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## AVIAN RESPONSE TO WILDFIRE IN INTERIOR COLUMBIA BASIN SHRUBSTEPPE

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**Abstract.** Wildfire and conversion of sagebrush (*Artemisia* spp.) shrublands to cheatgrass (*Bromus tectorum*) grasslands is a serious threat to the shrubsteppe ecosystem, but few studies have documented wildfire's effects on birds with multiple years of pre- and post-fire data. Using data from avian point counts recorded 4 years before and 7 years after a large-scale, severe wildfire in the Columbia Basin of south-central Washington, we found significant effects of fire on population trends or mean abundance of nearly all species investigated. The Sage Sparrow (*Amphispiza belli*), a sagebrush obligate, was decreasing at a high rate both pre- and post-fire. Among species inhabiting more open shrubsteppe or grasslands, the mean abundance of three (Grasshopper Sparrow, *Ammodramus savannarum*; Western Meadowlark, *Sturnella neglecta*; Vesper Sparrow, *Pooecetes gramineus*) was lower post-fire and one (Lark Sparrow, *Chondestes grammacus*) showed an initial, but short-lived, increase post-fire before dropping below pre-fire levels. Only one (Horned Lark, *Eremophila alpestris*) increased steadily post-fire and had higher post-fire mean abundance.

**Key words:** *Amphispiza belli*, cheatgrass, fire, *Pooecetes gramineus*, Sage Sparrow, sagebrush, shrubsteppe birds, Vesper Sparrow.

### Respuestas de las Aves a los Fuegos Silvestres en la Estepa Arbustiva del Interior de la Cuenca de Columbia

**Resumen.** Los fuegos silvestres y la transformación de los arbustales de *Artemisia* a pastizales de *Bromus tectorum* son una seria amenaza para el ecosistema de estepa arbustiva. Sin embargo, pocos estudios han documentado los efectos de los fuegos silvestres sobre las aves con base en datos de múltiples años anteriores y posteriores a los fuegos. Empleando datos de puntos de conteo de aves realizados cuatro años antes y siete años después de un fuego severo de gran escala en la cuenca de Columbia en el centro-sur de Washington. Encontramos efectos significativos del fuego sobre las tendencias poblacionales o la abundancia promedio en casi todas las especies investigadas. *Amphispiza belli*, una especie restringida a los arbustales de *Artemisia*, presentó altas tasas de disminución tanto antes como después del fuego. Entre las especies que habitaban los arbustales o los pastizales más abiertos, la abundancia promedio de tres especies (*Ammodramus savannarum*, *Sturnella neglecta* y *Pooecetes gramineus*) fue más baja después

del fuego y una especie (*Chondestes grammacus*) mostró un aumento inicial de corta duración después del fuego, para luego disminuir por debajo de los niveles previos al fuego. Sólo una especie (*Eremophila alpestris*) aumentó abruptamente después del fuego y tuvo una abundancia promedio mayor después del fuego.

Wildfire and the subsequent conversion of sagebrush (*Artemisia* spp.) to annual grasslands of the exotic cheatgrass (*Bromus tectorum*) is one of the most serious threats to remaining shrubsteppe habitat and shrubsteppe-obligate birds throughout the western United States (Knick and Rotenberry 1997, Knick 1999). Shrubsteppe is an imperiled ecosystem in the U.S., where much of the native sagebrush has been converted to exotic annual grasslands or sagebrush with an understory of exotic annual grasses (Mac et al. 1998, Knick et al. 2003). In the Interior Columbia Plateau of Washington, over 65% of the sagebrush has been lost, and much of the remaining Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) has been degraded or fragmented by agriculture, livestock grazing, and fire (McDonald and Reese 1998, Vander Haegen et al. 2000, Knick and Rotenberry 2002).

Historically, fires in Wyoming big sagebrush communities were probably infrequent (50 to >100 year intervals), patchy, and uneven, resulting in a mosaic of sagebrush and native bunchgrass communities in different stages of succession (Wright and Bailey 1982). Today's fires, fueled by the relatively densely growing and short-lived cheatgrass, are frequent, severe, and large and result in further conversion of native shrubsteppe to cheatgrass grasslands and sagebrush with cheatgrass understory (Young and Evans 1973, Knick and Rotenberry 1997, Knick 1999).

