

FRAGMENTATION BY AGRICULTURE INFLUENCES REPRODUCTIVE SUCCESS OF BIRDS IN A SHRUBSTEPPE LANDSCAPE

W. MATTHEW VANDER HAEGEN¹

Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501 USA

Abstract. Shrubsteppe communities are among the most imperiled ecosystems in North America as a result of conversion to agriculture and other anthropogenic changes. In the Intermountain West of the United States, these communities support a unique avifauna, including several species that are declining and numerous others that are of conservation concern. Extensive research in the eastern and central United States and in Scandinavia suggests that fragmentation of formerly continuous forests and grasslands adversely affects reproductive success of birds, yet little is known of the potential effects on avian communities in Western shrublands. I used multi-model inference to evaluate the potential effects of local and landscape variables on nest predation and brood parasitism, and behavioral observations of color-banded birds to evaluate the potential effects of habitat fragmentation on seasonal reproductive success of passerines in the shrubsteppe of eastern Washington State, USA. Reproductive success of shrubsteppe-obligate passerines was lower in landscapes fragmented by agriculture than in continuous shrubsteppe landscapes. Daily survival rates for nests of Brewer's Sparrows (*Spizella breweri*; $n = 496$) and Sage Thrashers (*Oreoscoptes montanus*; $n = 128$) were lower in fragmented landscapes, and seasonal reproductive success (percentage of pairs fledging young) of Sage Sparrows (*Amphispiza belli*; $n = 146$) and Brewer's Sparrows ($n = 59$) was lower in fragmented landscapes. Rates of parasitism by Brown-headed Cowbirds (*Molothrus ater*) overall were low (4%) but were significantly greater in fragmented landscapes for Brewer's Sparrows, and parasitism resulted in fewer young fledged from successful nests. Simple models of population growth using landscape-specific fecundity and estimates of adult survival derived from return rates of banded male Sage Sparrows and Brewer's Sparrows suggest that fragmented shrubsteppe in Washington may be acting as a population sink for some species. Immediate conservation needs include halting further fragmentation of shrubsteppe, restoring low-productivity agricultural lands and annual grasslands to shrubsteppe where possible, and convincing the public of the intrinsic value of these imperiled ecosystems.

Key words: agriculture; *Amphispiza belli*; brood parasitism; fragmentation; landscape effects; nest survival; *Oreoscoptes montanus*; seasonal productivity; shrubsteppe; *Spizella breweri*; Washington State, USA.

INTRODUCTION

An extensive literature has developed on the effects of habitat fragmentation on the reproductive success of passerine birds in forest environments (Thompson et al. 2002, Lampila et al. 2005). In general, increasing fragmentation has been linked to lower pairing success (Gibbs and Faaborg 1990, Villard et al. 1993, Hagan et al. 1996), greater rates of nest predation, and greater rates of parasitism by Brown-headed Cowbirds, *Molothrus ater* (Donovan et al. 1995, Robinson et al. 1995). These phenomena may be contributing to declining populations of some species (Temple and Cary 1988, Robinson et al. 1995, Donovan and Flather 2002). The ultimate cause of increased nest predation typically is attributed to agricultural or urban/suburban lands that

fragment forested landscapes and support increased numbers of generalist predators (Andr n 1992). Similarly, changes to the landscape that increase its suitability for cowbirds, such as introduction of livestock, pastures, and lawns, are blamed for the increased parasitism (Robinson 1999). These findings largely derive from eastern and central parts of the United States and from Scandinavia; research in the western United States, although sparse, suggests that these patterns may not hold where forests are naturally fragmented, predator populations vary, and cowbirds are a relatively recent addition (Tewksbury et al. 1998, Cavitt and Martin 2002).

More recently, studies in grasslands of the eastern and central United States have examined some of the same issues and reached similar conclusions. Nesting success of grassland birds can be affected negatively by decreasing patch size (Johnson and Temple 1990, Winter and Faaborg 1999, Herkert et al. 2003), proximity to edge (Johnson and Temple 1990, Winter et al. 2000), and

Manuscript received 12 June 2006; revised 5 September 2006; accepted 7 September 2006. Corresponding Editor: R. L. Knight.

