducted in July at four locations within a 50 m radius of each point-count station, and at five locations in each 25 m increment of a transect route. Those in common with the present study (as per Table 1) were live cover (%), and the percent of that cover that was either forbs or grass, estimated in Daubenmire frames. Also, visual obstruction measurements were taken using a Robel pole (see above; *HD* as per Table 1), where litter depth measurements were also made. Cover measurements were very similar to the present study, but either because of vegetation differences or because measurements were made later in the season, *HD* is, on average greater (mean = 4.7 dm; Fletcher and Koford 2002) than ours sampled in May (mean = 3.0 dm).

Statistical analysis

Statistical models were generated using R version 2.4.1 (R Development Core Team 2006). Prior to modeling each response, we reduced the 27 explanatory variables (summarized in Table 1) to a smaller group of candidate variables. From this, we generated global models using the retained variables and used mixed-effects logistic regression to model

occupancy, ordinal regression to model reproductive activity, and linear mixed-effects regression to model abundance. We accounted for temporal and possible spatial pseudoreplication in our data by including site and point-count station as nested random effects. We then chose the best-fit model as that which most reduced Akaike's Information Criterion (AIC; Akaike 1974). We further assess model fit by examining the parameter estimates of the final model and the variance associated with the random effects.

Predictive variables

We first accounted for the fact that abundance of each study species differed between sites, creating potential heterogeneity in detection probability. Although grassland birds occur in very open areas, and yield a high degree of detection during point-count surveys (particularly at ranges <50 m; Rotella et al. 1999), we accounted for any latent detection heterogeneity by *a posteriori* calculation of a 'conditional detection probability' (P_c ; Royle and Nichols 2003) for each site. We then used the resultant P_c as a covariate in all occupancy models.

We then reduced the set of 27 predictive variables by (1) eliminating the variable with the strongest collinearity within a pair (Graham 2003), and (2) using statistical criteria to select putatively important variables. To account for collinearity, we calculated r for each pairwise combination of variables. For those pairs with $r > 0.7$, we retained the variable we felt was more likely associated with habitat selection. For instance, because of persistent strong collinearity between May and June vegetation HD measurements, we used May samples, as they were more likely to be a cue used in territory establishment.

For models of occupancy and reproductive activity, candidate explanatory variables were selected, from those not eliminated because of collinearity, by retaining only those singular variables with a Mallows' C_p score (Mallows 1973) above that of a null model. The resultant set of candidate models contained the global model and all possible combinations of retained variables.

For abundance models, following the elimination of variables due to collinearity, candidate explanatory variables were selected by retaining only those above an arbitrarily set threshold of the upper 50% of the 27 candidate explanatory variables

with the highest individual F-statistic, which also had at least 0.10 $pr(|t|)$. The 50% threshold lacks statistical basis, but served to substantially reduce the dimensionality of models built from an otherwise complex set of variables. The candidate model set then contained the global model and all possible combinations of retained variables.

Variables were log transformed whenever it improved variance homogeneity and brought the model residual distribution closer to normality through visual assessment of qq-norm plots. However, for discussion purposes we present nontransformed variables (e.g., Table 1).

Models

We built mixed-effects logistic regression (function 'lmer' in package 'lme4' in R; version 0.9975-13, Bates and Sarkar 2007), incorporating a binomial distribution and logit link, to model point-count data, which were reduced to binary presence/absence (occupancy). Mean abundance of birds was modeled with linear mixed-effects regression (package 'nlme' in R; version 3.1-79, Pinheiro et al. 2006), maximizing the restricted log-likelihood to fit the model. In both cases, we included 'site' and 'point-count station' as nested random effects.

Because the reproductive activity data are ordinal (semi-quantitative) and cannot be fitted to a logistic model, we fitted an ordinal regression model using proportional odds (package 'Design' in R; version 2.0-12, Harrell 2005; see also Walker and Duncan 1967; Guisan and Harrell 2000). We identified that ordinal models met the equal slopes assumption of ordinal modeling by examining smoothed partial residual plots. We did not explicitly examine random effects in these models because the proportional odds structure applies the logit cumulatively, not separately, so as to estimate both random and fixed effects (Agresti 2002). In addition, the nature of the reproductive activity index is itself cumulative; in other words, its derivation is dependent upon temporal pseudoreplication.

