SUCCESSIONAL CHANGES AND HABITAT SELECTION IN HAYFIELD BIRD COMMUNITIES

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ABSTRACT.—I examined the effects of successional changes in vegetation on the breeding dispersion of grassland birds in hayfields in New York. I sampled vegetation and counted birds in 90 hayfields of various ages (i.e. number of years since planting) and sizes that were originally planted to a legume-dominated seed mixture. I also resampled a subset of these fields two years later. Over time, these hayfields changed from tall, dense, homogeneous stands of legume-dominated vegetation to short, sparse, patchy stands of grass-dominated vegetation. Fields of all ages were dominated by introduced plant species. Red-winged Black-birds (*Agelaius phoeniceus*), the most common bird species breeding in these fields, were most common in fields of intermediate ages, whereas numbers of Bobolinks (*Dolichonyx oryzivorus*), the second most abundant species, increased logarithmically with field age. Upland Sand-pipers (*Bartramia longicauda*), Eastern Meadowlarks (*Sturnella magna*), Grasshopper Sparrows (*Ammodramus savannarum*), and Henslow's Sparrows (*A. henslowii*) were most abundant in the oldest hayfields, whereas abundances of Savannah Sparrows (*Passerculus sandwichensis*, the third most common species) did not differ in fields of different ages. Bird-species richness and diversity increased linearly with hayfield age. Three species (Red-winged Blackbird, Bobolink, Savannah Sparrow) accounted for more than 90% of the breeding individuals. Vegetation structure, composition, and patch size were the most important proximate correlates of habitat selection for these species. Hayfield size was positively correlated with abundance for five of the seven most common species. Furthermore, those species that nested late in the season (Bobolinks, Grasshopper Sparrows, and Henslow's Sparrows) had low breeding densities in fields with early mowing dates the previous year. *Received 14 June 1993, accepted 6 September 1994.*

PREDICTION AND EXPLANATION of habitat selection in birds is a common focus of ornithological research (e.g. Hilden 1965, Cody 1985, Ganey and Balda 1994). Attributes of the vegetation usually are regarded as the most important determinants of avian habitat selection (James 1971, Rotenberry and Wiens 1980, Mills et al. 1991). However, other factors may modify and constrain habitat selection, including intraspecific competition (Fretwell and Lucas 1970, Wiens 1985, Andrén 1990), interspecific competition (Cody 1974, Diamond 1978), size of habitat patches (Whitcomb et al. 1981, Robbins et al. 1989), site tenacity (Hilden 1965, Wiens 1985), densities of predators and parasites (Brittingham and Temple 1983, Martin 1988, Johnson and Temple 1990), and anthropogenic factors (Bollinger et al. 1990, Frawley and Best 1991).

Studying habitat selection of grassland birds in eastern hayfields has several potential merits.

First, avian studies in grasslands of North America have been confined primarily to the midwestern prairies (e.g. Cody 1968, 1985, Wiens 1969, Zimmerman 1992). However, many species of grassland birds have expanded their ranges into, or become much more abundant in, the eastern United States as a result of land clearing and agricultural practices (Hurley and Franks 1976). Second, legume-dominated hay-fields undergo successional changes in vegetation that can be useful in studying habitat selection in birds. By looking at changes in densities of bird species as the vegetation changes over time, it may be possible to determine the optimum habitat(s) for species, as well as the range of acceptable habitats (Johnston and Odum 1956, Shugart and James 1973). Third, because the date of stand establishment can be determined for many hayfields, some of the effects of site tenacity can be assessed. Finally, the influence on habitat selection of hay-cropping, which can significantly reduce reproductive success for grassland birds (Bollinger et al. 1990), can be determined.

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My specific objectives were to: (1) describe the vegetation and avifauna of hayfields of different ages and to document the effects of hayfield succession on habitat selection in grassland birds; and (2) relate differences in bird species abundances among hayfields to differences in vegetation and to some of the other factors that may affect habitat selection.

METHODS

Study area.—This study was conducted in 1984–1986, primarily in central Madison and Tompkins counties, New York. I interviewed local landowners and obtained information on nearly 300 hayfields. From this group of fields, I selected a stratified-random sample of 90 fields originally planted to either a pure-legume mixture or a legume-grass mixture; field age, size, and soil type were strata. Fields were not adjacent to other hayfields and pastures or were separated from other grasslands by woody hedgerows.

Vegetation sampling.—Vegetation was sampled in each of the 90 fields along a transect line (Wiens 1969) randomly located such that it was more than 100 m from the edges of the field. Ten sampling locations were selected per field. For a 0.25-m² quadrat at each location, I visually estimated percent cover for all living vegetation, as well as for each genus of plant occupying 2% or more of the quadrate (Table 1). Vegetation was sampled between 20 and 29 May each year. The total area sampled per field was small but adequate given the relatively homogeneous vegetation.