The Fitzner–Eberhardt Arid Lands Ecology Reserve (ALE) Research Natural Area and Hanford Reach National Monument, of which ALE is a part, include some of the largest contiguous stands of shrubsteppe in the Interior Columbia Basin, including large expanses of threetip sagebrush (*Artemisia tripartita*)–bluebunch wheatgrass (*Pseudoregneria spicata*) communities and bluebunch wheatgrass communities. In June 2000, a wildfire burned nearly 66 368 ha, including all of ALE (31 200 ha). The fire caused >90% mortality of shrubs, grasses, and forbs over 85% of the area. Only 15% of the area burned in a mosaic fashion, and only 3500 ha of sagebrush habitat remained intact (USDI 2000). Because bird abundance is related to local (Rotenberry and Wiens 1980a, Rotenberry 1985, Wiens et al. 1987) and landscape-level habitat variables (Knick and Rotenberry 1995, Rotenberry and Knick 1999, Vander Haegen et al. 2000), a fire of this severity and scale is particularly likely to affect the abundance of shrubsteppe birds (Knick et al. 2005).

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Few studies have documented the effect of wildfire on shrub-steppe bird communities with multiple years of pre- and post-fire data at repeatedly monitored stations (reviewed by Petersen and Best 1999, Knick et al. 2005). We used avian point-count data from 33 points surveyed 4 years prior to and 7 years after the wildfire to quantify effects on abundance and trends in abundance for six native shrubsteppe species known to breed on the study site.

## METHODS

ALE lies near the confluence of the Columbia and Yakima rivers on the central Columbia Plateau of southeastern Washington. Although historically used for livestock grazing, ALE and the surrounding area has been largely closed to the public and livestock grazing since 1943 when acquired by the U.S. government. It was established as an ecological reserve in 1967 and has been managed by the U.S. Fish and Wildlife Service since 1997. The year 2000 wildfire we investigated was preceded by wildfires 7 and 10 years earlier on this study site and followed by an equally large and intense fire of late summer 2007.

ALE varies in elevation from 150 to 1050 m and encompasses the ridgetop and north-facing slope of Rattlesnake Mountain, portions of the Rattlesnake Hills and the Yakima Ridge, several valleys, and two major spring systems. Higher elevations (>600 m) are characterized by threetip sagebrush–bluebunch wheatgrass communities, intermediate elevations (300–600 m) by bluebunch wheatgrass with some Wyoming big sagebrush–bluebunch wheatgrass patches in lower areas of this zone (Sackschewsky and Downs 2001). Prior to the 2000 wildfire, lower elevations (<300 m), were covered about equally by Wyoming big sagebrush–cheatgrass communities and cheatgrass grasslands, with spiny hopsage (*Grayia spinosa*), Sandberg's bluegrass (*Poa secunda*), needle-and-thread grass (*Hesperostipa comata*), and Idaho fescue (*Festuca idahoensis*) often present.

## POINT COUNTS

The 33 points were located in six pre-fire cover types, defined by the principal cover type within a 100-m radius of the point (classification modified from Sackschewsky and Downs [2001]): bluebunch wheatgrass ( $n = 11$ ), threetip sagebrush–bluebunch wheatgrass ( $n = 5$ ), big sagebrush–native grass ( $n = 3$ ), black greasewood (*Sarcobatus vermiculatus*)–alkali saltgrass (*Distichlis stricta*) ( $n = 2$ ), big sagebrush–cheatgrass ( $n = 6$ ), and cheatgrass ( $n = 6$ ). Points were established in locations representative of ALE's biodiversity and in cover types roughly proportional to their availability on the study site, except that cheatgrass was slightly under-sampled (24% of available cover types and 18% of points) and black greasewood was slightly over-sampled (< 1% of available cover types and 6% of points).

