

## GHOSTS OF HABITATS PAST: CONTRIBUTION OF LANDSCAPE CHANGE TO CURRENT HABITATS USED BY SHRUBLAND BIRDS

STEVEN T. KNICK<sup>1</sup> AND JOHN T. ROTENBERRY<sup>2</sup>

<sup>1</sup>U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street, Boise, Idaho 83706, USA.

<sup>2</sup>Center for Conservation Biology and Department of Biology, University of California, Riverside, California 92521 USA

**Abstract.** Models of habitat associations for species often are developed with an implicit assumption that habitats are static, even though recent disturbance may have altered the landscape. We tested our hypothesis that trajectory and magnitude of habitat change influenced observed distribution and abundance of passerine birds breeding in shrubsteppe habitats of southwestern Idaho. Birds in this region live in dynamic landscapes undergoing predominantly large-scale, radical, and unidirectional habitat change because wildfires are converting shrublands into expanses of exotic annual grasslands. We used data from field surveys and satellite image analyses in a series of redundancy analyses to partition variances and to determine the relative contribution of habitat change and current landscapes. Although current habitats explained a greater proportion of total variation, changes in habitat and measures of habitat richness and texture also contributed to variation in abundance of Horned Larks (*Eremophila alpestris*), Brewer's Sparrows (*Spizella breweri*), and Sage Sparrows (*Amphispiza belli*). Abundance of birds was insensitive to scale for nonspatial habitat variables. In contrast, spatial measures of habitat richness and texture in the landscape were significant only at large spatial scales. Abundance of Horned Larks, Western Meadowlarks (*Sturnella neglecta*), and Brewer's Sparrows, but not Sage Thrashers (*Oreoscoptes montanus*) or Sage Sparrows, was positively correlated with changes toward stable habitats. Because dominant habitat changes were toward less stable conditions, regional declines of those birds in shrubsteppe habitats reflect current landscapes as well as the history, magnitude, and trajectory of habitat change.

**Key words:** birds, passerine; Brewer's Sparrow (*Spizella breweri*); Geographic Information Systems; habitat association model; Horned Lark (*Eremophila alpestris*); Idaho, USA; landscape change; remote sensing; Sage Sparrow (*Amphispiza belli*); Sage Thrasher (*Oreoscoptes montanus*); shrubsteppe; Western Meadowlark (*Sturnella neglecta*); wildfire.

### INTRODUCTION

Habitat associations of animal species often are developed to predict consequences of habitat change for conservation or management plans. Despite recognizing the potential effect of future changes, a site's historical contribution is often ignored as a component when developing models of habitat associations. The habitat at any point is a function not only of surrounding habitats currently in the landscape, but also its history, magnitude, and trajectory of change at multiple spatial and temporal scales (Southwood 1977, Allen and Starr 1982, Holling 1992, Levin 1992, Rosenzweig 1995). Our interpretation of processes in ecological systems necessarily relies on understanding relationships between components of habitat change and species response. Therefore, the potential contribution of the historical component has important management and ecological implications, particularly for regions in which the dependent animal community is subjected to short-term, radical disturbance. In addition, time lags

in species response can potentially confound design and interpretation of experiments involving habitat manipulation or natural change.

We tested our hypothesis that current distribution and abundance of passerine birds is a combined function of habitat change and current landscapes in a 200 000-ha region of shrubsteppe habitat that included portions of the Snake River Birds of Prey National Conservation Area (116° W, 43° N) in southwestern Idaho. Highly flammable exotic annuals, especially cheatgrass (*Bromus tectorum*), invaded the system around the turn of the century facilitated by overgrazing and failed agricultural homesteads (Yensen 1981). In a synergistic feedback mechanism, the exotic annual understory increased fire spread and loss of big sagebrush (*Artemisia tridentata*), winterfat (*Kraschenninikovia lanata*), and shadscale (*Atriplex confertifolia*) communities, and further accelerated the spread of annuals (Whisenant 1990, Knick and Rotenberry 1997). Frequent and extensive wildfires from 1979 to 1995 fragmented and reduced shrublands from 51% to 30% of the total area; the fire interval during that period was 27.5 yr compared to 80.5 yr from 1950 to 1979 (U.S. Department of the

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Interior 1996). The problem is widespread because similar disturbance patterns throughout the Great Basin and Upper Snake River Plains have created large expanses of exotic annual grasslands from which natural shrub recovery is unlikely (Klemmedson and Smith 1964, Young and Evans 1978, D'Antonio and Vitousek 1992). Therefore, birds in those systems live in landscapes undergoing radical habitat changes that are predominantly large in scale and unidirectional.

