A Comparison of Landscapes Occupied by Increasing and Decreasing Populations of Grassland Birds

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Abstract: *For several decades, many grassland bird species have been declining in abundance throughout the Midwest and Great Plains regions of the United States, possibly due to loss of natural grassland habitat and increasing urbanization. I used 20 years of data from the North American Breeding Bird Survey to identify increasing, decreasing, and stable populations of 36 grassland-nesting bird species. I characterized the immediate landscape (circle with radius = 30 km) surrounding each population based on data from the National Resources Inventory. For each landscape, I calculated the proportion of eight different land-cover types: restored grassland, rangeland, cultivated cropland, pasture, noncultivated cropland, forest, urban land, and water. Using a null model, I compared landscape composition of increasing, decreasing, and stable populations. As predicted on the basis of the habitat preferences of grassland birds, increasing populations inhabited landscapes that contained significantly more restored grassland and rangeland but significantly less forest land and urban land than landscapes inhabited by decreasing populations. There was no significant difference in the proportion of cropland within the landscapes of increasing and decreasing populations, although cropland composed a large proportion (>30%) of many landscapes. In contrast, restored grassland typically composed a very small proportion (<3.5%) of total land cover, yet it was significantly more common in the landscapes of increasing than decreasing populations. These results suggest that grassland birds may benefit from government initiatives, such as the Conservation Reserve Program, that promote the restoration of grassland at a landscape scale.*

Keywords: bird population trends, Conservation Reserve Program, randomization test, urbanization

Una Comparación de Paisajes Ocupados por Poblaciones Crecientes y Decrecientes de Aves de Pradera

Resumen: *Durante varias décadas, la abundancia de muchas especies de aves de pradera ha estado declinando en las regiones del Medio Oeste y las Grandes Planicies de los Estados Unidos, posiblemente debido a la pérdida de hábitat de pastizales naturales y el incremento de la urbanización. Utilicé datos de 20 años del North American Breeding Bird Survey para identificar poblaciones crecientes, decrecientes y estables de 36 especies de aves que anidan en praderas. Caractericé el paisaje inmediato (círculo con radio = 30 km) alrededor de cada población con base en datos del Inventario Nacional de Recursos. Para cada paisaje, calculé la proporción de ocho tipos de cobertura de suelos: pastizal restaurado, pradera, terreno agrícola cultivado, pastizal, terreno agrícola no cultivado, bosque terreno urbano y agua. Mediante un modelo nulo, comparé la composición de poblaciones crecientes, decrecientes y estables. Tal como se pronosticó con base en las preferencias de hábitat de las aves de pradera, las poblaciones crecientes habitaban paisajes que contenían significativamente más pastizal restaurado y praderas, pero significativamente menos bosque y terreno urbano que los paisajes habitados por las poblaciones decrecientes. No hubo diferencia significativa en la proporción de terrenos agrícolas en los paisajes con poblaciones crecientes y decrecientes, aunque los terrenos agrícolas comprenden una amplia proporción (>30%) de muchos paisajes. En contraste, los pastizales restaurados típicamente comprenden una proporción muy pequeña (<3.5%) de la cobertura total del suelo, aunque es significativamente más común*

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en los paisajes con poblaciones crecientes que con poblaciones decrecientes. Estos resultados sugieren que las aves de praderas pueden beneficiarse de las iniciativas del gobierno, como el Programa de Conservación de Reservas, que promueve la restauración de praderas a escala de paisaje.

Palabras Clave: Programa de Conservación de Reservas, prueba aleatoria, tendencias poblacionales de aves, urbanización

Introduction

For several decades, many bird species that nest in grassland and scrub habitats have been declining in abundance throughout much of their range. Such declines have been documented in data from the annual North American Breeding Bird Survey (BBS), which began in 1966 (Herkert 1995; Igl & Johnson 1997; Peterjohn & Sauer 1999; Coppedge et al. 2001). Some researchers believe the declines started much earlier when natural grasslands in the Midwest and Great Plains regions of the United States were converted for use as agricultural land (Herkert 1991; Knopf 1994; Peterjohn & Sauer 1999). Other land conversion trends, such as increasing urbanization and encroachment of woody vegetation, may have contributed to the declines (Jones & Bock 2002; Chapman et al. 2004*a*; Grant et al. 2004).

Of most importance, the declines of grassland birds have been more substantial than declines in other groups of birds (Peterjohn & Sauer 1993; Herkert 1995; Sauer et al. 2003*a*). Successful efforts to reverse these negative trends may come from a better understanding of how landscape composition (i.e., the relative proportions of different land-cover types in a landscape) affects the population dynamics of grassland-scrub bird species. One of the goals of this study was to evaluate the effectiveness of restored grassland in promoting the population growth of grassland-nesting birds over a wide geographic scale.

Restored grassland as wildlife habitat is one of the many potential benefits of the various land-conservation programs (e.g., Conservation Reserve Program [CRP]) administered by the federal government in the United States. The CRP provides private landowners with financial support to revegetate cropland with natural or seminatural vegetation. In the Midwest and Great Plains, this vegetation is primarily grasses (Heard et al. 2000). As of 2000, there were over 12.7 million ha of private land enrolled in the CRP nationwide, mostly in states of the Great Plains and Midwest (Heard et al. 2000).