¹ E-mail: vandemwv@dfw.wa.gov

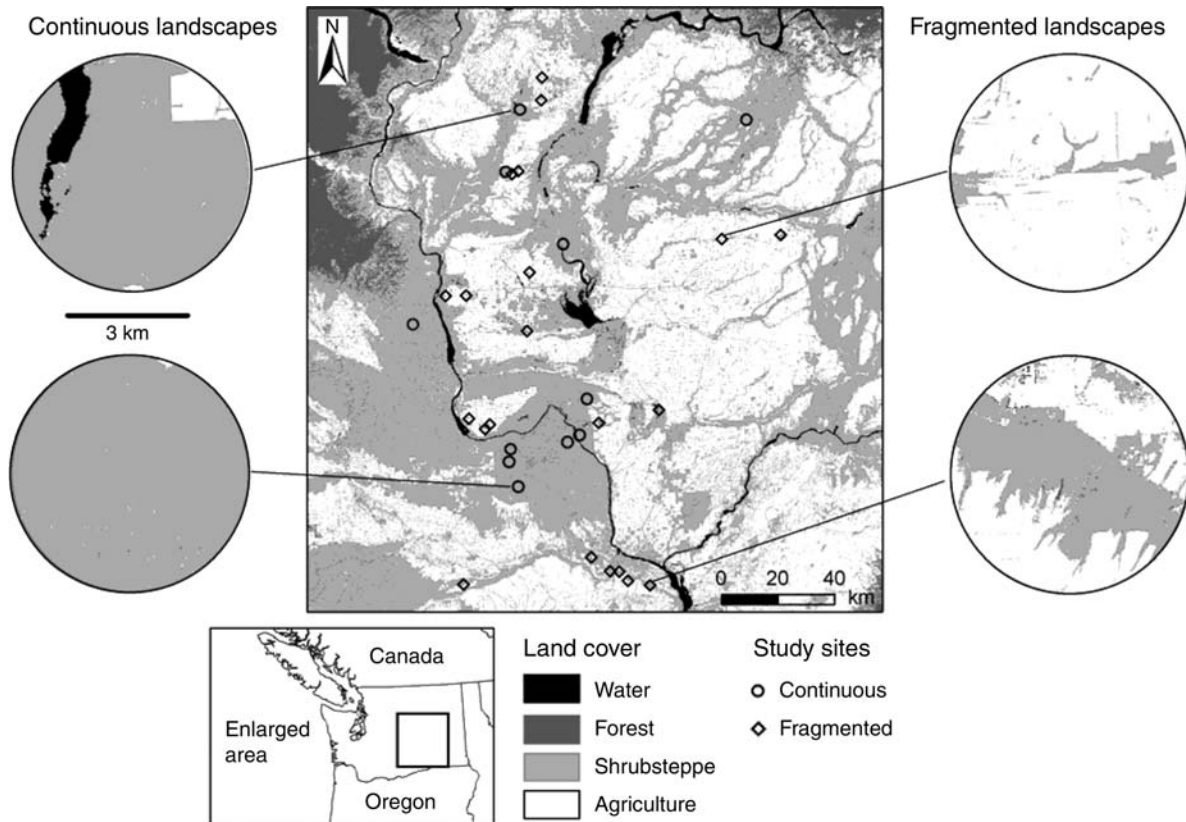


FIG. 1. Study area in eastern Washington State, USA, showing location of study sites and representative continuous and fragmented shrubsteppe landscapes. Land cover is derived from Landsat scenes dated 1993 and 1994.

regional abundance of cowbirds (Herkert et al. 2003). Few studies have examined landscape effects on the reproductive success of grassland and shrubland birds in western North America; similar to forests, the few studies that have examined these issues suggest that patterns may differ from those in the East and Midwest (Bolger 2002, Morrison and Bolger 2002, Skagan et al. 2005). Grassland and shrubland birds are among the most threatened in North America, largely a result of habitat loss and degradation (Knopf 1994, Vickery et al. 1999). High rates of nest mortality demonstrated by birds that breed in these habitats may make their populations particularly vulnerable to habitat degradation (Martin 1993).

Shrubsteppe communities of the Intermountain West have a unique avifauna that includes several species that are declining (Saab and Rich 1997, Dobkin and Sauder 2004) and numerous others that are of conservation concern (Paige and Ritter 1999). Sagebrush habitats are among the most imperiled ecosystems in North America as a result of conversion to agricultural fields, removal of sagebrush and planting of introduced grasses to improve livestock forage, widespread energy development, and increasing fire frequency that converts shrubsteppe to annual grasslands (Knick et al. 2003; see Plate 1). Changes in shrubsteppe communities have

been particularly severe in Washington State, where half of the area historically in shrubsteppe has been converted to agriculture, resulting in high fragmentation of extant habitat and a disproportionate loss of deep-soil communities (Jacobson and Snyder 2000, Vander Haegen et al. 2000). Although there has been some research on how landscape affects the distribution of shrubsteppe birds (Knick and Rotenberry 1995, Vander Haegen et al. 2000), we know little about how fragmentation of the landscape influences reproductive success of birds in this system (Knick et al. 2003).

From 1996 to 1998, I studied the relationship between fragmentation of habitat by agriculture and nest survival, parasitism rates, and seasonal reproductive success of passerines in the shrubsteppe of eastern Washington. I focused primarily on three sagebrush obligates, Brewer's Sparrow (*Spizella Breweri*), Sage Sparrow (*Amphispiza belli*), and Sage Thrasher (*Oreoscoptes montanus*), species of conservation concern that largely define the avifauna of Intermountain sagebrush ecosystems (Braun et al. 1976, Knick et al. 2003).

STUDY AREA

The study took place in eastern Washington, USA, within the geographic region known as the Columbia Basin (Fig. 1). The region is characterized by hot, dry

summers and cold winters. Precipitation falls mainly during winter, with annual totals ranging from 15 to 55 cm, decreasing from north to south across the study area (Daubenmire 1970). Within the study area, topography is generally flat to rolling and slopes from ~750 m elevation in the north to <250 m in some areas in the south (Daubenmire 1970).

Historically, most of the land in the study area supported shrubsteppe vegetation communities (Daubenmire 1970; see Plate 1). Large-scale clearing of land for agriculture began in the late 1800s and expanded when irrigation became widespread after damming of the Columbia River in the 1930s (National Research Council 1995). Using historical and current land cover maps from the Interior Columbia Basin Ecosystem Management Project (Quigley and Arbelbide 1997), McDonald and Reese (1998) estimated that the mean patch size of sagebrush in Washington decreased from 13 420 to 3418 ha and the number of patches increased from 267 to 370. A considerable portion of the study area currently is farmed, with dryland wheat being the main crop in higher rainfall zones, whereas irrigated orchards, vineyards, and row crops prevail at lower elevations. Grazing by livestock began in the region in the late 1800s and has continued to varying degrees.