We considered alternate hypotheses in our analyses because short-term, local scale studies of shrubsteppe birds have had mixed results in developing models of habitat associations (Rotenberry and Wiens 1980, Wiens 1985, Wiens and Rotenberry 1985, Rotenberry 1986, Petersen and Best 1987, Rotenberry and Knick 1998). If birds quickly fill habitats by an optimal model (Fretwell and Lucas 1969) without time lags in response, birds would have stronger associations for current habitat compared to measures of change, even though habitat change might be an underlying but integral component in shaping current landscapes. However, if birds exhibit strong natal philopatry or site tenacity (Wiens 1985, Wiens and Rotenberry 1985), we expected little association among current habitats and bird distribution and abundance. To explain the relative contributions, we partitioned variances in bird distribution and abundance between current and past habitat change components.

## METHODS

### *Field surveys*

We sampled 121 sites for Horned Larks (*Eremophila alpestris*), Western Meadowlarks (*Sturnella neglecta*), Sage Thrashers (*Oreoscoptes montanus*), and Brewer's (*Spizella breweri*) and Sage (*Amphispiza belli*) sparrows, once each year from 1992 through 1995. We allocated our sampling effort to most efficiently sample widely distributed species over a relatively large area (Ralph et al. 1995). Sites initially were located by randomly determined coordinates; final map coordinates (estimated precision <6 m) of sites were determined by corrected GPS (Global Positioning System) readings for overlay on the satellite imagery in a Geographic Information System (GIS). We sampled sites in random order between 30 April and 25 June between 0500 and 1000 on mornings that had little wind (<12 km/h) and no rain (Knick and Rotenberry 1995). We recorded number of all birds seen or heard for an unlimited radius within a 5-min interval (Ralph et al. 1995) (after a waiting period of 1–2 min) upon arrival at the site. Sites were >400 m apart; we assumed that birds represented independent observations among sites because only 187/5757 detections were estimated >200 m from the observer. Surveys were conducted by five different observers following a training period of 1–3 wk; one observer participated in all four years, one for two years, and three for one year of the study.

### *Satellite imagery and GIS analysis*

We used spectral values in the near-infrared (0.7–0.8  $\mu\text{m}$ ) band of Landsat Multispectral Scanner (MSS) imagery to measure habitat change and current habitats. The near-infrared band is sensitive to vegetation biomass, retains high contrast in reflectance between soil and green leaf area, and also is relatively insensitive to atmospheric variation (Richardson and Wiegand 1977, Tucker 1978). In satellite imagery, spectral values abstractly represent vegetation and soil characteristics (Lillesand and Kiefer 1994). Low spectral values represent highly absorptive (dark) surfaces compared to highly reflective (bright) surfaces at higher values.

We used a multitemporal series of three satellite images, taken during similar phenological periods, to measure current habitats as well as determine components of habitat change. Images were geometrically rectified individually to common ground control points for overlay in the GIS. Image dates (and, in parentheses, root mean square error after rectification) were 12 May 1979 (38.02 m), 24 May 1988 (45.03 m), and 4 June 1992 (30.20 m). Resolution of the original MSS imagery was  $57 \times 79$  m (which we resampled to  $57 \times 57$ -m cells in the GIS); therefore spatial error was <1 pixel.

We detected the trajectory (either positive or negative), and magnitude of habitat change by image differencing in which spectral values of pixels in the current image are subtracted from values in corresponding pixels from an earlier date (Singh 1989). Areas of no landcover change have similar spectral values and differences between image dates lie within a threshold surrounding 0 (Jensen 1986, Fung and LeDrew 1988). In contrast, landcover change that affects spectral reflectance will have positive or negative differences. Before subtracting pixel values between image pairs, we radiometrically rectified images (Hall et al. 1991) to adjust the spectral values in the 1992 and 1988 (subject) images relative to the 1979 (reference) image.