Most researchers studying the effects of the CRP on birds have focused on documenting the extent to which various species use (e.g., for nesting and foraging) or occur in CRP fields (e.g., Johnson & Schwartz 1993; Millenbah et al. 1996; Patterson & Best 1996; Delisle & Savidge 1997; Koford 1999; Chapman et al. 2004*b*). These researchers most often visually observed birds or nests in fields over a specified time period (e.g., Patterson & Best 1996; Best et al. 1997; Koford 1999; Hughes et al. 2000). Logistically, such studies are limited in spatial extent and temporal duration; although a few are commendable for having surveyed multiple fields at multiple times over a span of years (e.g., Johnson & Schwartz 1993; Johnson & Igl 1995; Patterson & Best 1996; Best et al. 1997). These smaller-scale studies have provided crucial evidence that some grassland bird species do successfully nest in habitat produced by the CRP (Ryan et al. 1998).

In addition to the small-scale studies, there are studies that examine the relationship between temporal trends in bird populations and CRP land at very large regional scales (Brady & Flather 1998; Murphy 2003). Typically, estimates of population trend at this level are means (or other composite measures) of trends of many populations within the region. Likewise, estimates of CRP and other land-cover types within the regions are coarse and general (Brady & Flather 1998; Murphy 2003). Other researchers evaluated fewer populations but thoroughly characterized the landscape surrounding each population (Coppedge et al. 2001). I combined both approaches by analyzing 20 years of data from hundreds of populations of 36 grassland bird species throughout the Midwest and Great Plains states. I quantified the proportion of eight different land-cover types (including CRP land) in the landscape surrounding each population. This allowed me to compare the landscapes of increasing and decreasing populations of each species. I predicted that the landscapes of increasing populations should contain a larger percentage of grassland habitat (e.g., CRP land, rangeland) than the landscapes occupied by decreasing populations.

Methods

Identifying Increasing and Decreasing Bird Populations

I used data from the North American BBS to identify increasing and decreasing "populations" of bird species that nest in grassland and scrub habitat. The BBS is an annual survey of the bird species found along more than 3000, 39.2-km routes throughout North America. I refer to the individuals of each species found along a route as a "population." However, the true population of a given species might actually consist of individuals from multiple adjacent routes, or conversely, a given route might have more than one population. My use of the term *population* is not meant to imply a closed, self-sustaining population. Routes of the BBS are typically secondary highways and roads. In late spring (typically May or June), an observer drives each route and records the number of individuals of each species heard or seen at regular stopping points along the route. Although the survey protocol is standardized, the enormous geographic coverage and temporal duration (the survey has been conducted since 1966) of the survey requires the participation of hundreds of volunteers. A more detailed description of the protocol is in Sauer et al. (1994) or Sauer et al. (2003*b*).

The vast majority of BBS routes have been surveyed by multiple observers over the years. That is, the data for a given route usually were collected by at least three or more observers, each recording data for a few consecutive years or more. Because observers vary in their ability to estimate bird abundance, an observer effect exists in BBS data (Sauer et al. 1994). This effect is the differences in yearly counts of a species due to differences in observers. The observer effect can lead to spurious positive or negative population trends (Fig. 1). To control for the observer effect, I used a randomization test developed to analyze single-species population trends for 10 or more years of data collected by multiple observers (Veech 2006). The test requires a minimum of 2 years of data from each observer in any temporal order; observers on most BBS routes have recorded data for at least four consecutive years.

The randomization test first involves calculating the slope of a least-squares regression of abundance versus year for the observed count data of a species on a given route for a specified time period. The slope of the observed data is then compared with a distribution of slopes obtained from the data (over the same specified time period) after randomizing the order of yearly counts within an observer (Fig. 1). The randomization thus removes any trend within an observer without changing the observed counts (only the temporal order of the count data is randomized). The mean count over time (years) recorded by an observer is conserved in the randomization. If the count data were randomized among observers, then the mean count for an observer would not be conserved. By randomizing within an observer, the randomization test produces random trends within the time periods covered by each observer. Finally, statistical significance of the observed population trend is assessed as the proportion of random slopes greater than or less than the observed slope, respectively, for positive and negative observed slopes (or trends). Essentially, this proportion is a p value. In the randomization test, the slope is used as the test statistic, and statistical significance indicates whether a given observed slope (or population trend) is significantly different from zero (positive or negative) but does not indicate how well the slope fits the data.