The variables that I selected to examine vegetation succession and habitat selection are described in Table 1. Alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*), and birdsfoot trefoil (*Lotus corniculatus*) are the three most common legumes planted for hay in New York (Pardee unpubl. report). Dandelion (*Taraxacum officinale*) was the most abundant weed in the hayfields I sampled, and its seeds are a common food item for some hayfield-nesting birds (pers. obs.). Grasses represent the second major group of forage plants; stout-stemmed grasses (e.g. brome grass [*Bromus inermis*], orchard grass [*Dactylis glomerata*]) were frequently used to support nests by Red-winged Blackbirds. I included total cover, litter cover, and vegetation height because of documented effects of these parameters on grassland bird densities in other studies (Tester and Marshall 1961, Wiens 1969, Rotenberry and Wiens 1980, Kantrud 1981, Zimmerman 1988). Coefficients of variation for vegetation height and total cover were used to index vertical and horizontal vegetation patchiness (Rotenberry and Wiens 1980). I also randomly selected 14 fields that were originally sampled in 1984 to resample in 1986. Seven fields were selected from each of two age categories (≤3 years and ≥10 years). The following vegetation

TABLE 1.   Description of habitat variables measured on 90 hayfields in central New York. Variables 1–12 based on means for 10 0.25-m² plots.

1. Percent total cover.—Percent cover of all living vegetation.
2. Percent alfalfa.—Percent cover of *Medicago sativa*.
3. Percent clover.—Percent cover of *Trifolium* (primarily red clover, *T. pratense*).
4. Percent trefoil.—Percent cover of *Lotus corniculatus*.
5. Percent grass.—Percent cover of all grasses.
6. Percent stout grass.—Percent cover of all stout-stemmed grasses (e.g. orchard grass, *Dactylis glomerata*; smooth brome grass, *Bromus inermis*).
7. Percent dandelion.—Percent cover of *Taraxacum officinale*.
8. Litter index.—Percent ground cover of dead vegetation, mean of index: (1) <5%; (2) 5–25%; (3) 26–50%; (4) 51–75%; (5) >75%.
9. Plant richness.—Number of plant genera/0.25-m²/plot (only genera with ≥2% cover included).
10. Vegetation height.—Height (in centimeters, 5-cm intervals) at which a Robel stick (Robel et al. 1970) is totally obscured by vegetation when viewed from 2 m away at 60 cm off ground.
11. Vertical patchiness.—Coefficient of variation of variable 10.
12. Horizontal patchiness.—Coefficient of variation of sum (by plot) of the percent coverages of all plant genera.
13. Field size.—Field size in hectares (determined from aerial photographs and by pacing field perimeters).
14. Field age.—Number of years since the stand of hay was established.
15. Percent field border in woods.—Percent of field perimeter bordered by woods (determined by pacing).

variables were measured: percent legume cover, percent grass cover, percent total vegetation cover, and percent litter cover.

Bird counts.—I used line transects (Burnham et al. 1980) to estimate bird abundance in hayfields. In all years, counts were completed between 0530 and 0800 EST from 29 May to 12 June under certain weather restrictions (see Robbins and VanVelzen 1969). Birds were counted along each transect twice, with one count during each week. One of the counts was completed between 0530 and 0700 and the other after 0700. Means of the two counts were used in data analysis.

In addition, I counted birds in 1986 in a subset of the fields originally counted in 1984. All fields in which no major changes had occurred either within (e.g. part of field plowed) or adjacent (e.g. hedgerow removed) to the field were recounted. All bird counts and vegetation sampling were completed before hay-cropping commenced (usually mid-June). After a field

TABLE 2. Description of hayfields used to determine breeding dispersion of grassland birds in central New York. All hayfields were originally planted to a legume or legume/grass mixture.

Age class (years)[a]	No. fields	Mean age (years)	Field size (ha; $\bar{x}$ and range)
1	12	1.0	9.6 (2–17)
2–3	20	2.4	10.0 (3–22)
4–7	20	4.8	8.3 (3–15)
8–14	20	9.7	9.5 (2–26)
≥15	18	18.8	9.8 (3–20)

[a] Number of years since stand established. First-year fields were in first full-production year; age classes used to stratify sample and to illustrate successional patterns. All other analyses (including all regression models) used exact age.

was mowed, it was no longer used as a breeding site by Red-winged Blackbirds (*Agelaius phoeniceus*) and Bobolinks (*Dolichonyx oryzivorus*) and overall breeding densities dropped over 90% (unpubl. data; see also Frawley and Best 1991).

Data analysis.—I examined vegetation succession in hayfields by considering vegetation differences among fields of different ages as well as vegetation changes within the same fields two years later. For among-field comparisons, I used stepwise multiple-regression techniques (SAS Institute 1982) with vegetation parameters as the dependent variables and field age, age^2, age^3, and ln(age) as the candidate independent variables. Only significant variables (i.e. $P < 0.05$, sequential sums of squares) were included in the models. For within-field comparisons, I used paired *t*-tests to evaluate changes in vegetation parameters between years.