We used the continuum of values within the spectral range of the near-infrared band to represent current habitats and habitat change. We associated the spectral values in the satellite imagery with vegetation at 528 ground sites sampled once from 1991 through 1994. Percent ground cover of vegetation was determined by point interception frame (Floyd and Anderson 1982). Sites were located throughout the study area at random coordinates; final coordinates were determined by GPS for overlay on the satellite imagery (U.S. Department of the Interior 1996). We grouped vegetation into high density shrub (>15% ground cover), low density shrub (>5% and <15% ground cover), grassland, and disturbed (bare ground or >15% ground cover of Russian thistle [*Salsola kali*]) classes. Spectral values were compared among vegetation classes by ANOVA followed by pairwise *t* tests (Bonferroni adjustment) to determine significantly different means (SAS Institute

TABLE 1. Relationship between spectral values in Landsat multispectral scanner satellite imagery and vegetation class for a shrubsteppe region in southwestern Idaho.

Current vegetation class	<i>n</i>	Current (1992) spectral value*	Spectral difference	
			1988–1992*	1979–1992*
Disturbed	49	56.9 <sup>A</sup>	7.6 <sup>A</sup>	8.1 <sup>A</sup>
Grassland	252	51.2 <sup>B</sup>	4.6 <sup>B</sup>	4.3 <sup>B</sup>
Low density shrubland	190	49.8 <sup>B</sup>	6.2 <sup>A</sup>	–0.2 <sup>C</sup>
High density shrubland	37	43.4 <sup>C</sup>	5.8 <sup>A</sup>	–5.5 <sup>D</sup>

Note: Vegetation classes with different superscript letters within columns differed significantly ( $P < 0.05$ ) in pairwise comparisons of Landsat near-infrared spectral values.

\* $P < 0.001$  (ANOVA).

1989). Because we conducted field sampling for vegetation at the scale of a satellite image pixel (Knick et al. 1997), we could not calibrate satellite measures of habitat richness and texture with actual field measures.

We determined mean habitat, and measured habitat richness and spatial texture in the landscape for each bird survey point by centering that point in ~150-, 1000-, and 5000-m boxes (actual box sizes were 171-, 969-, and 5073-m because of the  $57 \times 57$ -m cell dimension in the GIS) on each satellite image. For each site and box size, we determined the mean spectral (=habitat) value from all map cells. In addition, we determined the Shannon index (a nonspatial measure that increases with greater habitat richness), and the angular second moment (a measure of spatial texture that reaches a maximum of 1 when all cells within the block are identical) (Baker and Cai 1992, Musick and Grover 1991). We determined the current habitat components from the 1992 image; change components were determined from the differences between 1979–1992 and 1988–1992 in the image pairings.

#### Statistical analysis

We used the redundancy analysis (RDA) in canonical correlation (ter Braak 1995) for each bird species to determine habitat variables most correlated with the linear axis of species abundance. The response variable was the median value counted for each species at a site in the 4 sample years. We separated species response into current habitat and change components in a series of partial RDAs analogous to partialling out variance due to environmental and spatial components (ter Braak and Looman 1988, Borcard et al. 1992, Legendre 1993). Partialling out the components of variation takes the form: (1) determine variation in bird species data explained by current habitat variables (which contains variation due to change components), (2) determine variation in bird species data explained by change variables (which contains variation due to current components), (3) determine variation in bird species data explained by current habitat variables but remove variation due to habitat change by including change variables as covariates, and (4) determine variation in bird species data explained by change variables but remove variation due to current habitats by including current

habitat variables as covariates. The total variation in bird species explained by both current habitat and change variables is the sum of steps 1 + 4 or 2 + 3 (total unexplained variation is one minus this value). The variation in species abundance due solely to current habitat variables (the nonchange component) is step 3; variation due solely to change variables (the noncurrent component) is step 4.

## RESULTS

### Habitat and satellite image relationships

Disturbed or grassland habitats, which consisted of highly reflective bare ground or Russian thistle, had higher spectral values in the 1992 satellite image (current habitat) compared to more absorptive shrubland habitats (Table 1). Positive differences in spectral values between 1979 and 1992 were related to sites that currently were in disturbed or grassland habitats; negative differences during that period were associated with shrublands (Table 1). The relationship between habitat and spectral change was less clear for the 1988 to 1992 image differences.