The resultant set of top models were compared to the reduced models (i.e., only variables with analogs in our study) for Iowa and Wisconsin data on mean abundance and occupancy (reproductive activity data were not available). From this model set, we then compared the top models to determine which variables were retained in common across the three study regions. Uncertainty about the importance of

a variable in Nova Scotia models was considered 'reduced' (i.e., prediction success was higher) if Iowa or Wisconsin models retained the same variables.

RESULTS

For each response variable modeled, the predictive variables retained for model building are listed in Table 2. In general, conditional detection probability estimates (P_c) were similar among sites. There was a slight difference in P_c between sites for all study species (Table 1) but was not strong enough to be retained as a candidate variable in model sets for any response.

All top models describing occupancy (Table 2), abundance and reproductive activity were associated with AIC values substantially below that of the global models. Except for the model describing overall, i.e., both sex, abundance of Bobolinks, little variance was associated with the random effects of site and point-count station. Parameter estimates for each model are presented in Table 3.

Abundance models

The top model (Table 2) for Bobolink abundance (both sexes combined) indicated positive relationships to *HD* and the abundance of Orthoptera and Hemiptera (many of which were meadow plant bugs [*Leptopterna dolabrata*, suborder Heteroptera] and others in family Miridae). The positive relationship between *HD* and Bobolink abundance was particularly strong (Fig. 1). However, this model had the highest variance associated with the random effects of 'site' and 'point-count station' of any model assessed. A similar model was selected for female abundance (Table 2), showing a positive relationship with *HD* and Hemiptera abundance. Among Bobolink models, the model for female abundance also showed the least variance associated with random effects. The top male abundance model (Table 2) was a positive relationship with vegetative cover (%) and a negative relationship with the presence of alfalfa.

Models for the two sparrow species could be constructed only for the sexes combined because

they are sexually monochromatic. For both species, the variance associated with random effects was trivial. The best Savannah Sparrow abundance model (Table 2) was a positive association with flies (Diptera) and a negative relationship to both *HD* and centipedes (Chilopoda). The strong negative relationship to *HD* (Fig. 2) is in contrast to the positive relationship seen with Bobolink abundance. The top model for Nelson's Sparrow abundance (Table 2) was a positive relationship with abundance of grasshoppers (Orthoptera) and ditches, and a negative relationship with presence of alfalfa. The relationship between Nelson's Sparrow abundance and ditches was remarkably strong (Table 3).

Occupancy models

The top model (Table 2) for presence/absence of Bobolink (sexes combined) indicated a positive relationship to *HD* and a negative relationship to forb cover. The top Savannah Sparrow model (Table 2) showed their presence/absence was related positively with the number of beetles in pitfall traps (Coleoptera, primarily Carabidae) and related negatively with vegetation *HD* and forb cover. The negative influence of *HD* was the strongest among the variables in the top model of Savannah Sparrow occupancy. The top Nelson's Sparrow model (Table 2) showed positive relationships with caterpillars, spiders (Aranea), and ditches. Again, the models for the two sparrow species were not influenced by the variance associated with the random effects.

Reproductive activity models

The top Bobolink reproductive activity model (Table 2) was a positive relationship with *HD*, spiders, flies, and damselflies (Odonata). The influence of *HD* on Bobolink reproductive activity was particularly strong compared to the remaining variables in the top model (Table 3). The top Savannah Sparrow reproductive activity model (Table 2) was a positive association with harvestmen (Opiliones) and a negative association with forb cover. The top model for Nelson's Sparrows, like Bobolinks, showed a positive relationship to *HD* and spiders. The relationship between Nelson's Sparrow reproductive and ditches was the strongest of any assessed in the study (Table 3). Because of the proportional odds structure of

Table 2. Top models from the Nova Scotia study area for abundance, occupancy, and reproductive activity of Bobolink, Savannah Sparrow, and Nelson’s Sharp-tailed Sparrow. Model notation follows Table 1. For comparison, the value of Akaike’s Information Criterion (AIC) is provided for the global and final models. The variance associated with the random effects of site and point-count station is provided for models with mixed effects. Parameter estimates and standard errors are presented in Table 3. Footnotes indicate the retained variables used in model building for each model set. For occupancy and reproductive activity models, variables were retained if they had a Mallow’s Cp score (Mallow 1973) above that of a null model. Variables were retained for abundance models if they were within the upper 50% of highest individual F-statistics and had at least 0.10 pr (|t|).