During point counts, the observer recorded each bird seen or heard in an unlimited radius around the point during a 10-min period; fly-overs are not included in this analysis. One of two observers (NL or WL) recorded point-count data during one to four visits to each station each year between 7 April and 8 June 1997–2007. The average annual survey date was 6 May, with a range in annual means from 23 April to 13 May and a median of two visits per station annually. For each station, we averaged results from multiple visits in a year. In all years except 2004–2006, most stations (83%) were visited at least twice annually; from 2004 to 2006, most stations (87%) were visited once annually. Having multiple surveys within a year reduces potential bias resulting from some surveys being conducted early or late relative to a given species' breeding phenology. To compensate for

potential bias resulting from a difference in survey dates across years (relative to singing males' phenology), especially because some points were visited only once in some years, we added the average survey as a covariate to the models (see Statistical Analyses). Surveys were conducted 0–3.5 hours after sunrise and not during periods of rain or wind >20 km hr<sup>-1</sup>. We limit our analysis to six native species considered shrubsteppe or grassland associates that are known to breed on the study site and that occurred at ≥14 of the 33 stations.

## STATISTICAL ANALYSES

We used repeated-measures mixed-effects models (Proc Mixed, SAS Institute 2004) to investigate the effect of the wildfire on each species' abundance and trend in abundance, with 11 annual surveys repeated at each of 33 points and a first-order autoregressive covariance structure (typical of time-series analysis, Littell et al. 2006). The occurrence of fire in each year was coded as 0 for pre-fire (1997–2000) and 1 for post-fire years (2001–2007). The first five candidate models were the null model and models containing “year,” “fire,” “year + fire,” and “year + fire + year × fire” as fixed-effect independent variables. Two potentially confounding covariates were considered: average survey day (in later years surveys tended to be conducted at earlier dates than in earlier years) and total precipitation in the preceding growing season (October–May; data from the Hanford Meteorological Station, <http://hms.pnl.gov>). For species having either average survey day (Grasshopper Sparrow and Horned Lark) or precipitation (Western Meadowlark) or both (Lark Sparrow) as a significant univariate predictor ( $P < 0.05$ ), the covariate was added to the five previously mentioned models for a total of 10 or 15 candidate models per species.

We used Akaike's information criterion corrected for small samples (AIC<sub>c</sub>) to choose the best subset of models (Burnham and Anderson 2002). The model with the lowest AIC<sub>c</sub> score was considered the most parsimonious, and models within four AIC<sub>c</sub> units of it were included in the subset of best models. We used model averaging across the best subset of models to calculate the unconditional regression coefficient ( $\pm$  unconditional SE) for year (i.e., the population trend across time) and other parameters (Burnham and Anderson 2002).

If the model-averaged coefficient for the interaction term was significant ( $P < 0.05$ ), it indicated that the slope of the relationship between abundance and year pre-fire differed from that post-fire. If the interaction term was not significant, model-averaged coefficients for year and fire were calculated from the remaining models in the best model subset (i.e., those not containing the interaction term). If the model-averaged coefficient for fire was significant, it indicated that fire had a significant effect on mean abundance, given the observed trend.

## RESULTS

Among the two species occurring primarily in big sagebrush (Table 1), the Sage Sparrow declined at a high rate throughout the period ( $t_{131} = 2.5$ ,  $P = 0.01$ ) (Fig. 1), without significant effects of fire on mean abundance or trend (on the basis of model-averaged coefficients of the best model subset, Tables 2 and 3). The Lark Sparrow also was decreasing both before and after the fire, but fire had the initial effect of increasing mean abundance (coefficients for year and fire were marginally significant,  $P = 0.09$  and 0.07, respectively; Fig. 1, Table 3). The effect of precipitation was also marginally significant ( $P = 0.09$ ), with fewer individuals recorded in wetter years.

TABLE 1. Mean abundance (average individuals per count point) of species across the four main pre-fire cover types after the fire (2001–2007).<sup>a</sup>

Species	Cheatgrass <sup>b</sup>	Bluebunch wheatgrass <sup>b</sup>	Big sagebrush <sup>b</sup>	Threetip sagebrush <sup>b</sup>	<i>F</i>	<i>P</i>
Horned Lark	2.72 (0.74) A	7.09 (0.72) B	1.53 (0.42) A	3.52 (1.12) A	13.9	<0.0001
Western Meadowlark	6.72 (0.42)	5.7 (0.75)	6.44 (0.36)	4.84 (0.54)	1.4	0.27
Vesper's Sparrow	0.31 (0.26) A	1.77 (0.44) B	0.25 (0.25) A	4.04 (1.04) C	10.1	0.0001
Grasshopper Sparrow	0.66 (0.17) AC	2.0 (0.40) B	0.03 (0.03) A	1.52 (0.49) BC	8.1	0.0005
Sage Sparrow	0.06 (0.04) A	0.02 (0.02) A	2.31 (0.40) B	0 (–) A	25.9	<0.0001
Lark Sparrow	0.02 (0.02) A	0.01 (0.01) A	0.18 (0.07) B	0 (–) A	4.7	0.009