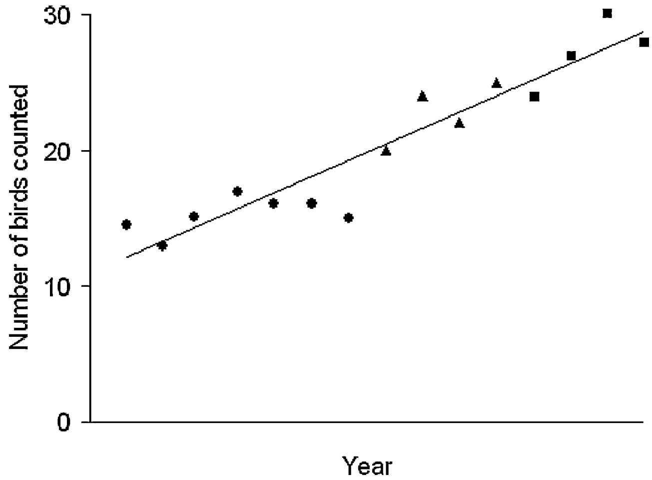

Figure 1. A hypothetical example of the observer effect in data of the Breeding Bird Survey (BBS). Observer 1 (circles) recorded counts of individuals of the bird species for 7 years. Observers 2 (triangles) and 3 (squares) recorded counts for 4 years. The least-squares regression line (solid line) indicates a positive trend (slope = 1.2) in the population. However, the three observers may also differ in their observational abilities given that observer 1 counted 15.1 individuals/year, on average. Observers 2 and 3 counted 22.8 and 27.3 on average, respectively. Therefore, the positive trend could be due to an observer effect.

I used the randomization test to identify increasing, decreasing, and stable populations of bird species that prefer to nest in grassland and scrub habitat (Peterjohn & Sauer 1990; Sauer et al. 2003*b*). An increasing population was indicated by a significantly positive slope ($p < 0.05$), a decreasing population by a significantly negative slope, and a stable population by a slope not significantly different from zero. The randomization test was applied to the raw count data instead of data adjusted for differences in species detection probabilities even though the detection probability for each species was probably <1. There was no need to adjust the raw data given that population trend can be identified as either positive, negative, or stable (with the randomization test) without estimating the true unknown population size for a species. To some extent, detection probability depends on observer ability, and the latter is accounted for in the randomization test. However, the test does assume a constant detection probability for each year of a given species–observer combination.

I limited the analyses to the BBS routes within 18 states in the Midwest and Great Plains regions of the United States (Fig. 2). Historically, these states had substantial areas of natural grassland and prairies. In addition, the CRP

Figure 2. Locations of the 859 BBS route landscapes used in this study.

is active in these states. One of my goals here was to evaluate the effect of the CRP on grassland birds. I further limited the analyses to only those BBS routes and bird species in which there was at least 10 years of abundance data between 1982 and 2002. In general, 10 or more years of data are needed for the randomization test to consistently identify positive and negative population trends (Veech 2006). I used 1982 as a starting date because the CRP began in the mid-1980s. Although Peterjohn and Sauer (1999) list 78 species as grassland and scrub-nesting birds, I included only species in which there were at least four increasing and four decreasing populations. Thus, I performed all subsequent analyses on 36 species. For each species, I assigned populations to either a group of increasing, decreasing, or stable populations on the basis of the outcome of the randomization test (a list of the 36 species and populations assigned to each group is available from the author).

Quantifying Land-Cover Composition within Landscapes

I defined the landscape of each BBS route as a 30-km radius circle centered on the midpoint of the route. Other researchers have also used landscapes of similar size centered on BBS routes (Flather & Sauer 1996; Boulinier et al. 2001; Donovan & Flather 2002; Vance et al. 2003). Data from the National Resources Inventory (NRI; Natural Resources Conservation Service, U.S. Department of Agriculture) were used to quantify the relative proportions of eight land-cover types within each landscape. The NRI is a broad-scale assessment of agricultural conditions and land-use practices on privately owned land within the United States (Nusser et al. 1998). The inventory was first conducted in 1982 and since then in 1987, 1992, and 1997. Much of the data in the NRI are derived from more than 800,000 semirandomly located sampling points that are surveyed every 5 years. At the lowest level, there are 1–3 NRI points per quarter section of a semirandomly selected section and township within a county. That is, the NRI uses a stratified random sampling design based on the county–township-section classification of the Public Land Survey to obtain a random yet thorough distribution of sample points (Nusser et al. 1998).

The NRI includes many different types of agricultural data. I used data of the "broad use land cover" classification scheme that assigns the land cover at a point to 1 of 12 categories. From 10 of these 12, I defined eight land-cover types (Table 1). I predicted the effect of each land-cover type on grassland birds on the basis of whether the land-cover type provided open "habitat" that could be used by

Table 1. Land-cover types and their predicted effects on population trends of grassland bird species.

*Land-cover type**	*Description*	*Predicted effect*
CRP (Conservation Reserve Program)	enrolled in CRP; generally planted with native or non-native grasses	positive
Cultivated cropland	planted with row crops or close-grown crops that are harvested annually; typically fallow over winter	positive
Pasture	planted with one or a few grasses and typically grazed by livestock; usually actively managed (e.g., weed control, application of fertilizer, reseeding)	positive
Rangeland	natural condition of native grasses, forbs, shrubs; used for grazing and browsing by livestock; managed less than pasture land	positive
Noncultivated cropland	planted permanently with a crop, such as perennial hayfields and orchards	negative
Forest	consists of woody plant species at least 4 m tall at maturity with a canopy cover >25%; includes only areas of at least 0.4 ha (1 acre) and >30 m wide; rows and small clusters of trees not included	negative
Urban or developed	residential, industrial, commercial, and institutional; includes rural highways and roads	negative
Water	permanent water bodies >0.81 ha and >25% open water; includes lakes, large ponds, rivers, and streams	negative