I selected study sites in two contrasting landscapes: fragmented landscapes where past conversion to agriculture left shrubsteppe existing only as islands or as interconnected fragments in an agricultural matrix, and continuous landscapes where shrubsteppe communities were primarily unaffected by agriculture (Fig. 1). Agricultural land enrolled in the Conservation Reserve Program (CRP) was considered part of the agricultural matrix. In each continuous site ($n = 11$), I established a 20-ha study plot consisting of five 100-m diameter point-count circles spaced 200 m apart along a transect. Study plots in continuous landscapes had a minimum buffer of 1.5 km to a developed edge. In fragmented landscapes ($n = 11$), study plots of 8–12 ha were established in 1–3 shrubsteppe patches, each containing 2–4 point-count circles. The 22 shrubsteppe patches sampled in fragmented landscapes ranged from 10 to 1261 ha (495 ± 19 ha, mean \pm SE). Fragment sites were selected to be as similar as possible in vegetation cover to continuous study sites.

METHODS

Site-level vegetation and landscape measurements

I quantified the vegetation on all study sites between May and July 1996. Each point-count circle was sampled along a 100-m transect running due east or due west from the center point, the direction alternating on successive circles. I used the line-intercept method (Canfield 1941) to quantify shrub cover by species and I measured the height of each shrub along the 100-m transect on alternate circles. I used a 0.1-m² sampling frame (Daubenmire 1959) placed at 5-m increments along each transect (20 samples/circle) to estimate

percent cover of herbaceous vegetation, litter, rock, and bare ground. I quantified the landscape surrounding each study site by generating a circle of 5 km radius centered on the study site in a geographic information system, ArcGIS 9.1 (ESRI 2004), and calculating the percent cover in native shrubsteppe vs. altered land use types (cropland, CRP, and suburban/urban development). I used a land cover database created from Landsat thematic mapper data collected in 1993 and 1994 (Jacobson and Snyder 2000).

Nest success

Trained field crews located nests by following behavioral cues of banded and unbanded birds and by random searches. A single flag was placed ≥ 8 m from nests to mark their location and nests were revisited every 2–4 days until they fledged or failed. The number of eggs and nestlings and presence of cowbird eggs and chicks was noted at visits. I considered nests as depredated when eggs or young nestlings disappeared from the nest or when empty nests appeared damaged or torn, as if by a predator. I considered a nest to have fledged when (1) the nest was empty and I saw fledglings near the nest or adults were seen nearby carrying food and/or scolding, or (2) the nest was empty and the median date between the last nest check during which the nest was active and the final nest check when the nest was empty was within two days of the predicted fledging date (BBIRD protocol, *available online*).² I defined successful nests as those that fledged ≥ 1 host young and I used the last count of nestlings before fledging as an estimate of the number of fledglings produced.

I used the logistic-exposure method of Shaffer (2004) to examine temporal, spatial, and vegetation effects on the fates of individual nests. Logistic regression has the benefit of including both categorical and continuous variables in modeling a dichotomous outcome variable, in this case, nest fate (Hosmer and Lemeshow 2000). Logistic exposure accounts for the differing exposure periods among nests by using nest observation intervals as sample units and incorporating interval length in a modified link function (Shaffer 2004). I used this method to examine factors influencing both nest success (fledging, not fledging) and brood parasitism (parasitized, not parasitized). The data set used for analysis of nest success included all nests in which eggs were laid and that could be tracked sufficiently to their conclusion (98.6% of all nests found). I excluded nests that were abandoned immediately following extreme weather events (e.g., severe rain or hail) and those that were abandoned immediately following parasitism by Brown-headed Cowbirds (both total <1%). The data set used to examine brood parasitism included all nests that were found before the hatching of young and that reached the

² (<http://pica.wru.umt.edu/BBIRD/protocol/monitor.htm>)

TABLE 1. Reproductive conclusions for focal male Brewer's Sparrows and Sage Sparrows derived from behavioral observations of color-banded birds in the field.

Conclusion	Evidence required
Lone male	Male was on territory ≥ 4 weeks but showed no indication of pairing.
Paired only	Male seen consorting with a female, but no evidence of nesting.
Attempted nesting	Female seen carrying nesting material, or nest found, or male or his mate found feeding nestlings.
Successful reproduction	Male or his mate seen feeding fledglings or nest of focal pair known to have successfully fledged.
Attempted renesting	Female seen carrying nesting material, or nest found, or male or mate found feeding nestlings after successfully fledging a nest.
Successful renesting	Male or his mate seen feeding fledglings from a second brood or second nest of focal pair known to have successfully fledged.

laying stage, and excluded all interval observations after the first egg hatched.

I developed a set of eight a priori models and evaluated their relative value in describing observed nest fate within an information-theoretic framework (Burnham and Anderson 2002). A landscape model included a single variable that differentiated nests in sites located in a continuous shrubsteppe landscape from those in landscapes fragmented by agriculture. A temporal model included variables for year and day of the year (days after 1 January), the latter equaling the last day in each exposure period. A vegetation model included variables for percent shrub cover and percent cover by perennial grasses, two variables that describe potentially important elements of nesting cover for shrub- and ground-nesting birds that probably showed the least among-years variation of all the parameters measured (vegetation was sampled in only one of the three years). The complete model set included all combinations of these variable sets, a global model with all variables, and a null model.