I examined the bird-count data for changes in bird detectability relative to season (i.e. first count week vs. second count week), time (i.e. early [0530–0700] vs. late [after 0700]), and year (1984–1986) for each species and sex with a sufficient number of observations. Chi-square tests indicated no changes in detectablity over season (all $P > 0.05$), time (all $P > 0.20$), or year (all $P > 0.10$). For most species I used the number of birds/100 m of transect as an index of bird abundance. For Bobolinks and Red-winged Blackbirds (the two species with obvious sexual dimorphism), I used number of males/100 m of transect because this index was more highly correlated with total density for Bobolinks than when sexes were combined (Bollinger 1988). To document changes in the density of each bird species occurring as a result of hayfield succession, I used methods analogous to those used to document vegetation succession. I also looked at the effects of succession on bird species richness and diversity.

A stepwise multiple regression also was used to determine which habitat variables (Table 1) were significant predictors of the abundances of the various

grassland bird species. Although the approach I used considered only linear relationships (and population densities of birds may not respond in linear fashion to changes in habitat features; Wiens 1985, Best and Stauffer 1986), I had little *a priori* reason to expect strongly nonlinear patterns among the variables I considered. Residual plots also indicated that my data met the assumptions of linear regression analysis. I transformed bird abundances ($\log[x + 1]$) where needed to equalize variances.

First, I considered all 90 hayfields and looked for relationships between bird densities and the variables shown in Table 1. To determine the importance of date of hay cropping (first cutting) the previous year in affecting bird dispersion, I ran a second series of regressions including the Julian date of hay cropping along with the original 15 variables. First-year fields were omitted from the latter analysis.

RESULTS

Description of hayfields and birds.—Field size and transect length did not vary with field age (ANOVA, $P > 0.50$; Table 2); neither did the proportion of fields planted to pure legume (vs. a legume-grass mixture; chi-square test, $P > 0.20$). Red-winged Blackbirds, Bobolinks, and Savannah Sparrows (*Passerculus sandwichensis*) were the three most commonly encountered birds in these hayfields and were detected, respectively, in 95, 73, and 66% of the fields. Eastern Meadowlarks were the next most abundant, being found in 33% of the fields.

Vegetation and avifauna succession in hayfields.—Vegetation differed markedly among hayfields of different ages (Figs. 1 and 2). Vegetation variables that declined significantly ($P < 0.001$) with field age included legume cover (percent alfalfa + percent clover + percent trefoil), total cover, and vegetation height. Variables that increased with field age included both vertical and horizontal patchiness, litter index, plant richness, and plant diversity. Grass cover and stout-stemmed-grass cover displayed a more complex, quadratic relationship with field age (Figs. 1C and 2A). Fields of all ages were dominated by introduced plant species.

The vegetation changes within fields between 1984 and 1986 agreed rather closely with those found among fields of different ages (Fig. 1). Fields up to three years old in 1984 showed significant declines in legume cover and total cover and significant increases in grass cover and litter cover by 1986 ($P < 0.05$, paired *t*-tests).