**Land-cover types are from the National Resources Inventory broad-use land-cover classification scheme with the following modifications: cover types 7 ("urban and built-up land") and 8 ("rural transportation") were combined into "urban or developed," cover types 9 ("small water areas") and 10 ("census water") were combined into "water," cover types 6 ("minor land") and 11 ("federal land") were not included.*

the birds (Table 1). Each of the BBS route landscapes typically contained 100 or more NRI sampling points (mean = 350 points). These points enabled me to calculate the relative proportions, c_i, of each of the $i = 1$–8 land-cover types in each landscape as n_i/N, where n_i is the number of points representing land-cover type i, and N is the total number of points in the landscape (Veech 2006). The mean density of points (350/2826 km^2 or 1 point/8 km^2) may seem to indicate that landscape composition was quantified at a coarse scale. However, an unpublished analysis (available from the author) of county-level data verified that this method of quantifying land-cover types is generally accurate to within 5% of the actual absolute value, even for relatively infrequent cover types such as urban land and CRP land. The method was also used in an analysis of the effect of landscape composition on Northern Bobwhite (*Colinus virginianus*) populations (Veech 2006).

For each BBS route landscape and land-cover type, I combined data from the 1982 and 1987 NRI and refer to those landscapes as "1987 landscapes"; likewise, I combined data from 1992 and 1997 NRI for the "1997 landscapes." It was necessary to combine data in this way to limit the number of landscape variables tested, and was justified because for each landscape, the percentage of each land-cover type usually did not change much (<5%) over the 1982–1997 time span of the NRI. For each of the 36 bird species, I determined the mean landscape composition for the group of increasing populations and the group of decreasing populations by obtaining the average c_i for each land-cover type in each group. Thus, for each species, this provided a "mean" landscape occupied by increasing populations and a mean landscape occupied by decreasing populations that could be compared. A similar approach was taken by Fuhlendorf et al. (2002).

Comparing Landscapes of Increasing and Decreasing Populations

I developed a nonparametric, random-sampling, null model to determine whether mean landscapes of increasing (and decreasing) populations were significantly different from the mean landscape of "stable" populations (i.e., those in which there was neither an increase nor a decrease). A stable population was defined as one in which the randomization test (see "Identifying Increasing and Decreasing Bird Populations") indicated no significant increase or decrease in the population. In addition, the slope of abundance versus year (i.e., the population trend) of a stable population had to be less than the mean slope of the group of increasing populations (of the given species) and greater than the mean slope of the decreasing populations to be included in the analysis. That is, stable populations had nonsignificant slopes within the interval between the mean slopes of the increasing and decreasing populations. This latter prerequisite was needed because the randomization test is prone to Type II error (i.e., misclassifying truly positive or negative trends as stable) for the unusual cases where trends within each observer are consistently negative (or positive), yet each successive observer records higher counts. Therefore, for each species, I had a group that included only populations that truly were stable. For all species, there were substantially more stable populations than either increasing or decreasing populations.

For a given species, the null model was used to test whether the mean landscape (i.e., mean c_i for land-cover type i) of a group of increasing populations was significantly different from the mean landscape of a randomly selected group of the same number of stable populations. For example, there were 6 increasing and 65 stable populations of upland sandpiper; thus, 6 populations (and corresponding BBS route landscapes) were selected from the group of 65 and a mean of the 6 was determined for each c_i. I repeated this random selection process 1000 times so as to generate a null distribution of the mean c_i for each land-cover type for a group of 6 stable populations. I also used the null model to test the significance of the mean c_i values for the decreasing populations of each species. In this case, BBS route landscapes were again randomly selected from the group of stable populations, and the number selected matched the actual number of decreasing populations (e.g., 21 for the Upland Sandpiper [scientific names not provided in text are in Table 2]).

I then compared the values of each mean c_i for the increasing (and decreasing) populations with the appropriate null distribution to obtain a p value or the proportion of null values greater than (or less than) the observed mean c_i, depending on the predicted effect of the land-cover type (Table 1). For instance, CRP land was predicted to have a positive effect on grassland birds (Table 1), so the mean c_{CRP} for landscapes occupied by increasing populations of upland sandpiper should be significantly greater than that of the stable populations. Hence, the p value would be the proportion of null values greater than the observed mean c_{CRP}. Likewise, the mean c_{CRP} for landscapes occupied by decreasing populations should be significantly less than that of the stable populations; hence, the p value is the proportion of null values less than the observed mean c_{CRP}.