<sup>a</sup>Number of points per cover type was 6 in cheatgrass, 11 in bluebunch wheatgrass, 9 in big sagebrush, and 5 in threetip sagebrush. Big sagebrush cover type includes points with native grass or cheatgrass understory; the two points in black greasewood/alkali saltgrass are not included in the cover-type means or ANOVA.

<sup>b</sup>SE given in parentheses. Columns within species sharing a letter do not differ statistically (Fisher's least significant difference used for pairwise comparisons if the one-way ANOVA was significant).

Of the two species occurring primarily in threetip sagebrush and bluebunch wheatgrass (Table 1), the year  $\times$  fire interaction term was significant for the Grasshopper Sparrow, indicating that pre- and post-fire trends differed (Table 3, Fig. 1). Grasshopper Sparrows were decreasing significantly prior to the fire and stabilized after the fire at a mean abundance lower post-fire than pre-fire (0.56 vs. 1.03,  $t_{32} = 3.5$ ,  $P = 0.002$ , based on paired  $t$ -tests). The model-averaged coefficient for “mean survey day” was also

significant, indicating that more individuals were recorded later in the spring (Table 3). For the Vesper Sparrow, only the fire coefficient was significant, indicating that the post-fire mean was lower than the pre-fire mean (Fig. 1, Table 3). However, the trend in abundance across years was clearly nonlinear (Fig. 1). Abundance declined in the first two years post-fire, increased for the following three years until it reached approximately pre-fire levels, and then declined in the final two years.

TABLE 2. Models in the best model subset, i.e., those within 4  $AIC_c$  units of the most parsimonious model (the model with the lowest  $AIC_c$ ),  $-2LL$  (negative 2 log likelihood),  $K$  (number of parameters), change in  $AIC_c$  (difference in  $AIC_c$  from model with lowest  $AIC_c$ ), and Akaike weight.

Species	Model <sup>a</sup>	$-2LL$	$K$	$\Delta AIC_c^b$	Akaike weight
Grasshopper Sparrow	Yr + Fire + Yr $\times$ Fire + Srvday	764.8	8	0	0.52
	Fire + Srvday	772.4	6	0.79	0.35
	Yr + Fire + Yr $\times$ Fire	771.2	7	2.91	0.12
Western Meadowlark	Yr + Fire + Yr $\times$ Fire	1336.4	7	0	0.85
	Yr + Fire + Yr $\times$ Fire + Precip	1336.4	8	3.52	0.15
Horned Lark	Yr + Fire + Yr $\times$ Fire + Srvday	1593.9	8	0	0.52
	Yr + Srvday	1601.8	6	1.08	0.30
	Yr + Fire + Yr $\times$ Fire	1599.5	7	2.05	0.18
Lark Sparrow	Yr + Fire + Precip	20.6	7	0	0.35
	Fire + Srvday	26.0	6	2.13	0.12
	Srvday	29.0	5	2.18	0.12
	Yr + Fire + Yr $\times$ Fire + Srvday	19.4	8	2.31	0.11
	Precip	29.3	5	2.41	0.10
	Yr + Fire + Srvday	23.4	7	2.85	0.08
	Yr + Fire + Yr $\times$ Fire + Precip	20.6	8	3.52	0.06
	Yr + Fire	27.7	6	3.82	0.05
	Fire	955.3	5	0	0.52
Vesper Sparrow	Yr + Fire + Yr $\times$ Fire	950.2	7	1.18	0.29
	Yr + Fire	955.2	6	2.97	0.12
	Yr	959.0	5	3.73	0.08
	Yr	669.4	5	0	0.49
Sage Sparrow	Yr + Fire	667.2	6	0.86	0.32
	Fire	672.1	5	2.72	0.12
	Yr + Fire + Yr $\times$ Fire	666.9	7	3.77	0.07

<sup>a</sup>Abbreviations for model parameters are Yr (year), Srvday (average survey day), Precip (precipitation during the preceding growing season, October–May).