Wildfires were related to composition of current vegetation as well as to areas of greatest habitat change during both analysis periods (Fig. 1a, b, c). Spectral values at 174 sites sampled for vegetation in burned areas were higher than for 354 unburned sites in the 1992 satellite image (54.1 vs. 49.0,  $t = 6.54$ ,  $P < 0.001$ ) primarily because wildfires had eliminated shrubs. The average spectral value also increased more in burned compared to unburned areas during the 1988–1992 (6.6 vs. 5.0,  $t = 2.59$ ,  $P < 0.01$ ) and 1979–1992 (5.4 vs. 0.8,  $t = 6.72$ ,  $P < 0.001$ ) image analysis periods, again because landcover changed from shrubland to more highly reflective grassland or bare ground surfaces.

The primary trajectory of habitat change in our entire study area was toward grassland and disturbance land surfaces as opposed to an opposite trajectory towards shrublands. From 1979 to 1992, 22.2% of all image cells ( $n = 584\,075$  cells) increased in reflectance by more than +1 SD, which indicated loss of shrub and increased grass cover, compared to 7.8% of the cells that decreased below 1 SD. From 1988 to 1992, 33.8% of the image cells increased  $> +1$  SD compared to only 3.3% that decreased.

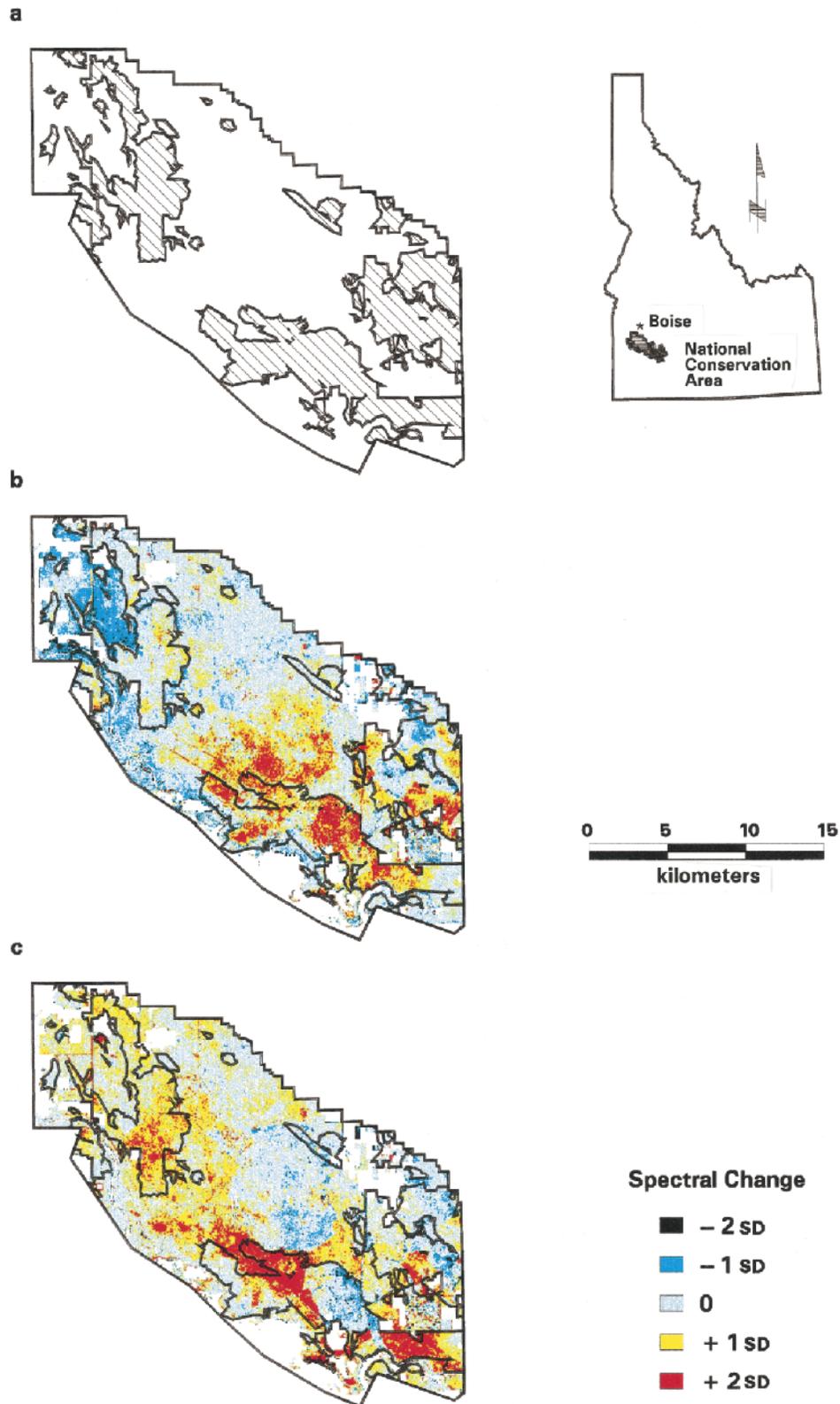


Fig. 1. Relationship between wildfires in a shrubsteppe region of southwestern Idaho and spectral change in MSS imagery. (a) Wildfires from 1979 to 1992; (b) changes in MSS imagery between 1979 and 1992; (c) changes in MSS imagery between 1988 and 1992. For illustration, we grouped spectral change values into categories based on standard deviations and centered at the mean value. Boundaries of burns are from U.S. Bureau of Land Management records. Fires were not recorded for the central portion, a military training site, before 1988.

TABLE 2. Differences in habitat variables in Landsat multispectral scanner satellite imagery between 1988 and 1992 and between 1979 and 1992 at 121 bird sampling sites for three spatial scales. Landscape measures of habitat richness and texture are not comparable among scales.

Habitat variable	1988–1992				1979–1992			
	Difference			<i>P</i>	Difference			<i>P</i>
	Mean	1 SE	Paired <i>t</i>		Mean	1 SE	Paired <i>t</i>	
Mean habitat†								
150 m	+6.06	0.50	12.65	< 0.01	+2.14	0.69	3.10	< 0.01
1000 m	+6.30	0.43	14.67	< 0.01	+2.17	0.61	3.58	< 0.01