Because the analysis included increasing and decreasing populations of 36 species and 16 landscape variables (eight land-cover types in both the 1987 and 1997 landscapes), many p values (1152) were generated by the null model. Because I was not primarily interested in differences between species and to both control Type I error rate and increase the power of testing for effects due to land-cover type, I used consensus-combined p values to summarize and further test the results of the null model. A consensus-combined p value is calculated from a set of constituent p values (e.g., 36 p values representing the null model results for each bird species). The constituent

Table 2. Bird species for which there was a significant ($p < 0.05$) difference between the 1997 landscapes of increasing populations (inc.) and decreasing populations (dec.) for percentage of Conservation Reserve Program (CRP) land, rangeland, and urban land.*

	CRP land (%)		Rangeland (%)		Urban land (%)	
Species	*inc.*	*dec.*	*inc.*	*dec.*	*inc.*	*dec.*
Bobolink *Dolichonyx oryzivorus*	5.4	2.9	17.2	2.6	2.4	6.5
Chestnut-collared Longspur *Calcarius ornatus*	7.4	3.3	—	—	—	—
Clay-colored Sparrow *Spizella pallida*	—	—	17.2	1.1	3.9	8.8
Common Yellowthroat *Geothlypis trichas*	3.9	2.5	15.3	6.1	—	—
Eastern Meadowlark *Sturnella magna*	2.9	1.8	—	—	—	—
Field Sparrow *Spizella pusilla*	3.6	2.2	29.2	3.4	3.0	6.4
Grasshopper Sparrow *Ammodramus savannarum*	—	—	38.7	22.1	—	—
Indigo Bunting *Passerina cyanea*	3.5	2.3	20.7	1.9	—	—
Ring-necked Pheasant *Phasianus colchicus*	—	—	—	—	1.7	5.0
Savannah Sparrow *Passerculus sandwichensis*	4.2	2.3	21.0	6.1	1.7	8.6
Upland Sandpiper *Bartramia longicauda*	7.1	3.0	—	—	0.5	3.4
Vesper Sparrow *Pooecetes gramineus*	—	—	26.1	9.9	1.9	5.0
Western Meadowlark *Sturnella neglecta*	—	—	31.1	19.0	2.0	3.7

Results for 1987 landscapes (not shown) were also significant, except CRP land for Common Yellowthroat, Indigo Bunting, Savannah Sparrow, and Upland Sandpiper.

p values are combined to obtain the quantity, $-2\Sigma\ln(p_j)$, for $j = 1$ to J constituent p values (Fisher 1954; Sokal & Rohlf 1995; Quinn & Keough 2002). The quantity has a chi-square distribution with $2J$ df, which thus provides the consensus-combined p value. If the combined p value is significant at a prescribed alpha level (e.g., $p < 0.05$), then one can conclude there is an overall effect of the tested factor on the response variable (Fisher 1954; Sokal & Rohlf 1995; Quinn & Keough 2002) even if none of the constituent p values are significant. Of course, by chance alone, I still expect to get two significant p values (i.e., $p < 0.05$) for each set of 36 constituent p values ($36 \bullet 0.05 = 1.8$ or $\cong 2$). I generally obtained between 4 and 10 significant p values in each set; thus, the null model was not prone to study-wide Type I errors.

Combining p values is a well-established statistical technique that is frequently used to interpret multiple significance tests (Rice 1990; Caudill & Hill 1995; Zaykin et al. 2002). I used the technique to test whether the mean proportions of each land-cover type (in landscapes occupied by increasing and decreasing populations) are significantly different from the proportion expected in landscapes where populations are stable. For the stable populations, I used the means of the null distributions. For each of the eight land-cover types in the 1987 and 1997 landscapes, I calculated combined p values separately for the group of increasing and decreasing populations. That is, each combined p value was derived from a set of 36 constituent p values representing the 36 species. Therefore, I was able to separately test for the predicted effect of each land-cover type (Table 1) on the entire set of grassland bird species.

Results

Bird Population and Landscape Trends

My results confirm the overall decline in grassland bird species that has been documented in other studies in which BBS data were analyzed (e.g., Sauer et al. 2003*a*). That is, across all 36 species, 1633 populations decreased between 1982 and 2002, whereas only 963 populations increased during the same time period. Twenty-one species had a greater number of decreasing than increasing populations and 15 had more increasing than decreasing populations. The majority of the populations of each species was stable between 1982 and 2002. Averaged over all 36 species, the mean size (per year) of decreasing populations was 21.4 individuals (range: 4.2–115.2), and the mean size of increasing populations was 22.0 (range: 4.3–129.4). On average, the size of decreasing populations was 102.8% of increasing populations. Furthermore, the mean number of years of BBS data per population (averaged over all 36 species) was 16.2 (range: 13.3–19.2) for decreasing populations and 15.6 (range: 12.7–17.8) for increasing populations. Thus, for all 36 species, increasing and decreasing populations differed very little in recorded number of individuals and number of years of recorded data.

The most common land-cover types (averaged over 1987 and 1997) in the 859 landscapes surrounding BBS routes were cultivated cropland (32%), rangeland (18%), and forest (18%). On average, the proportion of cultivated cropland and rangeland decreased slightly (−3% and −0.5%, respectively) between 1987 and 1997, whereas forested land increased slightly (0.5%). Pasture composed, on average, 9% of the landscapes and declined slightly (−0.6%) between 1987 and 1997. Noncultivated cropland (i.e., horticulture and permanent crops) composed about 4% of the landscapes and changed little between 1987 and 1997. In contrast, the proportions of CRP land and urban land increased between 1987 and 1997. The 1987 landscapes consisted of only 1% CRP, but by 1997 that proportion had increased to about 3% on average. Likewise, urban land composed 3.5% of the landscape cover in 1987 and about 4% by 1997. On average, the landscapes did not change much in each land-cover type (except perhaps CRP land) between 1987 and 1997.