(A) PERCENT TOTAL COVER

$Y=93.55-6.11(LnX)-0.88X$
$r = 0.77$

(B) PERCENT LEGUME

$Y=82.20-27.00(LnX)$
$r = 0.90$

(C) PERCENT GRASS

$Y=11.86-5.58X+32.26(LnX)$
$+0.0036X^3$ $r = 0.61$

(D) LITTER INDEX

$Y=1.31+0.19(LnX)$
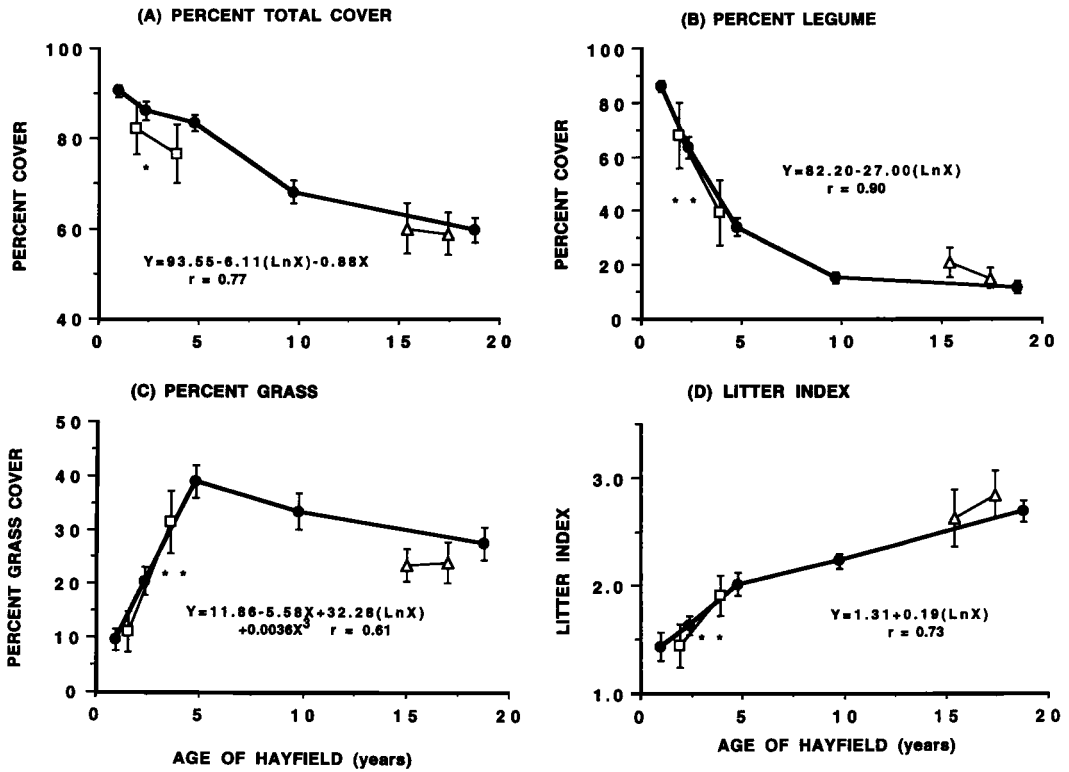$r = 0.73$

AGE OF HAYFIELD (years)

AGE OF HAYFIELD (years)

Fig. 1.   Relationships between hayfield age (in years since seeding) and various vegetation parameters for 90 hayfields in central New York. All fields originally planted to a legume or legume/grass mixture. Solid circles represent mean values (±SE) for the various age classes of fields (see Table 2). Open squares and triangles represent, respectively, values for seven "young" (≤3 years in 1984) and seven "old" (≥10 years in 1984) fields sampled in both 1984 and 1986 (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; paired t-tests). Also shown are regression models, where Y is the vegetation parameter, X is hayfield age, X^2 is age^2, X^3 is age^3, and LnX is log$_e$ (age). Models are significant ($P < 0.001$).

Both the direction and magnitude of these changes agreed with among-field patterns. Fields more than 10 years old in 1984 did not show significant changes in these variables between 1984 and 1986; however, for three of the four variables the direction of the change was the same as that found among fields.