<sup>b</sup> $AIC_c$  calculated on the basis of 33 points.

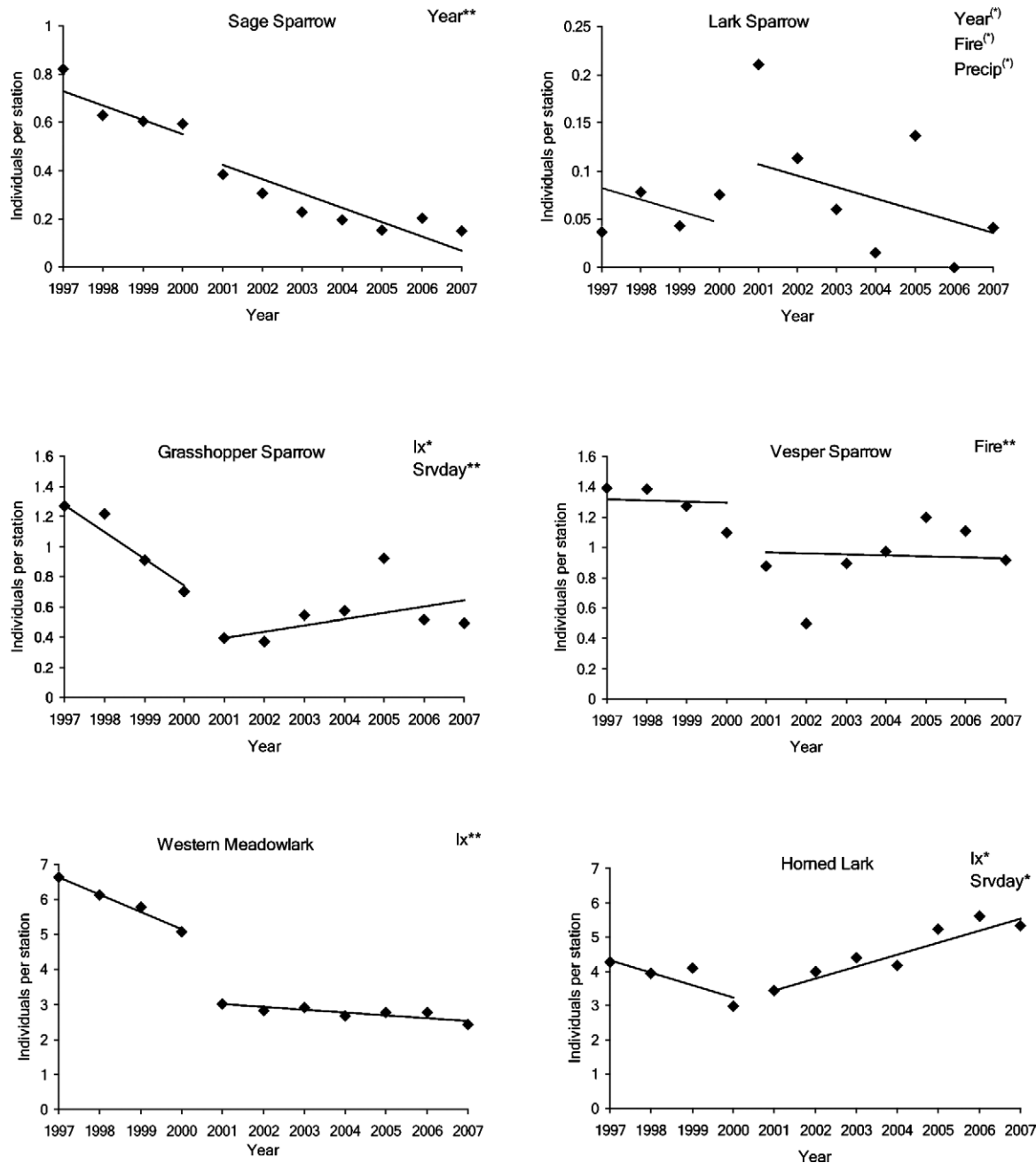


FIGURE 1. Average individuals per count point before (1997–2000) and after (2001–2007) fire; regression trend lines were calculated with model-averaged coefficients (Table 3); parameters with significant coefficients listed in upper right where (\*) $P < 0.10$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , and abbreviations are Ix (year  $\times$  fire interaction), Srvday (survey day), and Precip (precipitation).