There was also little difference in the change in each land-cover type between the two groups of populations (increasing and decreasing) of a species. Therefore, temporal changes in each land-cover type were not included as landscape variables in this study. Instead, the study focused on analyzing the static composition of landscapes (in 1987 and 1997) occupied by increasing and decreasing populations of each bird species.

Comparison of Landscapes

Over all 36 bird species, there was a greater-than-expected proportion of CRP land in the 1997 landscapes occupied by increasing populations (3.18% CRP) than those occupied by stable populations (2.88%), but no difference in 1987 (Table 3). The proportion of CRP land in the 1997 landscapes occupied by decreasing populations was almost identical to the proportion in landscapes of stable populations (2.86% vs. 2.88%). Increasing populations of eight species occupied landscapes with significantly more CRP land than the landscapes of decreasing populations (Table 2).

As predicted, increasing populations occurred in landscapes that had a greater proportion of rangeland in 1987 and 1997 (almost 20%) than the landscapes of stable populations (slightly more than 15%) (Table 3). However, contrary to the prediction, decreasing populations occurred in landscapes with slightly more rangeland (about 16%) than the landscapes of stable populations (Table 3). Despite this unexpected result, on average, the landscapes of increasing populations did have more rangeland than those of decreasing populations. When examined individually, nine species had significantly more rangeland in landscapes occupied by increasing populations than in those occupied by decreasing populations (Table 2).

Also as predicted, the 1987 and 1997 landscapes occupied by increasing populations tended to have significantly less forest land (16–17%) than the landscapes of stable populations (slightly more than 20%) or decreasing populations (slightly less than 20%) (Table 3). There was slightly but significantly less pasture in landscapes of decreasing populations (mean of 8.97% for 1987 and 8.36% for 1997) than in the landscapes of stable populations (mean of 9.31% for 1987 and 8.57% for 1997). Decreasing populations also inhabited landscapes with a greater proportion of urban land (mean of 3.77% for 1987 and 4.37% for 1997) than the landscapes of stable populations (mean of 3.5% for 1987 and 4.07% for 1997) (Table 3). When examined individually, eight species had significantly more urban land in the landscapes of decreasing populations than in those occupied by increasing populations (Table 2).

Table 3. Composition of landscapes occupied by increasing, decreasing, and stable populations of grassland bird species in 1987 and 1997.

	1987			*1997*		
Cover type (%)[a]	*increasing*	*decreasing*	*stable*	*increasing*	*decreasing*	*stable*
CRP	1.06	1.06	1.07	3.18[b]	2.86	2.88
Cultivated cropland	32.68	34.37	33.60	29.88	31.66	30.87
Pasture	9.13	8.97[c]	9.31	8.56	8.36[c]	8.57
Rangeland	19.56[d]	16.22[c]	15.56	19.00[d]	15.83[c]	15.23
Noncultivated cropland	3.60	3.30	3.56	3.74	3.60	3.85
Forest	16.64[d]	19.62	20.11	17.06[d]	19.98	20.56
Urban	3.43	3.77[c]	3.50	3.99	4.37[c]	4.07
Water	0.59[b]	0.63[c]	0.64	0.61[c]	0.64[c]	0.66

[a] *Percent cover type is a mean for the landscapes occupied by increasing, decreasing, and stable populations among all 36 bird species.*
[b] *Mean percentage of cover type is significantly greater than or less than ($p < 0.01$) the percentage in landscapes of stable populations based on Fisher's consensus-combined* p *value test ($n = 36$ constituent* p *values, $df = 72$).*
[c] $p < 0.05$.
[d] $p < 0.0001$.

On average, all of the landscapes had very little water compared with the other land-cover types. Landscapes of increasing populations had significantly lower proportions of water than the landscapes of stable populations although the difference was small (Table 3). The two remaining land-cover types, cultivated and noncultivated cropland, differed little and in nonsignificant ways between landscapes of increasing, stable, and decreasing populations (Table 3).

Discussion

There were definite and significant differences in the landscapes occupied by increasing and decreasing populations of grassland bird species. In general, the differences in land-cover composition were either as predicted (Table 1) or not great enough to be detected. That is, increasing populations tended to inhabit landscapes that had more CRP land and rangeland and less forest land and urban land than the landscapes inhabited by decreasing populations. Of the eight land-cover types I examined, rangeland and CRP land had the greatest potential of having a positive effect on grassland birds. Both land-cover types are open habitats dominated by grasses and disturbed by anthropogenic processes (e.g., grazing by livestock or mowing) at low intensity or not at all. Thus, as predicted, landscapes with large proportions of rangeland were associated with increasing populations of grassland birds (more so, than landscapes with less rangeland). Likewise, the 1997 landscapes of increasing populations had more CRP land than 1997 landscapes of decreasing populations even though, on average, CRP land did not constitute a large percentage (2.9–3.2%, 82–90 km^2) of either type of landscape. The 1987 landscapes of increasing and decreasing populations had the same mean percentage (1.064%, 30 km^2) of CRP land. By 1987 the CRP had been in existence for only 2 years, so it is unlikely that the CRP would have had an effect on grassland bird species so quickly.