Model for	Top Model	Global AIC	Best AIC	σ^2 Site	σ^2 Point
Bobolink					
abundance (female + male) [†]	<i>HD + HEMI + ORTH</i>	386.4	364.4	0.337	0.324
abundance (female) [‡]	<i>COV - ALF</i>	272.2	234.2	0.149	0.131
abundance (male) [§]	<i>HD + HEMI</i>	151.7	123.5	0.043	0.036
occupancy	<i>HD - FORB</i>	149.3	142.8	0.123	0.114
reproductive activity [¶]	<i>HD + ARA + DIP + ODO</i>	152.2	149.8	--	--
Savannah Sparrow					
abundance [#]	<i>DIP - CHI - HD</i>	329.6	295.1	0.005	0
occupancy ^{††}	<i>COLP - FORB - HD</i>	49.3	42.2	0.007	0
reproductive activity ^{‡‡}	<i>OPIL - FORB</i>	107.6	101.8	--	--
Nelson’s Sparrow					
abundance ^{§§}	<i>DIT + ORTH - ALF</i>	8.4	-40.0	0.018	0
occupancy	<i>DIT + ARA + LHL</i>	235.1	228.8	0.001	0
reproductive activity ^{¶¶}	<i>HD + ARA - ALF</i>	-39.2	-44.1	--	--

[†] ALF, COV, FORB, HD, HEMI, LIT, ORTH, SPT

[‡] ALF, COV, DIP, DIPL, FORB, HD, HEMI, LIT, ODO, SPT

[§] ALF, DIP, HARV, HD, HEMI, HYM, LHL, LIT, ODO, ORTH

[|] COV, DIP, FORB, HARV, HD, LIT

[¶] ALF, ARA, COV, DIP, DIPL, GR, HD, HEMI, LIT, LUM, ODO, ORTH

[#] ALF, CHI, COLS, DIP, HARV, HD, ORTH, STY, YR

^{††} COLP, COLS, DIP, FORB, HD, LIT

^{‡‡} ALF, ARA, CHI, COLS, FORB, HPY, LUM, OPIL, ORTH, STY, YR

^{§§} ALF, ARA, DIT, HARV, HEMI, LIT, ODO, ORTH, SPT, STY

^{||} ALF, ARA, DIT, LHL, LIT, HARV, SPT

^{¶¶} ALF, ARA, HD, LIT, LUM, YR

Table 3. Model coefficients with standard errors in parentheses for variables retained in final models (Table 2) for abundance, occupancy, and reproductive activity of Bobolink, Savannah Sparrow, and Nelson's Sharp-tailed Sparrow in Nova Scotia. Model notation follows Table 1.

Model for	Variables retained in best model	β (SE)
<u>Bobolink</u>		
abundance (female + male)	<i>HD</i>	0.34 (0.19)
	<i>HEMI</i>	0.03 (0.02)
	<i>ORTHO</i>	0.71 (0.98)
abundance (female)	<i>COV</i>	0.34 (0.15)
	<i>ALF</i>	-0.36 (0.19)
abundance (male)	<i>HD</i>	0.17 (0.08)
	<i>HEMI</i>	0.02 (0.01)
occupancy	<i>HD</i>	0.68 (0.25)
	<i>FORB</i>	-0.19 (0.08)
reproductive activity	<i>HD</i>	1.14 (0.39)
	<i>ARA</i>	0.69 (0.20)
	<i>DIP</i>	0.07 (0.02)
	<i>ODO</i>	0.09 (0.03)
<u>Savannah Sparrow</u>		
abundance	<i>DIP</i>	0.02 (0.01)
	<i>CHIL</i>	-0.65 (0.38)
	<i>HD</i>	-0.37 (0.15)
occupancy	<i>COLP</i>	0.51 (0.21)
	<i>FORB</i>	-0.04 (0.02)
	<i>HD</i>	-1.12 (0.45)
reproductive activity	<i>OPIL</i>	1.87 (0.52)
	<i>FORB</i>	-0.19 (0.08)

(con'd)

Nelson's Sparrow

abundance	<i>DIT</i>	3.22 (0.93)
	<i>ORTHO</i>	0.05 (0.02)
	<i>ALF</i>	-0.14 (0.05)
occupancy	<i>DIT</i>	7.12 (10.89)
	<i>ARA</i>	0.06 (0.03)
	<i>LHL</i>	0.26 (0.12)
reproductive activity	<i>HD</i>	0.19 (0.06)
	<i>ARA</i>	0.03 (0.01)
	<i>ALF</i>	-0.49 (0.23)

ordinal regression, random effects were not modeled.