The seven most common bird species also tended to show changes in abundance among fields of different age classes (Fig. 3). Initially, the numbers of Red-winged Blackbirds increased rapidly, but they then declined as the fields aged. Bobolinks increased logarithmically, whereas Savannah Sparrows showed no significant variation in abundance with field age. Eastern Meadowlarks increased linearly with field age. Upland Sandpipers (*Bartramia longicauda*), Henslow's Sparrows (*Ammodramus henslowii*), and Grasshopper Sparrows (*A. savanna-*

rum) were only detected in the oldest fields, and their abundances were positively correlated ($r > 0.27, P < 0.05$) with field age.

Changes in bird abundance within fields I sampled in 1984 and 1986 were similar to differences that existed among fields of different ages (Fig. 3A–D). Both Red-winged Blackbirds and Bobolinks increased in abundance in the younger fields ($P < 0.05$, paired t-tests) and showed no significant changes in the older fields (although the decline in Red-winged Blackbirds approached significance; $P = 0.08$). Savannah Sparrows showed no significant changes within fields. Upland Sandpipers, Henslow's Sparrows, and Grasshopper Sparrows were not common enough in the fields that I resampled to make such comparisons meaningful.

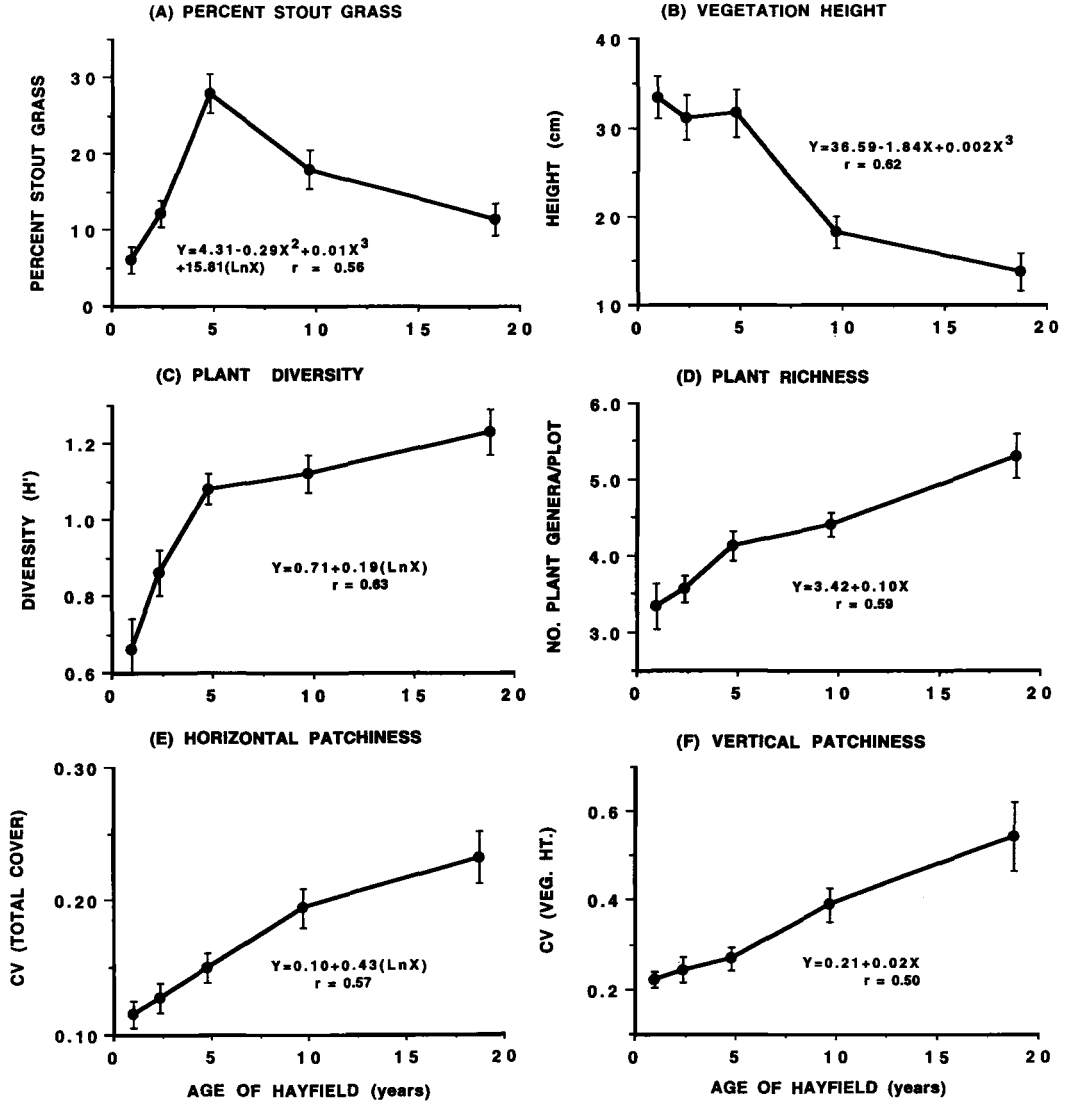Three species (Red-winged Blackbirds, Bobolinks, and Savannah Sparrows) comprised, on