The effect of urban land and forested land on grassland bird populations was as predicted. Both land-cover types were more common in landscapes occupied by decreasing populations than by increasing populations. Compared with other land-cover types, there are relatively few published studies of the effects of urban land (and urbanization) on grassland birds. Jones and Bock (2002) documented a 25% loss of bird species over a 100-year period in grassland patches near Boulder, Colorado. Another study at the same site revealed that urbanization can have detrimental effects because the edges of patches that border developed areas support fewer species and individuals (Bock et al. 1999). Two studies in Canada compared bird diversity within urban areas to diversity in natural grassland habitats, and in general there were fewer grassland species in the urban areas (Sodhi 1992; Edgar & Kershaw 1994). My results indicate that increasing populations of grassland birds tend to occupy landscapes with slightly, but significantly less, urban land than the landscapes of decreasing populations. Urban land was not a huge component of the majority of landscapes, rarely more than 10%. However, there was substantial variation among the 859 landscapes in the proportion of urban land, with some having <1% and a few having 50%. In addition, urban land increased in nearly all the landscapes between 1987 and 1997. Thus, given the ubiquity of urbanization and variation in its extent, there is tremendous opportunity (and need) to further analyze the effects of urbanization on grassland birds, particularly at the scale I used here.

As with urban land, forested land comprised a greater percentage of the landscapes of decreasing populations than increasing populations. Although forested land may be habitat for other bird species (including some Neotropical migrants that are declining), it is generally not suitable habitat for grassland bird species. Indeed, some studies have identified shrub encroachment into grassland habitat as a cause of declines in grassland birds (e.g., Coppedge et al. 2001; Rosenstock & Van Riper 2001; Chapman et al. 2004*a*). My results agree with the results of these previous studies inasmuch as shrub encroachment, and succession in general, lead to closed-canopy forests that cannot support populations of birds that need open habitat for foraging and nesting. On the other hand, land that was in the early stages of shrub encroachment and succession was most often classified as "rangeland," and I found a positive effect of rangeland on population trends of grassland birds.

For most land-cover types, the mean difference between landscapes of increasing, decreasing, and stable populations may seem negligible. However, these differences were often significant (Table 3) and almost always as predicted (Table 1). For each land-cover type, the null model tested whether the landscapes of increasing and decreasing populations of a species had a mean percent cover that could have been obtained by chance from any set of populations. Rejection of this null hypothesis indicated that the landscapes of increasing (or decreasing) populations were significantly different from landscapes of stable populations. Again, this is an average overall result that should be interpreted cautiously. The difference between landscapes of increasing and decreasing populations (e.g., on average, 9 km^2 for CRP land in 1997, 90 km^2 for rangeland in 1987 and 1997) should not be taken as a prescription for increasing populations of certain species or as conclusive evidence that a given land-cover type always has either a positive or negative effect on grassland birds.

Nonetheless, even a relatively small increase in favorable habitat within a large landscape (9–90 km^2 in a 2826-km^2 landscape) might substantially benefit populations of some species. Herkert (1994) found that 5–55 ha of habitat was needed to support at least one individual of some of the species positively affected by CRP and rangeland in my study (Table 2). For seven of the species in Table 2, Johnson and Schwartz (1993) estimated densities within CRP fields of 1 breeding pair (Vesper Sparrow) to 20 breeding pairs (Grasshopper Sparrow) per 100 ha. The other five species had 2–8 breeding pairs/100 ha. Thus, 900 ha of CRP land might be able to support 10 to almost 200 additional breeding pairs depending on the species.

The differences between the landscapes of increasing and decreasing populations were typically even greater when examining some species individually, particularly for CRP land, forest land, and urban land (Table 2). However, for each species and each land-cover type, the ranges of percent cover for both the landscapes of increasing and decreasing populations were generally large. For example, increasing populations typically occupied landscapes with 0% to 90% rangeland, whereas decreasing populations occupied landscapes that were almost as variable in rangeland. For most species, CRP land ranged from approximately 0% to 20% in landscapes of both increasing and decreasing populations. Urban land ranged from approximately 0% to 50% in landscapes of decreasing populations but only 0% to 15% in landscapes of increasing populations. Thus, no land-cover type had an exclusively positive or negative effect on population trends of the species examined. Some populations were increasing in landscapes with a relatively high percentage of urban land and low percentage of rangeland and CRP land, and some populations decreased in landscapes with relatively high percentages of rangeland and urban land.

The increasing and decreasing populations of three species (Bobolink, Field Sparrow, and Savannah Sparrow) differed significantly in all three land-cover types (CRP land, rangeland, and urban land) (Table 2, Fig. 3). For each species, CRP land and rangeland composed a greater proportion of the landscapes of increasing populations than the landscapes of decreasing populations. For decreasing populations of all three species, the proportion of urban land is greater than the proportions of CRP land and rangeland combined (Fig. 3). Results of the null-model analysis suggest that CRP land and rangeland are beneficial to these species, whereas urban land is detrimental.