Two species, the Western Meadowlark and Horned Lark, occurred commonly in all cover types, although Horned Larks were more common in bluebunch wheatgrass than elsewhere (Table 1). For both species, the model-averaged year  $\times$  fire interaction term was significant. Western Meadowlarks were decreasing significantly prior to the fire and stabilized after the fire (Table 3, Fig. 1) at a mean abundance lower post-fire than pre-fire (2.77 vs. 5.89,  $t_{32} = 11.1$ ,  $P < 0.0001$ , based on paired  $t$ -tests). Unlike all other species we investigated, the Horned Lark exhibited no trend in numbers prior to the fire, but increased significantly

after the fire (Table 3, Fig. 1) and had a higher abundance post-fire than pre-fire (4.58 vs. 3.81,  $t_{32} = 2.2$ ,  $P = 0.03$ ). For the Horned Lark, the model-averaged coefficient for “mean survey day” was also significant, indicating that more individuals were recorded later in the spring (Table 3).

Because the effect of fire on vegetative structure was not expected to be uniform across cover types, we, as a qualitative post-hoc analysis, visually compared trends across four major pre-fire cover types for four species having sufficient data in two or more cover types. Within each of the four species (Western



TABLE 3. Model-averaged coefficients (SE) and pre-fire and post-fire trends (i.e., coefficients for year term) for those species for which the year  $\times$  fire interaction term was or was not significant (best model subset given in Table 1).

Species	Model-averaged coefficients (SE) <sup>a</sup>		Population trends (SE) <sup>a,b</sup>	
			Pre-fire	Post-fire
Interaction term for year × fire significant				
	Year × Fire	Survey day		
Grasshopper Sparrow	0.12 (0.06)*	0.01 (0.004)**	−0.15 (0.06)**	0.04 (0.03)
Western Meadowlark <sup>c</sup>	0.42 (0.14)**	—	−0.50 (0.12)***	−0.08 (0.06)
Horned Lark	0.44 (0.20)*	0.03 (0.01)*	−0.28 (0.19)	0.34 (0.09)***
Interaction term for year × fire not significant				
	Year	Fire		
Lark Sparrow	−0.01 (0.007)(*)	0.08 (0.05)(*)		
Vesper Sparrow	−0.006 (0.01)	−0.33 (0.12)**		
Sage Sparrow	−0.05 (0.02)**	−0.10 (0.08)		

<sup>a</sup>Statistical significance based on *t*-tests: (\*) $P < 0.10$ , \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ .

<sup>b</sup>Pre- and post-fire trends calculated from models containing the interaction term (see Table 1).

<sup>c</sup>For Western Meadowlarks and Lark Sparrows, precipitation also entered the best model subset (coefficient =  $-0.00002 \pm 0.002$ ,  $t_{265} = 0.006$ ,  $P = 0.99$ , and coefficient =  $-0.004 \pm 0.002$ ,  $t_{325} = 1.68$ ,  $P = 0.09$ , respectively).

Meadowlark, Horned Lark, Grasshopper Sparrow, and Vesper Sparrow), patterns in each cover type were similar (Fig. 2).

## DISCUSSION

Species associated with more sagebrush cover and relatively unfragmented landscapes, such as the Sage Sparrow (Knick and Rotenberry 1995, 1999, Vander Haegen et al. 2000, Vander Haegen 2007), are expected to respond negatively to fire or sagebrush removal (Wiens and Rotenberry 1985, McIntyre 2003, Knick et al. 2005). In our study, Sage Sparrows were declining steeply in numbers prior to the fire and continued to decline at a similar rate after the fire, a pattern that reflects their decrease on Breeding Bird Survey routes throughout the Columbia Plateau physiographic region over the same period (1997–2007; Sauer et al. 2008). Although one might expect Sage Sparrows to have declined more rapidly post-fire, it is possible that their strong fidelity to breeding sites moderated any tendency to avoid burned areas (Wiens and Rotenberry 1985, Wiens et al. 1986, Knick and Rotenberry 2000).