Models from independent data sets

Comparing the best models from our study site to only analogous variables for each regional dataset yielded the top models in Table 4. Vegetation *HD* was most important in every model for Bobolink occupancy and abundance (sexes combined) and represents a strongly predictive variable. *HD* was also negatively related with Savannah Sparrow abundance in Iowa prairie/restored grasslands (as we observed in Nova Scotia hayfields), but positively associated with Savannah Sparrow abundance in Wisconsin pastures. *HD* was also retained as a positive term in the top models for Savannah Sparrow occupancy in Wisconsin (but was negative in Nova Scotia). Two very different models (Table 4) to predict male Bobolink abundance were chosen for Iowa and Nova Scotia. Wisconsin data were not available.

DISCUSSION

This study identified habitat characteristics important to three grassland bird species across a large geographic area. Moreover, the importance of

these habitat features was observed in agroecosystems under three different forms of land use. This allows for the development of some generalized conservation and habitat management prescriptions for the three species, which should benefit other species as a result. This study also illustrates the importance of confronting models with data from other regions and independent research, which makes our recommendations more likely to be applicable across a range of agricultural grasslands and regions.

For Bobolinks, higher and denser grass in May, i. e., the pre-breeding season, was associated with increased occupancy rates and abundance in each study region, i.e., Nova Scotia, Iowa, and Wisconsin, representing three agricultural landscape types: hayfield, pasture, and restored prairie. This is consistent with other reported correlations of Bobolink abundance from other regions (Herkert 1994, Bollinger 1995). It is worth noting that the high variance associated with random effects in Bobolink abundance models is likely related to the propensity of males to aggregate their territories, although this speculation warrants further examination. Reproductive activity, in Nova Scotia, was also positively related to vegetation height-density in May for both Bobolinks and Nelson's Sparrow. This highlights the general importance of vegetation height-density (see also Madden et al. 2000), which has been linked with fitness for other

Fig. 1. Mean abundance of Bobolink/point-count station as a function of vegetation height-density in dm, determined using method of Robel et al. 1970 in May. Although linear mixed-effects models were used, least-squares trendline is shown to illustrate direction of relationship.