Fig. 2. Relationships between hayfield age (in years since seeding) and various vegetation parameters for 90 hayfields in central New York (see Fig. 1 for details).

average, over 90% of the individuals counted in hayfields (Fig. 4). The youngest fields were dominated by Red-winged Blackbirds and Savannah Sparrows; Bobolinks were the most common species in the oldest hayfields. Overall, bird-species richness and diversity increased linearly with field age (Fig. 5).

Hayfield characteristics and bird abundance.—Stepwise multiple regressions indicated that percent cover by stout-stemmed grasses explained the most variability in Red-winged Blackbird abundance (Table 3). For Savannah Sparrows, the first variable included was the

percent of field edge in woods. Of the remaining five species, percent total cover was the first variable entered into regression models for Bobolinks, Eastern Meadowlarks, and Upland Sandpipers. These species reached highest densities in hayfields with lowest percent total cover. Field size was included in models (positive correlations explaining 3 to 26% of the variation in bird densities) for Bobolinks, Savannah Sparrows, Upland Sandpipers, Henslow's Sparrows, and Grasshopper Sparrows.

When a field's mowing date the previous year was evaluated in regression analyses along with
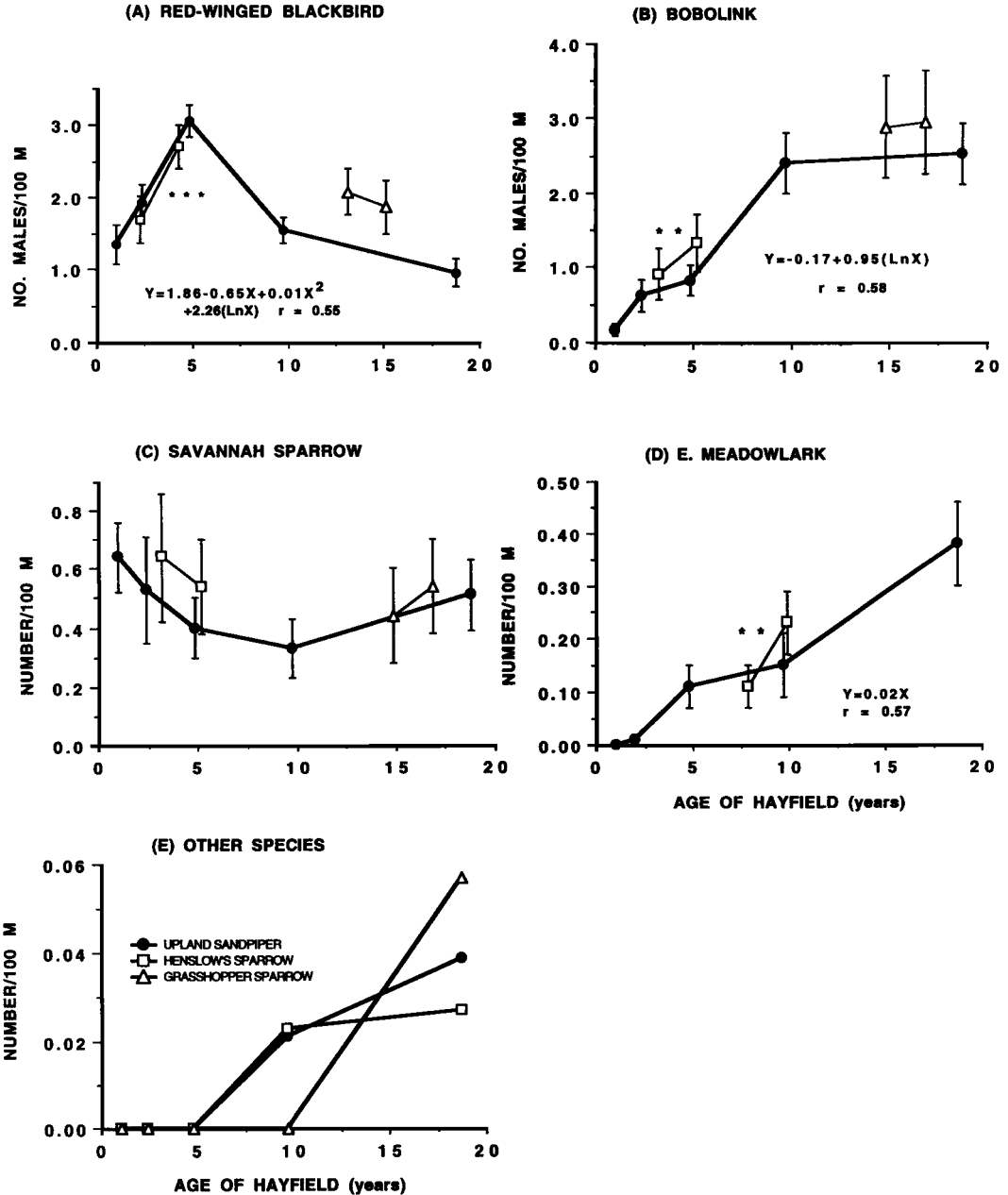
Fig. 3.   Relationships between hayfield age (in years since seeding) and abundances (number of birds/100 m of line transect) of seven most commonly detected bird species in 90 hayfields in central New York. Solid circles represent mean abundances ($\pm$SE) for the various age classes of fields (Table 2). Open squares and triangles represent mean values for 25 fields censused in both 1984 and 1986 (***, $P < 0.001$; **, $P < 0.01$; paired t-tests). Also shown are regression relationships between bird abundances and hayfield age (see Fig. 1 for details).

the other 15 variables, it was included in models for Bobolinks, Grasshopper Sparrows, and Henslow's Sparrows. It was marginally significant ($P = 0.09$, sequential sums of squares) for Up-

land Sandpipers. Fields with earlier mowing dates had densities of these species that averaged 18% lower than would be expected based on their habitat parameters.
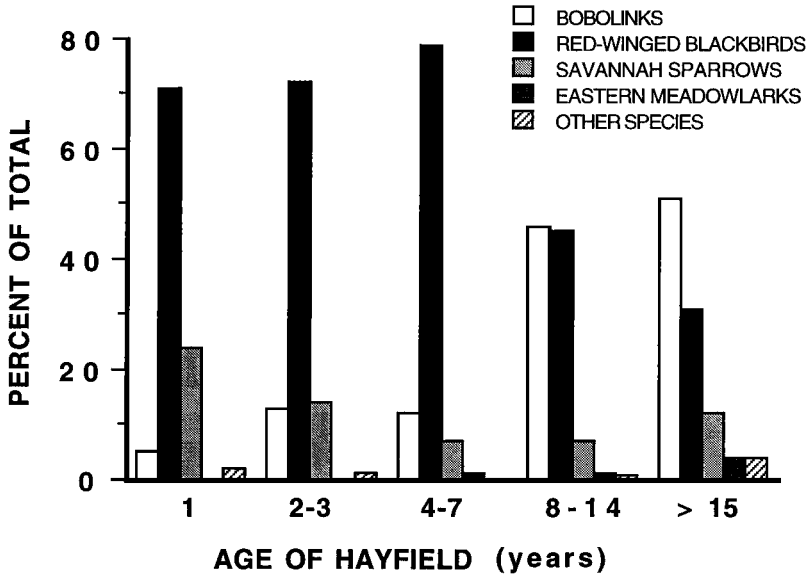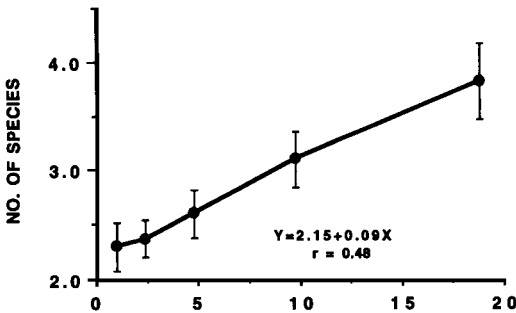
Fig. 4.   Species composition (percent of total detected) for five age classes of hayfields (n = 90) in central New York.