For each species, I tested the global model for goodness of fit using the Hosmer and Lemeshow (2000) goodness-of-fit test. I then used diagnostics within the GENMOD procedure (SAS Institute, Cary, North Carolina, USA) to examine standardized deviance residuals for the global model, where large values (≥ 3) would suggest outliers. I used the REG procedure (SAS Institute, Cary, North Carolina, USA) to examine multi-collinearity of continuous variables in the global model (Allison 1999). No models showed indications of significant outliers or multi-collinearity. I used code developed by Shaffer (2004) for the GENMOD procedure to fit models for each species and to calculate Akaike's Information Criterion (adjusted for small sample sizes; AIC_c) and Akaike weights (w) for the full model set. I used AIC_c to rank models from most to least supported (Burnham and Anderson 2002) and calculated ΔAIC_c as the difference between the current model and the model with greatest support. Akaike weights provided a measure of support for each model, summing to 1 over all models. Models with ΔAIC_c values ≤ 2 generally are considered as competing with the best-fit model and those ≤ 4 have some support (Burnham and Anderson 2002). To account for model

selection uncertainty, I calculated model-averaged coefficients for each variable, using a value of 0 for coefficients of variables that did not occur in a model (Burnham and Anderson 2002). I then calculated odds ratios from the model-averaged coefficients and confidence intervals (CI) based on unconditional standard errors (Burnham and Anderson 2002). I present interpretation for those variables where CIs for odds ratios do not include the value 1. I calculated daily nest survival rates using *estimate* statements in GENMOD (SAS Institute, Cary, North Carolina, USA) and the best-fitting model for each species.

Focal males

I collected behavioral information on individual males of two focal species to gain insight to seasonal reproductive performance. Male Sage Sparrows and Brewer's Sparrows were captured with mist nets using song playback and were banded with U.S. Fish and Wildlife Service numbered bands and unique color band combinations. Where present, one male of each species with a territory nearest each point-count center was banded during the first few weeks of each field season. If that male was not resighted on two subsequent visits, another male was banded. Focal males were visited at one-week intervals during the breeding season. During each visit, the observer spent a minimum of 60 minutes on the birds' territory and estimated the reproductive state of the male by noting behaviors such as associating with a female (indicating paired status), feeding fledglings (indicating successful reproduction), or feeding fledglings from a second successful nest (indicating successful renesting) (after Vickery et al. 1992). While conducting focal watches, observers also noted other clues to the male's reproductive status, such as presence of an active nest or presence of a female feeding young on his territory. At the end of each field season, each male was assigned a reproductive rank (Table 1) based on weekly observations and the fates of nests determined to belong to the focal pair.

Because some males disappeared from study plots and others were banded several weeks into the nesting season, the number of visits per male varied. I examined the percentage of males changing status with each subsequent visit to establish a minimum number of visits

TABLE 2. Comparison of vegetation and landscape variables measured on shrubsteppe study sites in continuous and fragmented landscapes in eastern Washington State, USA.

Variable	Continuous (<i>n</i> = 11 sites)		Fragmented (<i>n</i> = 22 sites)	
	Mean	SE	Mean	SE
All shrubs (% cover)	25.5	1.22	24.4	1.56
Sagebrush (% cover)	23.1	1.46	22.2	1.73
Shrub height (cm)	82.1	4.49	78.0	3.85
Perennial grasses (% cover)	32.7	4.84	32.4	3.79
Annual grasses (% cover)	12.8	4.22	14.7	4.01
Bare ground (% cover)	19.4	2.92	15.3	3.14
Percentage shrubsteppe (5 km circle)†	92.4	2.99	31.8	3.94

† Percentage of the land cover in native shrubsteppe (vs. altered land use types such as cropland) within a 5 km radius of the study site center.

for males to be included in analyses. I used likelihood ratio chi-square tests to examine differences in the percentage of males achieving specific reproductive ranks between landscapes.

Population models

I developed simple population growth models to examine whether observed differences in fecundity between landscapes might be of biological significance to local populations. I estimated population growth rate (λ) using a difference equation based on a simple stage projection model (Noon and Sauer 1992, Donovan and Thompson 2001):

$$\lambda = p + p_0m$$

where p equaled adult annual survival, p_0 was survival of juveniles to the next breeding season, and m was annual fecundity (females fledged/female in the adult population). Individuals of both species breed as yearlings and I assigned adults to a single age class because data on age-specific fecundity and survival are lacking for these species. I used return rates of color-banded adult males as an estimate of p . Male Sage Sparrows are known to exhibit high fidelity to breeding territories (Martin and Carlson 1998), whereas fidelity of Brewer's Sparrows probably is somewhat lower (Rotenberry et al. 1999). In at least one case during my study, a male Brewer's Sparrow established a territory on a site several kilometers distant from where he had bred the previous year (M. Vander Haegen, unpublished data). Survival of juvenile passerines to the next breeding season has rarely been measured but has been estimated to be approximately half that of adults (Greenberg 1980, Donovan et al 1995); I used $p \times 0.5$ as an estimate of juvenile survival. Data from focal males provided measures of annual reproductive success that incorporated multiple nesting attempts as well as double brooding. I used these values to estimate landscape-specific annual fecundity:

$$m = fy + f_2y$$

where f equaled the proportion of pairs successfully

fledging one nest, f_2 equaled the proportion of pairs successfully fledging a second nest, and y was one-half of the mean number of fledglings from successful nests. I allowed m to vary by 50% above and below the empirical estimate to evaluate the sensitivity of λ to fecundity. Because p was estimated from return rates and probably underestimated actual survival, I also estimated λ over a range of values of p beginning with the return-rate-derived estimate. I looked for significant differences in mean clutch size and mean number of young fledged among years and between landscapes by inspecting 95% confidence intervals for lack of overlap.