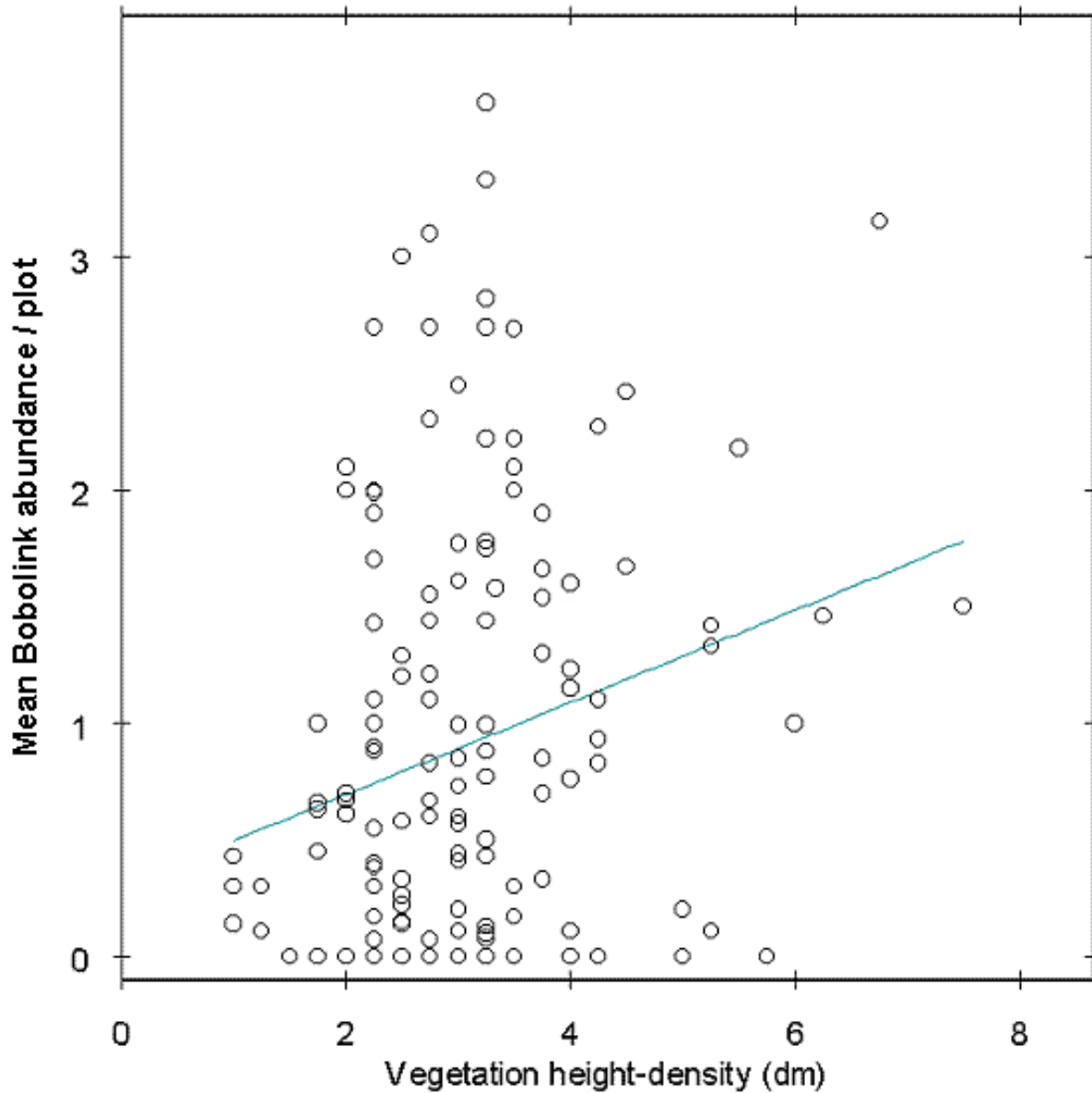


Fig. 2. Mean abundance of Savannah sparrow per point-count station as a function of vegetation height-density in dm, determined using method of Robel et al. 1970 in May. Although linear mixed-effects models were used, least-squares trendline is shown to illustrate direction of relationship.