(A) BIRD SPECIES RICHNESS
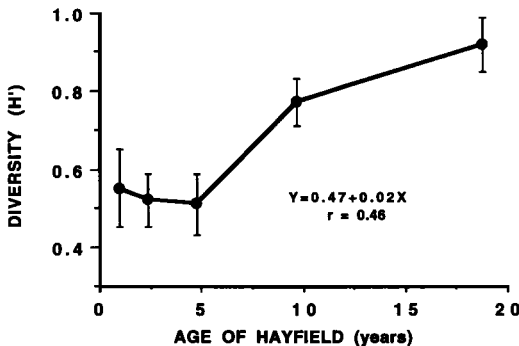

(B) BIRD SPECIES DIVERSITY

Fig. 5.   Relationships of hayfield age (in years since seeding) with (A) bird-species richness and (B) diversity (Shannon-Wiener H') for 90 hayfields in New York. Solid circles represent means (±SE) for the five age classes (Table 2).

DISCUSSION

Vegetation and avifauna succession in hayfields.— Vegetation in hayfields originally planted to a legume or legume/grass mixture changed in predictable patterns over time. As fields became older (i.e. more consecutive years of hay cropping), they shifted from dense, homogeneous, legume-dominated communities to sparse, patchy, grass-dominated communities as the legume crop died out. These patterns, although derived from fields of different ages, were supported by the short-term (two-year) vegetation changes that I measured within the same fields. In general, nutrient inputs to hayfields (manure, other fertilizers) are below the nutrients removed by hay cropping. Declining yields of both total biomass and alfalfa are primarily responsible for the current practice of rotating alfalfa fields to another crop after four years in New York (Bollinger 1988). The relative increase in grasses probably occurs because they tend to be more winter hardy and more tolerant of high soil moisture (Baylor and Vough 1985, VanKeuren and George 1985). The death of legume plants in certain portions of a stand also creates a "patchier" field; subsequent invasion of fields by weed species increases plant-species richness and diversity. Loss of cut vegetation during hay cropping (15–25% of potential yield;

TABLE 3. Independent variables included in stepwise multiple regressions of abundances of seven species of birds nesting in 90 hayfields in central New York. Candidate variables described in Table 1.

Species	r^2	Independent variables[a]
Red-winged Blackbird	0.78	+Stout grass (0.59), +Total cover (0.11), −Grass (0.05), +Dandelion (0.02), +Plant richness (0.01).
Bobolink	0.70	−Total cover (0.49), +Field size (0.16), −Vertical patchiness (0.02), +Trefoil (0.02), +Field age (0.02).
Savannah Sparrow	0.15	−Field border in woods (0.06), −Grass (0.06), +Field size (0.03).
Eastern Meadowlark	0.51	−Total Cover (0.38), −Vertical Patchiness (0.08), +Plant Richness (0.03), −Trefoil (0.02).
Henslow's Sparrow	0.35	+Field Size (0.26), −Vegetation Height (0.09).
Grasshopper Sparrow	0.38	+Plant Richness (0.25), +Field Size (0.08), −Litter (0.03), +Vertical Patchiness (0.02).
Upland Sandpiper	0.25	−Total Cover (0.15), +Field Size (0.07), −Vegetation Height (0.03).

[a] Independent variables listed in order in which they were included in model; all variables listed were significant ($P < 0.05$, sequential sum of squares); partial r^2 in parentheses; "+" before variable name denotes positive association with bird abundance; "−", a negative association.

Miller 1984) is largely responsible for the increase in litter cover over time.

Associated with these temporal changes in vegetation were changes in the avifauna. Red-winged Blackbirds were the most abundant bird in young hayfields, whereas Bobolinks were the most abundant bird in older hayfields (Graber and Graber 1963). As with the vegetation data, changes in bird species abundance within fields resampled two years later agreed closely with between field patterns. This strongly supports the hypothesis that the avifaunal differences I detected in fields of different ages were primarily the result of successional changes in the vegetation occurring within the fields.

In particular, changes in Red-winged Blackbird abundance seem related to successional changes in the availability of suitable nest support and cover. Red-winged Blackbirds were most abundant in fields with dense cover and dense stands of stout-stemmed grasses. Nests of this species found in hayfields were consistently supported by clumps of stout-stemmed grasses in dense patches of vegetation. As the largest of the common hayfield-nesting species, it is unlikely that its nesting dispersion was influenced markedly by potential avian competitors.

The other six species form a group that Rotenberry and Wiens (1980:1231) listed as "typical tallgrass prairie birds." Five of these species—Bobolinks, Eastern Meadowlarks, Upland Sandpipers, Henslow's Sparrows, and Grasshopper Sparrows—selected approximately the same types of hayfields. They were most abundant in the older fields with shorter, sparser,

patchier, grass-dominated vegetation and greater litter cover.

Studies of this group of species in midwestern grassland and shrub-steppe habitats have found that this group of species is most abundant in the tallest, densest vegetation (e.g. Rotenberry and Wiens 1980, Kantrud 1981, Zimmerman 1988). However, I feel that the apparent discrepancy in the vegetation height and density selected by these species is due to differences in the geographic locations of the studies (Wiens 1981). Eastern hayfields typically have greater primary production than most prairies (Bollinger 1988).