RESULTS

Site characteristics

Vegetation of study sites was similar between landscapes when examined in general categories (Table 2). All sites were characterized by a dominant overstory of big sagebrush (*Artemisia tridentata*) and an understory of bunchgrasses and forbs. Bunchgrasses included bluebunch wheatgrass (*Pseudroegneria spicata*), Sandberg's bluegrass (*Poa secunda*), Idaho fescue (*Festuca idahoensis*), and needle and thread grass (*Hesperostipa comata*). Common forbs on the sites included balsam root (*Balsamorhiza* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.). Cheatgrass (*Bromus tectorum*), an introduced annual grass, was ubiquitous on the study area and was present at low densities in even the least disturbed sites. Fragment sites were embedded in a landscape dominated by agricultural fields, whereas continuous sites were primarily surrounded by native shrubsteppe (Table 2).

Nest survival

In total, 1450 nests of 25 species were located and monitored over the course of the study. I developed models of nest survival for four species with the greatest number of nests: Brewer's Sparrow ($n = 496$ nests), Sage Sparrow ($n = 367$), Sage Thrasher ($n = 128$), and Vesper Sparrow (*Pooecetes gramineus*; $n = 113$). Predation was the dominant cause of nest loss (40% of nests were depredated), followed by abandonment for unknown cause (3%) and weather-related abandonment (<1%). Nests of species sensitive to parasitism (Brewer's Sparrow, Sage Sparrow, Vesper Sparrow) experienced 4% parasitism rate (43 of 970 nests). Of parasitized nests, 30% (20 of 43) were depredated, 16% were abandoned (7 of 43), 30% fledged at least one host young (13 of 43), and 7% fledged only cowbird young (3 of 43).

Brewer's Sparrow.—I monitored Brewer's Sparrow nests through 1745 intervals (350 in 1996, 583 in 1997, and 817 in 1998). The global model fit the observed values ($\chi^2 = 5.7$, $P = 0.68$) and also was the best-selected model with a weight of 0.797 (Table 3). The landscape and vegetation effects model also had support with a weight of 0.183. Model-averaged odds ratios for explanatory variables revealed a strong effect of landscape class (Table 4, Fig. 2), with odds of a nest

TABLE 3. Models used to examine factors influencing nest success of birds in shrubsteppe habitats in eastern Washington.

Model	K	Sage Thrasher (n = 533)		Brewer's Sparrow (n = 1745)		Sage Sparrow (n = 1211)		Vesper Sparrow (n = 364)	
		ΔAIC _c	w _i	ΔAIC _c	w _i	ΔAIC _c	w _i	ΔAIC _c	w _i
Landscape effects	2	2.15	0.170	15.70	0.000	3.85	0.073	0.79	0.315
Vegetation effects	3	7.35	0.013	13.40	0.001	0.00	0.499	3.53	0.080
Temporal effects	4	5.29	0.035	17.25	0.000	7.28	0.013	4.43	0.051
Landscape and temporal effects	5	0.00	0.498	10.83	0.004	8.29	0.008	5.33	0.033
Vegetation and temporal effects	6	4.19	0.061	7.94	0.015	4.33	0.057	7.89	0.009
Landscape and vegetation effects	4	4.71	0.047	2.94	0.183	1.96	0.188	4.76	0.043
Global model	7	2.17	0.168	0.00	0.797	6.24	0.022	9.35	0.004
Null model	1	8.31	0.008	23.76	0.000	2.55	0.140	0.00	0.466

Notes: Model terms are *n*, the number of nest intervals used to derive the model (Shaffer 2004); *K*, the number of estimable parameters in the model; ΔAIC_c, the difference between the Akaike information criterion for the strongest model and for the model under consideration; and *w_i*, the Akaike weight for the model. Lowest ΔAIC_c values (best-supported models) are shown in boldface.

surviving in continuous landscapes 68% greater than that of a nest in fragmented landscapes. Percent shrub cover also influenced nest success, with odds of nest survival increasing 30% with an increase of 5% in shrub cover (Table 4). Shrubs cover for sites included in the model ranged from 17% to 38%. Of the temporal variables, only year had a strong effect, with odds of a nest surviving in 1996 being 131% greater than that of a nest surviving in 1998. Daily nest survival rate derived from the global model was 0.968 (0.963–0.972, 95% CI). Projected nest survival over the 24-day nest period was 46%. Cowbirds parasitized 5.7% of Brewer's Sparrow nests that were found when active and tracked before hatching (*n* = 363 nests). Models of brood parasitism had nests available through 849 intervals (150 in 1996, 265 in 1997, and 434 in 1998). The global model fit the observed values ($\chi^2 = 4.7$, *P* = 0.79). The model containing landscape and vegetation variables was the best-selected model, with a weight of 0.860 (Table 5). The global model also had support, with a weight of 0.129. Model-averaged odds ratios for explanatory variables revealed a strong effect of landscape class (Table 6), with odds of a nest avoiding parasitism in continuous landscapes being 550% greater than those of a nest in fragmented landscapes. Perennial grass cover also influenced nest success, with odds of a nest avoiding parasitism decreasing 35% with an increase of 5% in perennial grass cover (Table 6). Perennial grass cover for sites included in the model ranged from 28% to 60%.

The mean number of Brewer's Sparrows fledged from parasitized nests (1.75 ± 0.41 fledglings/nest, mean \pm SE; *n* = 8 nests) was lower than that for nonparasitized nests (3.12 ± 0.05 , *n* = 295) (*t* = 4.6, *P* = 0.001).