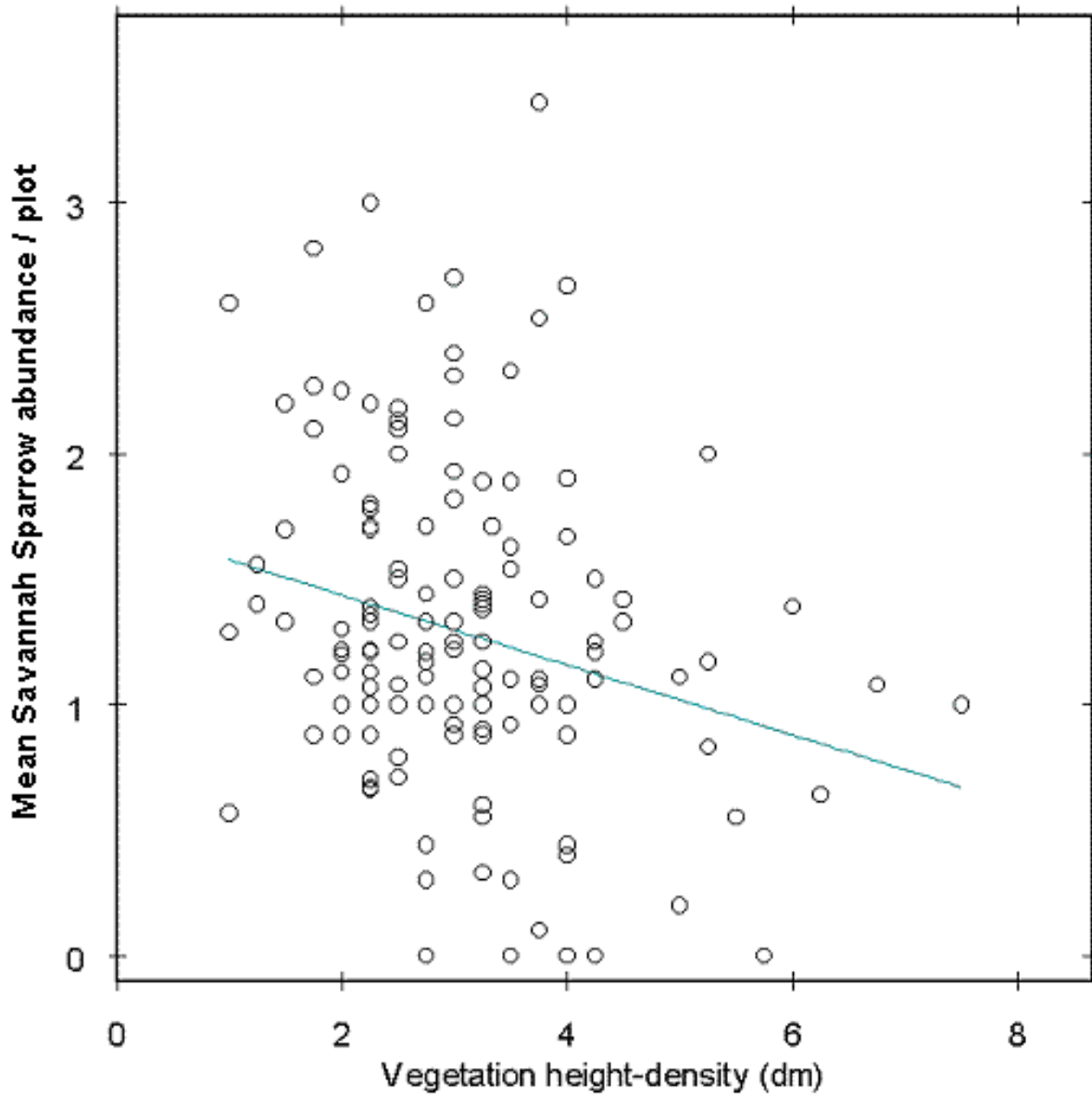


Table 4. Top models of vegetative correlates (notation as per Table 1) for presence/absence, i.e., occupancy, and abundance of Bobolinks and Savannah Sparrows from three different regions, habitat types, and studies: Nova Scotia, i.e., hayfields, this study, Wisconsin (pastures; Renfrew 2002), and Iowa (prairies and restored grasslands; Fletcher 2003). Only combined-sex Bobolink data were available for Wisconsin. Lower-case letters represent variables important to Nova Scotia models not sampled in Wisconsin or Iowa. Logistic mixed-effects models were created to model occurrence, and linear mixed-effects models for abundance. Variables in bold are shared in top models for all study sites.

	Region		
	Nova Scotia	Wisconsin	Iowa
Top model of:			
Bobolink occupancy	HD - FORB	HD	HD + LIT + COV
Bobolink abundance (female + male)	HD + hemi + orth	HD	HD + LIT + FORB + COV
Bobolink abundance (female)	COV - alf		HD
Savannah Sparrow occupancy	Colp - FORB - HD	HD - COV	LIT
Savannah Sparrow abundance	dip - chil - HD	HD + FORB	- COV - HD

species associated with farmland like the Magpie (*Pica pica*) and Meadow Pipit (*Anthus pratensis*) (Perkins et al. 2000). Increased height and density (in the spring) could indicate suitable nesting locations because it facilitates nest concealment and reduces detection by predators (Fondell and Ball 2004), and provides seeds for foraging granivores in both early- and late-season (Vickery and Gill 1999).