The least productive hayfields in my study were probably similar to the more productive prairie habitats in terms of vegetation density and height. However, direct comparisons are complicated by the use of different vegetation sampling techniques and the dominance of eastern hayfields by exotic vegetation (see Mills et al. 1989). In the eastern United States, the preference for hayfields with sparser vegetation is not simply due to preferences for grass-dominated fields (with the correlated decline in vegetation density). Each of these five species maintained a negative correlation with vegetation density among fields eight or more years old, which are all dominated by grasses (compare Fig. 1B with 1C).

The sixth species in this group, the Savannah Sparrow, appeared equally abundant in hayfields of all ages, from dense alfalfa-dominated fields to relatively sparse grass-dominated stands. However, Savannah Sparrows are found in a diverse array of open habitats including

prairies (e.g. Cody 1968, Wiens 1969), salt marshes (Bédard and LaPointe 1984), tundra (Weatherhead 1979), and eastern hayfields and pastures (Graber and Graber 1963, this study). Thus, this species may exhibit little habitat selection over the spatial and habitat scales that I considered in this study.

Relative importance of habitat-selection parameters.—Overall, vegetation variables were the most important predictors of patterns of bird abundance in hayfields. For five of seven species, a vegetation variable was the first variable entered into the overall regression model (explaining 15–59% of variation in bird densities). This is in agreement with the prevailing notion that vegetation structure, species composition, and volume usually are the most important proximate factors in avian habitat selection (Hilden 1965, James 1971, Cody 1981, Wiens 1985, Mills et al. 1991). However, given that 75 to 80% of the independent variables that I considered were vegetation variables, this interpretation of the overriding importance of vegetation structure and composition in determining breeding bird dispersions at my scale of measurement is cautiously made (Wiens and Rotenberry 1981, Wiens 1985, 1989).

Field size also was frequently included in the regression models, but was usually of secondary importance to characteristics of the vegetation. Densities of Henslow's Sparrows, Savannah Sparrows, Grasshopper Sparrows, Upland Sandpipers, and Bobolinks were positively correlated with field size. Lower densities or absence of many forest interior bird species from small woodland patches has been commonly documented (e.g. Whitcomb et al. 1981, Robbins et al. 1989), but similar "patch-size effects" have not been as extensively documented in grassland habitats (but see Samson 1980, Stauffer and Best 1980, Herkert 1994). For species that historically nested in large expanses of prairie habitat, there may be an innate attraction to large hayfields because they most closely mimic this open-area "gestalt" (James 1971).

A field's hay-cropping date the previous year was a positive correlate of density for Bobolinks, Henslow's Sparrows, and Grasshopper Sparrows, indicating that fields with early hay-cropping dates the previous year had lower bird densities than fields with later mowing dates. These three species have the latest nesting seasons of the species nesting in my hayfields (Wiens 1969, pers. obs.). Thus, mowing-induced

nest destruction appears responsible for lower densities of these species in early-mowed fields. Earlier hay-cropping dates have been implicated in the decline of grassland birds in the United States (Bollinger et al. 1990, Frawley and Best 1991).

Site fidelity has the potential for creating time lags in habitat selection patterns that could affect breeding dispersion patterns (Hilden 1965, Wiens 1985, 1989). Over a successional sequence of habitats, densities of a given species may be higher than expected in later seral stages, as birds continue to return to a site even after it is no longer optimum habitat. Thus, a hayfield's age, after controlling for succesional changes in vegetation, should be positively correlated with a species' density if site fidelity was an important determinant of breeding dispersion. However, this variable was included in only one of our regression models (as the last variable in the Bobolink model), suggesting that this factor has only a minor effect on breeding dispersion patterns in hayfields.

Interspecific competition also does not appear to be an important factor currently affecting the breeding dispersions of grassland birds in New York hayfields. Partial correlations among breeding densities of the different species ("corrected" for habitat preferences as in Mountainspring and Scott 1985) were never significantly negative (Bollinger 1988), indicating that these species were not limiting each other's densities (Wiens 1974, 1977, Rotenberry and Wiens 1980). However, inferring competition based on correlations should be done with caution (Carnes and Slade 1988, Sherry and Holmes 1988).

Avian species richness and diversity in hayfields.—Very few species of birds nested in the hayfields that I surveyed ($\bar{x}$ = 2.9/field). Comparable studies (e.g. similar average plot sizes) in mixed-grass and tallgrass prairies (i.e. Wiens 1974, Rotenberry and Wiens 1980) averaged about four species per plot. The depauperate avifauna of hayfields may reflect the generally high degree of homogeneity of the vegetation (Rotenberry and Wiens 1980), or the prevalence of exotic vegetation in hayfields (Mills et al. 1989, but see Warner 1994). The youngest hayfields had the fewest species, whereas the oldest fields, which had the least homogeneous vegetation (and the most native vegetation), had species-richness values approximately equal to those of the prairies. Few hayfields, however,

are left as hay for more than five or six years (Bollinger 1988). Hayfield succession, therefore, usually does not progress to the point where these fields are optimum breeding habitat for most grassland bird species

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