Sage Thrasher.—I monitored Sage Thrasher nests through 533 intervals (221 in 1996, 167 in 1997, and 145 in 1998). The global model fit the observed values ($\chi^2 = 5.7$, *P* = 0.68). The landscape and temporal effects model was the best-selected model, with a weight of 0.498 (Table 3). The landscape model and the global model also had support, with weights of 0.170 and 0.168. Model-averaged odds ratios for explanatory variables revealed a strong effect of landscape class (Table 4, Fig. 2), with odds of a nest surviving in continuous landscapes being 151% greater than those of a nest in fragmented landscapes. Daily nest survival rate derived from the landscape and temporal effects model was 0.969 (0.959–0.977, 95% CI). Projected nest survival over the 29-day nest period was 40%.

Sage Sparrow.—I monitored Sage Sparrow nests through 1211 intervals (294 in 1996, 515 in 1997, and 402 in 1998). The global model fit the observed values ($\chi^2 = 12.5$, *P* = 0.128). The vegetation effects model was the best-selected model, with a weight of 0.499 (Table 3). The landscape and vegetation effects model also had support, with a weight of 0.188. The null model also was a competing model, with a weight of 0.140. Model-averaged odds ratios for explanatory variables all were very close to 1, with confidence intervals that included 1,

TABLE 4. Odds ratios and 95% confidence intervals (CI) for explanatory variables in main models of nest success, based on model-averaged coefficients from seven models of species in shrubsteppe habitats in eastern Washington.

Variable	Sage Thrasher		Brewer's Sparrow		Sage Sparrow	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
Landscape class	1.85	3.08–1.12	1.68	2.32–1.22	0.97	1.11–0.85
Perennial grass cover	1.00	1.01–1.00	1.01	1.03–1.00	1.01	1.02–1.00
Shrub cover	1.00	1.02–0.99	1.05	1.08–1.02	0.99	1.03–0.96
Year (1996 vs. 1998)	1.51	2.69–0.85	1.59	2.31–1.09	1.02	1.07–0.98
Year (1997 vs. 1998)	0.85	1.53–0.47	1.17	1.54–0.89	1.00	1.04–0.97
Day of the year	0.99	1.00–0.98	1.00	1.01–1.00	1.00	1.00–1.00

Note: Variables with the strongest effect (CI does not include 1.00) are shown in boldface.

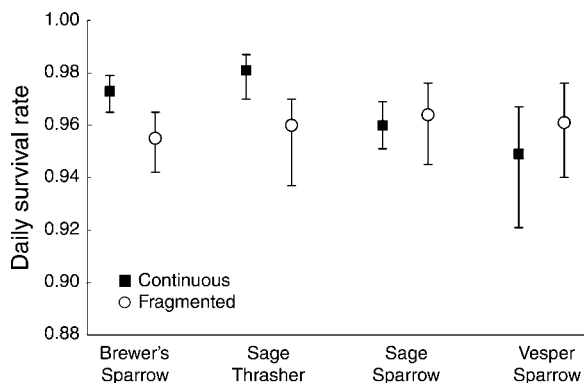


FIG. 2. Daily survival rates (mean and 95% CI) for Brewer's Sparrow ($n = 1745$ intervals), Sage Thrasher ($n = 533$), Sage Sparrow ($n = 1211$), and Vesper Sparrow ($n = 364$) nests in continuous and fragmented shrubsteppe landscapes in eastern Washington.

suggesting only weak relationships with nest success (Table 4). Daily nest survival rate derived from the vegetation effects model was 0.961 (0.954–0.966, 95% CI). Projected nest survival over the 26-day nest period was 36%.

Cowbirds parasitized 8.5% of Sage Sparrow nests that were found when active and tracked prior to hatching ($n = 247$). Models of brood parasitism had nests available through 575 intervals (132 in 1996, 230 in 1997, and 213 in 1998). The global model fit the observed values ($\chi^2 = 7.01$, $P = 0.54$). The model containing landscape and temporal variables was the best-selected model with a weight of 0.561 (Table 5). The temporal model also had support, with a weight of 0.297. Model-averaged odds ratios for explanatory variables revealed a strong effect of year (Table 6), with odds of a nest avoiding parasitism being greater in 1996 than in 1998. Day of the year also influenced nest success, with odds of a nest avoiding parasitism decreasing as the season progressed (Table 6). The mean number of Sage Sparrows fledged from successful parasitized nests (2.8 ± 0.49 fledglings/nest, mean \pm SE, $n = 5$ nests) was similar to that

for successful nonparasitized nests (2.94 ± 0.06 fledglings/nest, $n = 195$) ($t = 0.36$, $P = 0.72$).

Vesper Sparrow.—I monitored Vesper Sparrow nests through 364 intervals (101 in 1996, 126 in 1997, and 137 in 1998). The global model fit the observed values ($\chi^2 = 11.7$, $P = 0.166$). The null model was the best-selected model, with a weight of 0.466 (Table 3). The landscape effects model also had support, with a weight of 0.32. All competing models, including the landscape model, had deviance values similar to those of the null model, suggesting little improvement. Daily nest survival rate derived from the null model was 0.949 (0.935–0.960, 95% CI). Projected nest survival over the 26-day nest period was 26%. Cowbirds parasitized 3.6% of Vesper Sparrow nests that were found when active and tracked prior to hatching ($n = 84$). Only one of three parasitized nests fledged Vesper Sparrow young.

Model summary.—Of the three species with models of daily nest survival that were improvements over the null model, landscape occurred in all relevant models for Brewer's Sparrow and Sage Thrasher and also, for these two species, was a significant variable after model-averaging. Sums of the Akaike weights across all models that included landscape were 0.83 for Sage Thrasher and 0.97 for Brewer's Sparrow, but only 0.20 for Sage Sparrow.