Conversely, Savannah Sparrow abundance showed a negative relationship with vegetation height-density in both Nova Scotia and Iowa, but the reverse in Wisconsin pastures. This pattern of differential response to vegetation height-density has been documented before (see Madden et al. 2000), particularly for Savannah Sparrows (Fondell and Ball 2004). We attribute that vegetation height-density was negatively related with Savannah Sparrow abundance in Iowa and Nova Scotia, but positively associated with Savannah Sparrow abundance in Wisconsin pastures to an artefact either of pastures being so open that birds were using the tallest of what was otherwise very short grass, or were placing their nests in localized tufts of tall grass, but occurring throughout the pasture. This suggests a unimodal relationship between Savannah

Sparrow abundance and vegetation height-density that could be tested with additional data from areas with more mid-range vegetation height-density values than those examined here. This again highlights the ubiquity of the importance of vegetation height-density, but it is counter to the patterns that would benefit Bobolinks and Nelson's Sparrows. Although this species is limited by other physiographic factors, such as patch size (Vickery et al. 1994), it is not as much of a conservation concern because it is widespread and common (Dale et al. 1997).

Vegetation height-density in the pre-breeding season is an easily managed habitat characteristic. Ensuring fields are not cut late (e.g., after late August in Nova Scotia) in the preceding year, to allow for extra growth and height prior to winter, should promote reproductive activity for Nelson's Sparrow and Bobolink, and both Bobolink occupancy and abundance (see Fig. 1). In northern climes, this would mean forgoing either a third hay crop or a very late second crop for the year, usually harvested in September (Nocera and Milton, unpublished data). Refraining from cutting after August is a feasible practice, as third harvests of forage crops tend to be low yield (e.g., Kallenbach

et al. 2002) and are often harvested only to “clean up the field” rather than truly increase haylage stocks (Nocera and Milton, unpublished data). If a farm were in need of late-season harvests, simultaneous management could still be accomplished by staggering harvest across a farm so that some fields are cut after August to benefit species like Savannah Sparrows, while others are not cut after August to benefit other species. Vegetation heterogeneity in landscapes could be managed to benefit as many taxa as possible.

Birds can reproduce successfully in agricultural grasslands in which farmers delay their hay harvest until after fledging (Bollinger et al. 1990, Vickery et al. 2004, Nocera et al. 2005). Given the results of the current study, we suggest that, in addition to not harvesting too early (during the breeding period), it is likewise important to also not harvest some fields too late in the season (early fall), to ensure adequate growth in the spring. These recommendations would require that hay harvest be restricted to an optimal time window, which, in Nova Scotia, would be from early July to late August. We predict a large net conservation benefit from such a prescription for many species, which remains to be tested. Such benefits will also help agricultural landscapes shed the sometimes-unwarranted image of being reproductive sinks and “ecological traps” (Best 1986; Dale et al. 1997); a delayed first harvest will allow birds to reproduce successfully and a forgone late-season, often third, harvest will ensure adequate vegetative structure when they arrive in the spring. The farmer need not lose from this prescription, because hay of high nutritional quality can still be harvested (Nocera et al. 2005) during July and August.

An important connection to landscape physiography is the positive relationship between the total amount of ditch and Nelson’s Sparrow occupancy and abundance. Nelson’s Sparrows likely use hayfield ditches as foraging areas and saltmarsh surrogates, to fulfill a general requirement for dense, damp swards of vegetation (Greenlaw and Rising 1994; Hanson and Shriver 2006). Typically, ditches that remain uncut provide a damp environment with tall coarse vegetation. A simple management action that would benefit this species in agricultural lands during the breeding season is to ensure some ditches remain uncut. In Nova Scotia, farmers often cut grass in ditches and do not use the resultant hay (Nocera and Milton, unpublished data). This is

largely because the dominant grass species in ditches tends to be coarse and early maturing, e.g., reed canary grass, making it unpalatable for livestock. Therefore, an easily executed management action is to limit the cutting of ditch grass to only periods of maintenance, the benefits of which are not limited to Nelson’s Sparrow. For instance, in the UK, species of some conservation concern such as Whitethroats (*Sylvia communis*), Yellowhammers (*Emberiza citrinella*), and Reed Buntings (*E. schoeniclus*) can all benefit from proper ditch management (Vickery et al. 2004).

Prey did not influence whether Bobolinks occurred at a site. Savannah Sparrow occupancy patterns, however, did show a positive relationship with the abundance of pitfall-trapped beetles, i.e., primarily ground beetles, Carabidae. This is consistent with the finding that beetles constitute a substantial proportion of the Savannah Sparrow diet (>33%, Wheelwright and Rising 1993; Kobal et al. 1998), particularly during years of low grasshopper abundance (Miller and McEwen 1995). Additionally, Nelson’s Sparrow occupancy was positively associated with abundance of caterpillars and spiders, both of which represent important prey items for adults and nestlings (Greenlaw and Rising 1994; particularly spiders, Montagna 1942).