5000 m	+6.06	0.31	19.86	< 0.01	+1.90	0.51	3.71	< 0.01
Habitat richness‡								
150 m	+0.19	0.04	4.62	< 0.01	+0.02	0.04	0.54	NS
1000 m	+0.14	0.03	5.20	< 0.01	+0.17	0.03	5.49	< 0.01
5000 m	-0.09	0.02	-4.32	< 0.01	+0.21	0.02	8.74	< 0.01
Habitat texture§								
150 m	-4.97	1.41	-3.53	< 0.01	+0.06	0.83	0.08	NS
1000 m	-1.37	0.18	-7.52	< 0.01	-0.19	0.08	-2.21	< 0.05
5000 m	-0.44	0.05	-8.63	< 0.01	-0.16	0.03	-4.13	< 0.01

† Increases represent habitat changes toward grassland or disturbance habitats; decreases represent habitat changes toward shrublands.

‡ Increases represent landscape changes that increase habitat richness.

§ Increases represent landscape changes that increase spatial homogeneity.

Spectral change at our 121 sites sampled for birds also indicated increased grassland or disturbance cover during both change analysis periods (Table 2). Habitat richness increased, except at 5000 m between 1988 and 1992, and homogeneity of the landscape decreased at all three spatial scales during the change analysis periods (Table 2).

#### *Current habitats, habitat change, and breeding birds*

Current abundance and distribution of all species, except for Sage Sparrows, was most strongly correlated with the pure current habitat component (Fig. 2). Although secondary to measures of current habitat, the component for pure habitat change was significantly correlated with abundance of Horned Larks and Brewer's sparrows during 1979–1992 and 1988–1992 periods and with Sage Sparrow numbers for 1988–1992 (Fig. 2). The pure habitat change component was not significantly related to abundance of Sage Thrashers and Western Meadowlarks. Current and change variables explained largely separate partitions of the variation in bird abundance; the variation explained by combined variables was small relative to the pure components (Fig. 2).

Abundance of all species was most strongly correlated with nonspatial measures of current habitat at each spatial scale (Table 3). Habitat richness and texture in the current habitat, when significant, were correlated with bird abundance only at the 5000-m spatial scale. For habitat change, nonspatial variables again were significantly correlated with bird abundance (Table 4). Only large-scale decreases in habitat richness and spatial heterogeneity were correlated with bird abundance.