Among species using open shrublands or grasslands, one might expect fewer negative long-term effects of fires that decrease sagebrush cover (Knick and Rotenberry 2002, Knick et al. 2005), but these species' short-term response will likely reflect immediate post-fire plant mortality. Throughout the study area and in all cover types, there was substantial loss of vegetation immediately post-fire, and shrubs had shown little recovery when vegetation monitoring ended 4 years later. Big sagebrush cover decreased from 20% pre-fire to 0% and 0.3% in years 1 and 4 post-fire, respectively; threetip sagebrush cover decreased from 8% to 1.4% and 2.8%, native perennial grass cover decreased from 39% to 19% and 30%, and cheatgrass cover decreased from 14% to 3% and 10% in years 1 and 4 post-fire, respectively (Evans and Lih 2005). Each of the five open shrubland or grassland species we investigated exhibited post-fire effects in keeping with this loss of vegetation.

Three of the five open shrubsteppe or grassland associates had lower mean abundance post-fire. Western Meadowlarks were decreasing prior to the fire and stabilized after the fire at a lower overall mean abundance. Other studies have reported neutral,

positive, and negative effects of fire on Western Meadowlark abundance (reviewed in Knick et al. 2005), a result possibly related to the species' use of a variety of shrubsteppe and grassland habitats (Lanyon 1994). The Vesper and Grasshopper Sparrows, two species associated with perennial grasslands (Vander Haegen et al. 2000), were also less common post-fire overall. Both species exhibited a short-term increase to near pre-fire levels beginning in years 3 or 4 post-fire, but neither post-fire trend was statistically significant over the 7-year period. For the Vesper Sparrow, other studies also have reported short-term increases in abundance after a fire or sagebrush removal, with a 1-to 2-year lag, presumably related to an initial decrease and subsequent increase in grass and forb cover (Wiens and Rotenberry 1985, Petersen and Best 1987, McIntyre 2003). In other western shrublands Grasshopper Sparrows avoid burned areas (Bock and Bock 1987, 1992), but in mid-western tallgrass prairies they prefer frequently burned, and thus more sparsely vegetated, areas (Reinking 2005, Powell 2008). Although findings in the West and Midwest at first appear contradictory, it is not surprising that fire-induced thinning of vegetation has a positive effect on this species in relatively dense tallgrass prairies but not in sparse bunchgrasses of the arid West.

The remaining two open shrubsteppe or grassland associates increased either immediately or gradually post-fire. Lark Sparrow abundance increased immediately post-fire, a pattern that may reflect the increase in bare ground in the study area post-fire (Evans and Lih 2005), then declined to pre-fire levels and below. In other studies, Lark Sparrow abundance increased at a site where fire increased bare ground (Bock and Bock 1987) but not at a site where bare ground changed little (Bock and Bock 1992). Horned Larks, unlike the other species investigated here, increased steadily post-fire and had higher mean abundance post-fire, indicating a long-lasting positive effect. This positive response is consistent with their preference for less sagebrush cover (Knick and Rotenberry 1995, Vander Haegen et al. 2000) and less herbaceous vegetation (Bock and Webb 1984, Wiens et al. 1987) and consistent with other studies in which they increased after fire (Petersen and Best 1987, McIntyre 2003, and Knick et al. 2005).

Local population dynamics may be influenced by both local and regional processes (Boulinier et al. 2001). In our study,