Seasonal reproductive success

I color-banded 177 male Sage Sparrows and 71 male Brewer's Sparrows over three years of study. The percentage of males that increased in status declined from visits 6–12 (Fig. 3), with $\leq 10\%$ of males changing status after nine visits. Because the sample size of males diminished with increasing number of visits, I selected nine visits as the cut point to include individual males in analyses. Trends between landscapes in percentage of males achieving different reproductive levels were similar among years, so I combined data across years to increase sample size.

Brewer's Sparrow.—Reproductive success for Brewer's Sparrows was derived from 31 males at four

TABLE 5. Models used to examine factors influencing parasitism rates of broods in shrubsteppe habitats in eastern Washington.

Model	K	Brewer's Sparrow ($n = 856$)		Sage Sparrow ($n = 575$)	
		ΔAIC_c	w_i	ΔAIC_c	w_i
Landscape effects	2	14.81	0.000	26.42	0.000
Vegetation effects	3	11.58	0.002	29.37	0.000
Temporal effects	4	19.28	0.000	1.27	0.297
Landscape and temporal effects	5	16.16	0.000	0.00	0.561
Vegetation and temporal effects	6	12.26	0.002	4.66	0.054
Landscape and vegetation effects	4	0.00	0.776	28.91	0.000
Global model	7	2.53	0.219	3.73	0.087
Null model	1	19.24	0.000	26.01	0.000

Notes: Model terms are n , the number of nest intervals used to derive the model (Shaffer 2004); K , the number of estimable parameters in the model; ΔAIC_c , the difference between the Akaike information criterion for the strongest model and for the model under consideration; and w_i , the Akaike weight for the model. Lowest ΔAIC_c values (best-supported models) are shown in boldface.

TABLE 6. Odds ratios and 95% confidence intervals (CI) for explanatory variables in main models of brood parasitism, based on model-averaged coefficients from seven models of birds in shrubsteppe habitats in eastern Washington.

Variable	Brewer's Sparrow		Sage Sparrow	
	Odds ratio	CI	Odds ratio	CI
Landscape class	6.51	20.80–2.04	0.46	1.19–0.18
Perennial grass cover	0.93	0.98–0.89	1.00	1.01–0.99
Shrub cover	1.04	1.14–0.96	1.00	1.03–0.97
Year (1996 vs. 1998)	0.96	1.39–0.67	10.95	86.88–1.38
Year (1997 vs. 1998)	0.83	1.19–0.57	1.74	4.41–0.69
Day of the year	1.00	1.00–0.99	0.95	0.97–0.93

Note: Variables with the strongest effect (CI does not include 1.00) are shown in boldface.

continuous sites and 28 males from four fragment sites (633 total visits; 10.7 ± 0.15 visits/individual, mean \pm SE). Almost all focal males paired (Fig. 4) and the percentage of paired males fledging young was greater in continuous landscapes (79%) than in fragmented landscapes (44%) ($\chi^2 = 7.4$, $df = 1$, $P = 0.006$). Four males fledged second broods: three in continuous landscapes and one in a fragmented landscape. Of paired males that were found not to fledge young, most (five of six in continuous landscapes and 13 of 15 in fragmented landscapes) showed evidence of attempting to nest. Of males that fledged a brood, few showed evidence of attempting a second nest (two of 23 males in continuous landscapes and three of 12 in fragmented landscapes). I documented 1.7 ± 0.11 nesting attempts (mean \pm SE, range 1–3, $n = 31$) for pairs that fledged at least one brood and 1.7 ± 0.21 (range 1–3, $n = 18$) attempts for pairs that showed evidence of nesting but did not fledge young.

Sage Sparrow.—Reproductive success for Sage Sparrows was derived from 106 males from 10 continuous sites and 40 males from five fragment sites (1640 total visits; 11.2 ± 0.13 visits/individual, mean \pm SE). Of male Sage Sparrows, 84% paired (Fig. 4); pairing success

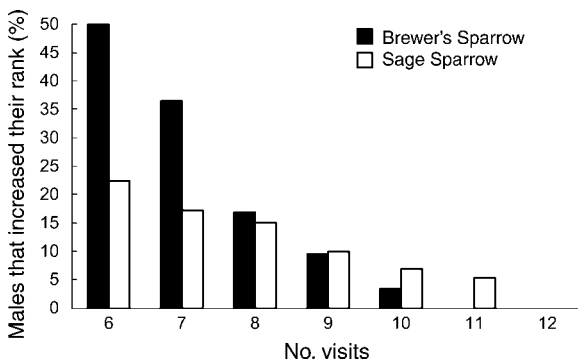


FIG. 3. Percentage of color-banded focal males that increased their reproductive rank. This was less than 10% after nine visits. Males were visited weekly over the breeding season to determine their reproductive status.