#### DISCUSSION

Competing processes of short-term response and species inertia caused by site fidelity (Rotenberry and Wiens 1980, Wiens 1985, Wiens and Rotenberry 1985) were reflected in the relative variation explained by change and current habitat components. How long might we expect effects of habitats past to persist due to philopatry and site tenacity? Assume, for example, that a site changes such that it becomes completely unsuitable (i.e., no successful reproduction occurs) for a species. If the species is highly site-tenacious, its abundance in subsequent years primarily reflects annual survivorship. Given adult passerine mortality rates of ~40–60%/yr, we would expect to see ~5% of the original population still present at the site 4–7 yr after the alteration. To the extent that the changed habitat permits reproduction (even at below replacement rates), any philopatry will further extend the species occupancy of the site.

Wildfires, the major disturbance altering landscapes in our study area, burn primarily from July through early September. Therefore, most habitats change when birds either are not tied to a specific location during nesting, or are absent on migratory grounds. Birds in our study area likely respond predominantly to changes in the landscape upon returning from wintering ranges by a process of redistribution among the new configuration of suitable habitats.

Horned Larks, Western Meadowlarks, and Brewer's Sparrows, but not Sage Thrashers or Sage Sparrows, were positively correlated with decreased habitat richness and increased spatial homogeneity at large spatial scales, which have greater inherent stability or persistence for either shrubland or grassland habitats relative

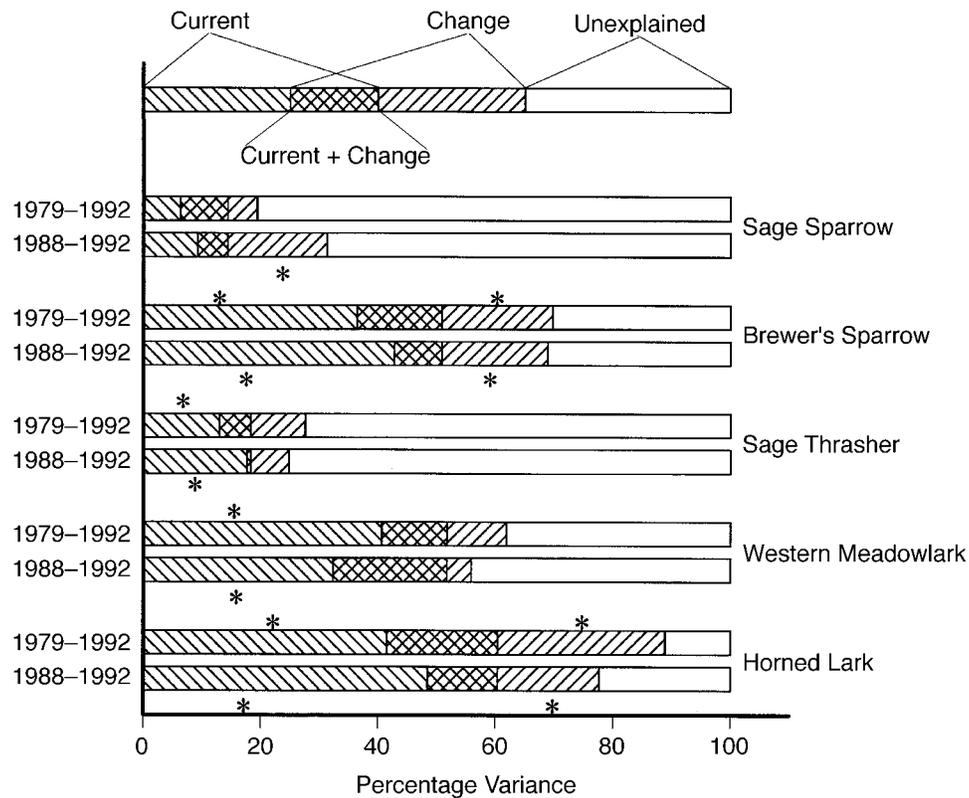


FIG. 2. Contribution of current and change variables in explaining current distribution and abundance of breeding passerine birds in a shrubsteppe region of southwestern Idaho. Significance of canonical  $R^2$  for the pure component was determined from Wilks'  $\lambda$ .  
\*  $P < 0.05$ .

TABLE 3. Correlation coefficients with the first axis of bird abundance in a redundancy analysis of current habitat variables at three spatial scales.