Overall, rangeland appeared to be at least as beneficial to grassland birds as CRP land. For most species, the landscapes of increasing and decreasing populations differed more in percent rangeland than CRP land (Table 2). However, three species (Chestnut-collared Longspur, Eastern Meadowlark, and Upland Sandpiper) were positively affected by CRP land but not rangeland. The landscapes occupied by increasing populations of these species had significantly more CRP land than the landscapes of decreasing populations but no significant difference in rangeland (Table 2).

At the very least, a conclusive demonstration of the positive or negative effects of each land-cover type would require more detailed demographic data for each population (territory size of nesting pairs, reproductive and

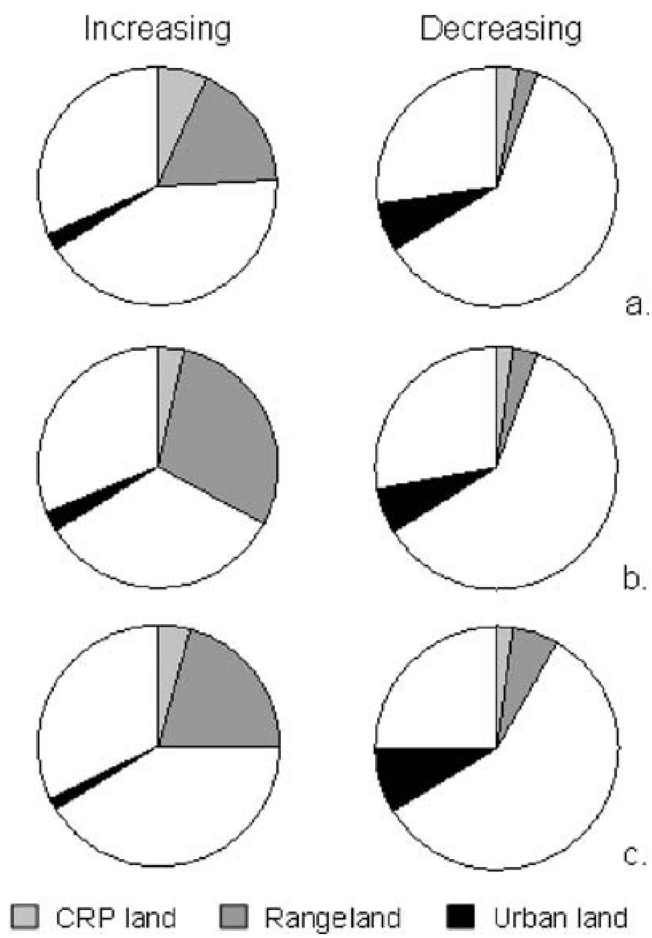

Figure 3. Differences between the mean 1997 landscapes of increasing and decreasing populations of (a) Bobolink, (b) Field Sparrow, and (c) Savannah Sparrow for proportion of Conservation Reserve Program land, rangeland, and urban land.

survival rates) and knowledge of the relationships among populations (source vs. sink) that might belong to the same metapopulation. Furthermore, my results provide only an initial indication that increases in some land-cover types (e.g., CRP land and rangeland) and limits to others (e.g., urban land) will assist in maintaining populations of grassland birds. It remains to be discovered how much CRP land within a landscape is needed to maintain populations of different bird species.

In addition, my results may be scale dependent. Some grassland bird species may perceive and utilize landscape features at a scale different from the 2826-km^2 circular landscapes I examined. The effect of landscape composition on population dynamics of grassland birds depends on the extent to which different land-cover types (and their spatial arrangement) either facilitate or inhibit processes such as mate finding and nest building. These processes directly influence population persistence and therefore should be considered. However, at the very least, the basic autecology and presumed habitat preferences of grassland bird species can be used to generate predictions of how grassland birds are affected by different land-cover types (Table 1). These predictions can then be tested with a geographically broad, multispecies analysis (as in this study) to confirm whether the different land-cover types do, in general, have the predicted effects. Efforts to maintain and increase populations of grassland birds can then be directed at those land-cover types identified as having the greatest positive effect.

Results of other studies (e.g., Fahrig 2001 and references within; Vance et al. 2003) have revealed that the minimum amount of habitat necessary for population persistence within a landscape depends on annual reproductive output of the organisms. Moreover, the total amount of suitable habitat may be as important to population persistence as is the configuration (fragmentation and patch size) of that habitat and the quality of the intervening matrix (Fahrig 2001). My results are evidence that the amount of grassland habitat (CRP land and rangeland) within a landscape can affect population trends in grassland birds, regardless of the spatial configuration of CRP fields or rangeland parcels. Granted, the spatial configuration might have an additional effect beyond the effect that amount of grassland habitat has.

Comparing the landscapes of declining and increasing populations of any species allows the identification of the land-cover types that are beneficial and those that are detrimental to population persistence. My results demonstrate that the restored grassland habitat of land enrolled in the CRP and the natural habitat of rangeland is beneficial to the population growth of grassland birds. Urban land, however, is detrimental to population growth and may have contributed to declines in grassland birds (landscapes with decreasing populations had more urban land than landscapes where populations have increased). These results (e.g., identification of positive effects of CRP land and negative effects of urban land) are likely to be broadly applicable due to the large geographic scale of the study and the degree to which population trends were analyzed in the context of local landscapes.

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