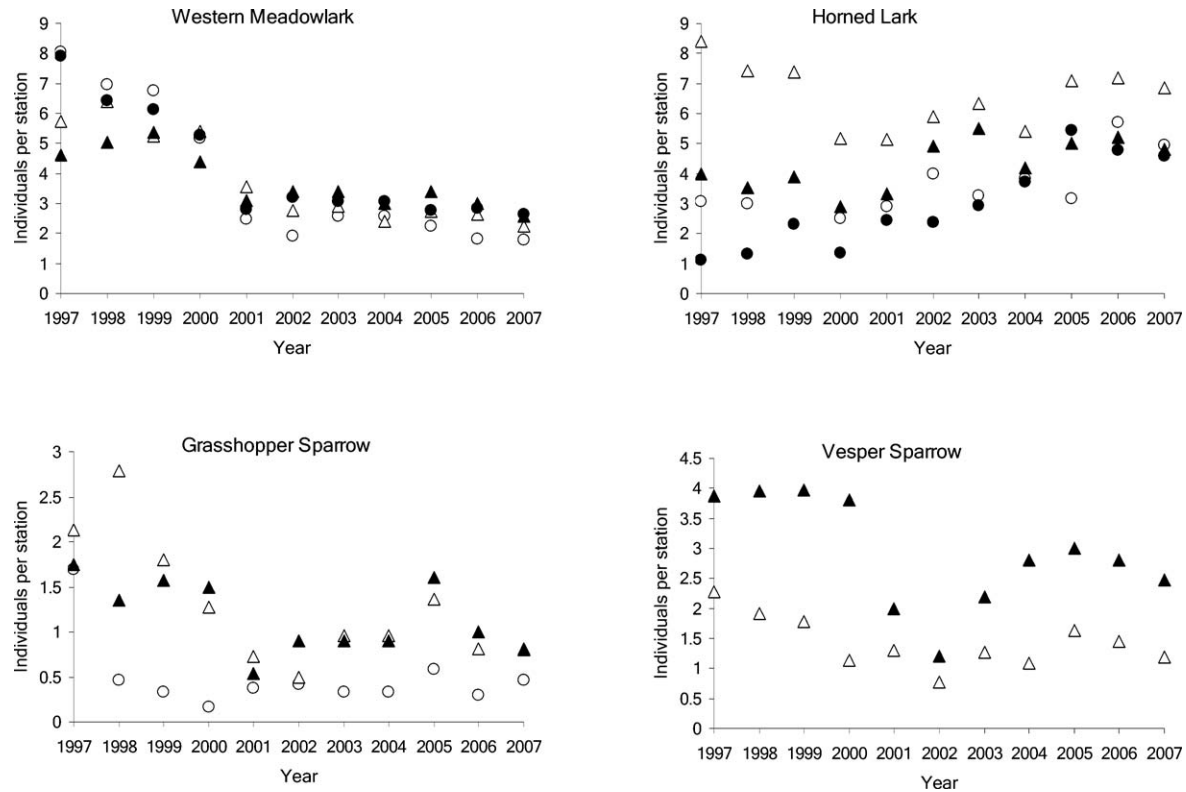


FIGURE 2. Average individuals per count point before (1997–2000) and after (2001–2007) fire for four species for which data were sufficient for trends among two or more pre-fire cover types to be visually compared. Pre-fire cover types are big sagebrush (filled circle), cheatgrass (unfilled circle), threetip sagebrush–bluebunch wheatgrass (filled triangle), and bluebunch wheatgrass (unfilled triangle).

of the four species whose pre-fire or overall trend was significant or marginally significant, two had similar trends in the Columbia Plateau physiographic region (Sage Sparrows  $-4.3\%$ ,  $P = 0.003$ ; Western Meadowlark  $-3.0\%$ ,  $P < 0.001$ ; BBS data 1997–2007, Sauer et al. 2008), suggesting congruence between local and larger-scale processes for these two species. Not surprisingly, given the local post-fire vegetation changes, the single significant post-fire trend (an increase in Horned Larks) did not correspond to a significant regional trend ( $-1.34\%$ ,  $P = 0.23$ ).

Avian populations may respond to one or several potential types and spatial scales of fire-induced vegetation changes (Knick et al. 2005). Birds may respond to immediate post-fire mortality in sagebrush or herbaceous cover, changes in composition of herbaceous species (in particular, the replacement of native bunchgrasses by cheatgrass), the patchiness or complexity of the burn, and the loss of sagebrush across the landscape. The fire investigated here produced considerable plant mortality across  $>66\,000$  ha, and we interpret the substantial changes in the abundance and trends of the six avian shrubsteppe associates over 7 years post-fire primarily as a response to plant mortality. For future studies, vegetation monitoring at the points and over a longer time would be useful in distinguishing the direct effects of plant mortality from those of changes in composition of the sagebrush and herbaceous communities.

Because our 7 years of post-fire data comprise a complete interfire interval (i.e., the site reburned immediately after the study), this study will aid in interpreting subsequent post-fire dynamics on this site and serve as an example of the effects of frequent fires in shrubsteppe. As today's shrubsteppe fires become

more severe and frequent (Knick and Rotenberry 1997), long-term monitoring across multiple fire intervals, especially if coupled with vegetation and demographic monitoring, will become increasingly important in understanding spatial and temporal responses of avian populations.

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