On the other hand, arthropod prey was more often associated with how many individuals resided in an area. This does not suggest that the species are limited by prey availability (Wiens 1969), but rather indicates a simple tendency to settle in areas of greater resources. Bobolink abundance (in models for females and both sexes combined) was positively associated with true bugs; one of the top four prey groups fed to nestling Bobolinks (Wittenberger 1982). Hemipterans have one of the highest levels of gross energy content and fat composition among insects in agro-ecosystems (Robel et al. 1995), particularly members of family Miridae (plant bugs), which constituted the bulk of Hemipterans sampled in this study. Nelson’s Sparrow abundance was likewise positively related to grasshopper abundance; an important link given that grasshopper species representing four different families are known to be food for nestlings (Greenlaw and Rising 1994). Abundance of Savannah Sparrows also showed positive correlation to the abundance of flies, another known prey item (Wheelwright and Rising 1993; Kobal et al. 1998).

Reproductive activity, for all three species, was positively related to the abundance of spiders and their allies. The abundance of spiders caught in pitfalls was retained in the top model for Bobolink and Nelson's Sparrow reproductive activity, while harvestmen were in the top model for Savannah Sparrow. We suggest that, although spiders are important prey for most grassland birds, they may not contribute directly to reproductive activity but are likely associated with a latent variable. This prediction warrants further examination.

An important caveat to our prey relationship models is that our taxonomic information was very coarse. This is a common problem in grassland bird literature. Most studies do not identify arthropod prey beyond family or order, largely because they must examine partially digested regurgitate or highly fragmented prey, e.g., recoveries from nestlings with ligatures around their necks to prevent swallowing, which renders detailed taxonomic identification impossible, and is usually biased towards detecting hard-bodied insects (Wheelwright and Rising 1993). Additionally, prey availability, and hence, what a bird may or may not eat, is notoriously difficult to estimate because it is a complex function of abundance, body size, nutrients, energy (calories), life stage, palatability, and ease of capture (Poulin and Lefebvre 1997). Therefore, particularly when size or nutrient value varies greatly within a group, more precise taxonomic identification of prey would yield more informative results (Poulin and Lefebvre 1997). This level of detail is an important and untouched aspect of grassland bird ecology that future studies should try to consider.

Our assessment of models across regions highlights the ubiquitous importance of the variables retained in top models. However, we acknowledge that not all relationships, such as those we observed, could be expected to be consistent across space and time. For instance, Davis (2004) found temporal variation in relationships between grassland birds and habitat between years. We found little important variation between years; we included year as a factorial explanatory variable and it was never retained in any best-fit models. Secondly, habitat use patterns can vary across space, sometimes substantially (Johnson and Igl 2001). Such spatial variation has been suggested for Nelson's Sparrow (Nocera et al. 2007), so it is unfortunate that we were unable to procure independent data to test our habitat models for Nelson's Sparrow in other parts of its range. Our

models for this species are thus only truly pertinent to our study area. However, because the habitat features in our models were at least adequate to support Nelson's Sparrow in Nova Scotia, our management recommendations likely pertain elsewhere, or are at least unlikely to elicit adverse effects. Therefore, we caution that our models have not defined "high-quality" Nelson's Sparrow habitat; this needs further study at a broader landscape scale than we performed.

Nonetheless, the models we present provide a robust assessment of resource use by some grassland birds in agro-ecosystems and the association with their occurrence, abundance and measures of reproduction. This is an important distinction, because models typically include only one population response parameter of interest, which may be misleading when trying to assess or manage for several aspects of population dynamics (Van Horne 1983). The net benefit derived from any of the management suggestions presented here are all the more likely to be greater if incorporated into sympathetic agro-ecosystem management that provides for habitat heterogeneity. In our study, we examined three response variables from among many other measurable variables. It will be worthwhile for future research to examine how model development when confronted with population parameters that may behave very differently, such as mortality and fledging success. Regardless of the variables chosen, further studies that include multiple responses, study sites, and broad habitat assessments are likely to accrue even greater conservation benefit.

Responses to this article can be read online at:
<http://www.ace-eco.org/vol2/iss1/art7/responses/>

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