Habitat variable	Bird species				
	Horned Lark	Western Meadowlark	Sage Thrasher	Brewer's Sparrow	Sage Sparrow
Mean habitat†					
150 m	0.73*	-0.67*	-0.23*	-0.66*	-0.22*
1000 m	0.73*	-0.70*	-0.30*	-0.68*	-0.23*
5000 m	0.70*	-0.66*	-0.34*	-0.65*	-0.18*
Habitat richness‡					
150 m	0.11	-0.02	0.04	-0.06	-0.13
1000 m	0.05	0.01	0.13	-0.06	-0.06
5000 m	0.24*	-0.20*	-0.05	-0.21*	0.06
Habitat texture§					
150 m	-0.09	0.02	-0.01	0.02	0.05
1000 m	-0.14	0.05	0.05	0.02	0.13
5000 m	-0.26*	0.14	0.02	-0.08	0.00

Note: Significance of correlations were determined by univariate  $F$  ( $P < 0.05$ ).

† Positive coefficients represent associations with grassland or disturbance habitats; negative coefficients represent greater associations with shrublands.

‡ Positive coefficients represent associations with landscapes containing greater habitat richness.

§ Positive coefficients represent associations with habitats having greater spatial homogeneity.

TABLE 4. Correlation coefficients with the first axis of bird abundance in a redundancy analysis of habitat change variables at three spatial scales.

Habitat variable	Horned Lark		Western Meadowlark		Sage Thrasher		Brewer's Sparrow		Sage Sparrow	
	1988–1992	1979–1992	1988–1992	1979–1992	1988–1992	1979–1992	1988–1992	1979–1992	1988–1992	1979–1992
Mean habitat†										
150 m	0.20*	0.58*	0.07	-0.27*	-0.07	-0.17	0.08	0.41*	0.00	-0.39*
1000 m	0.24*	0.58*	0.05	-0.22*	-0.08	-0.23*	0.08	0.39*	0.00	-0.40*
5000 m	0.32*	0.62*	0.26*	-0.21*	-0.17	-0.22*	0.27*	0.36*	-0.15	-0.37*
Habitat richness‡										
150 m	0.01	0.03	0.01	0.05	-0.04	-0.02	-0.13	0.00	0.08	-0.02
1000 m	-0.23*	-0.32*	-0.16	0.05	0.06	0.09	-0.29*	-0.14	0.14	0.10
5000 m	-0.43*	-0.30*	-0.23*	-0.04	0.16	-0.02	-0.21*	-0.03	0.16	0.14
Habitat texture§										
150 m	0.11	-0.01	0.12	-0.09	0.02	-0.01	0.24*	0.11	-0.23*	-0.01
1000 m	0.16	0.15	0.37*	-0.05	-0.05	0.06	0.46*	0.11	-0.13	-0.01
5000 m	0.26*	0.17	0.33*	0.09	-0.05	0.09	0.38*	0.06	-0.07	-0.10

Notes: Analyses did not include covariables. Increases in mean spectral value indicate habitat change toward grassland or disturbed area; decreases indicate increased shrub cover. Increases in values for habitat texture indicate greater spatial homogeneity. Significance of correlations was determined by univariate  $F$  (\*  $P < 0.05$ ).

† Positive coefficients represent associations with habitat changes toward grassland or disturbance habitats; negative coefficients represent greater associations with habitat changes toward shrublands (Table 1).

‡ Positive coefficients represent associations with landscape changes that increase habitat richness.

§ Positive coefficients represent associations with landscape changes that increase spatial homogeneity.

to more heterogeneous landscapes. Larger shrubland patches tend to remain because cheatgrass is less abundant in the patch interior to facilitate fire spread (Knick and Rotenberry 1997). Thus, large shrubland patches are less likely to be destroyed by wildfire than highly fragmented shrublands embedded in a grassland matrix, which are susceptible to cheatgrass invasion and subsequent fires. In contrast, large expanses of exotic annual grasslands also are a spatially stable habitat primarily because frequent, large-scale fires prevent shrub regeneration and maintain the grassland system.

The average changes in habitat across our sites, towards increased habitat richness and spatial heterogeneity, were associated with lower abundances of birds. Of the five species, populations of Horned Larks, Western Meadowlarks, and Brewer's and Sage sparrows have declined significantly in Breeding Bird Surveys across their range since the mid-1960s (Peterjohn and Saurer 1993, 1999). For Brewer's sparrows, Horned Larks, and perhaps Sage Sparrows, those declines likely are a function of components for habitat change as well as current landscapes.

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