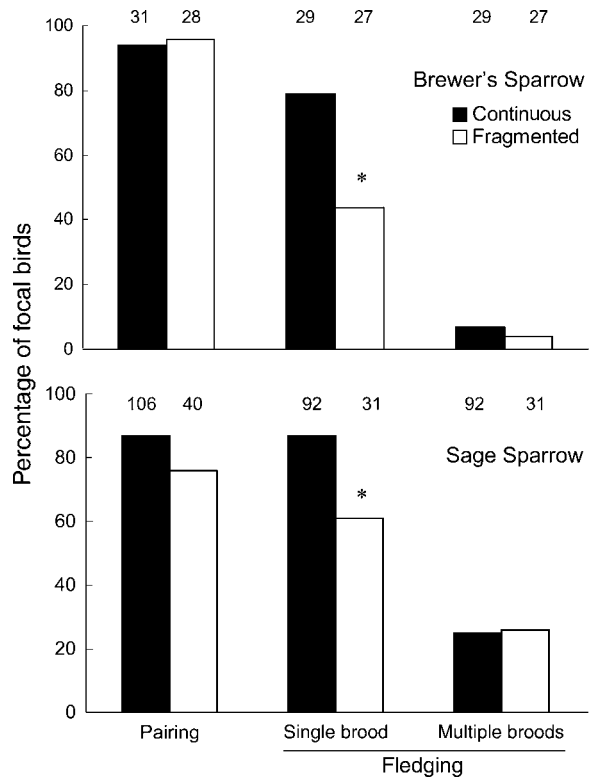


FIG. 4. Percentage of color-banded Brewer's Sparrow and Sage Sparrow males that paired, and percentage of pairs that fledged young and fledged multiple broods on study sites in continuous and in fragmented shrubsteppe landscapes in eastern Washington. Sample sizes are given above bars.

* $P < 0.01$, likelihood ratio chi-square test.

did not differ between landscapes ($\chi^2 = 1.78$, $df = 1$, $P = 0.18$). Of those males that paired, fewer fledged young in fragmented landscapes (61%) than in continuous landscapes (87%; $\chi^2 = 8.2$, $df = 1$, $P = 0.004$). The percentage of males fledging second broods was similar between landscapes (25%; Fig. 4) ($\chi^2 = 0.0008$, $df = 1$, $P = 0.98$). Three males fledged three nests in one season: two in continuous landscapes and one in a fragmented landscape. Of the paired males that were found not to fledge young, most (11 of 12) in continuous landscapes showed evidence of nesting attempts compared to only half (six of 12) in fragmented landscapes. Of males that fledged a brood, about half showed evidence of attempting a second nest (37 of 80 in continuous landscapes and eight of 19 in fragmented landscapes). I documented 1.8 ± 0.07 nesting attempts (mean \pm SE, range 1–3, $n = 99$) for pairs that fledged at least one brood, compared with 1.5 ± 0.20 (range 1–4, $n = 16$) attempts for pairs that showed evidence of nesting but did not fledge young.

Clutch size and number of fledglings

The number of eggs laid in completed clutches did not differ substantially among years for most species examined, although the 95% confidence intervals suggest

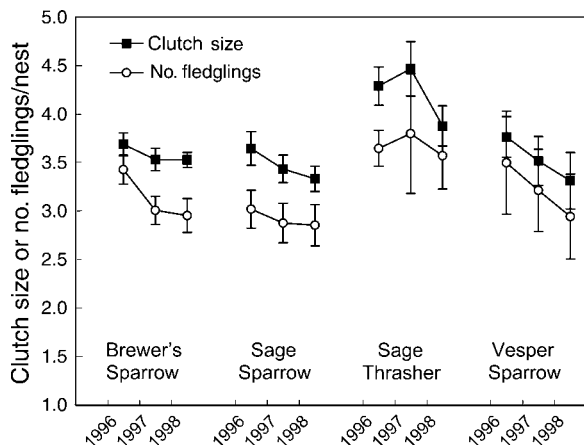


FIG. 5. Mean (with 95% CI) values for clutch size (for all nests in which the clutch was completed) and number of fledglings (for successful nests only) for shrubsteppe passerines in eastern Washington, 1996–1998.

lower clutch size for Sage Thrashers in 1998 (Fig. 5). The number of fledglings produced from successful nests exhibited a similar trend, although the 95% confidence intervals suggest more fledglings in 1996 than in subsequent years for Brewer's Sparrows. Neither parameter varied between landscape classes for any of the four species examined (Table 7).

Population models

Adult survival.—Six sites were searched thoroughly for color-banded male Sage Sparrows in 1997 and 14 sites were searched in 1998. Return rate was 52% in 1997 (15/29 birds) and 58% in 1998 (41/71birds). Eight sites were searched for male Brewer's Sparrows in 1998, with a return rate of 38% (17/45 birds). On one site in 1998, 23 male Brewer's Sparrows were color-banded as adults and 48% returned in 1999 (B. Walker, *personal communication*). Because fidelity to breeding sites for these species has not been quantified and is probably <100%, I used the larger of the two annual estimates as an approximation of adult annual survival.

Lambda.—Population growth rates derived from landscape-specific fecundity estimates were lower in

fragmented landscapes for both Brewer's Sparrows and Sage Sparrows (Fig. 6). Using *p* based on band-return data and empirical values for *m*, Sage Sparrows had a negative rate of growth in fragmented landscapes and positive rate of growth in continuous landscapes. This dichotomy was sensitive to *p* and disappeared with an increase in this variable of 0.04 (Fig. 6c). For Sage Sparrows, λ was sensitive to large changes in fecundity; raising or lowering *m* by 50% moved λ above or below 1, respectively, regardless of the value of *p*. Lambda values for Brewer's Sparrow were extremely low at *p* derived from band-return data, suggesting that this was not an adequate estimate of adult annual survival (Fig. 6b, d). It required an increase in *p* to 0.6 to achieve a positive lambda value; however, even at this rate of *p* lambda in fragmented landscapes was considerably below that in continuous landscapes. Moreover, raising *m* by 50% also failed to elevate λ above 1 for Brewer's Sparrows in fragmented landscapes (Fig. 6d).

DISCUSSION

Reproductive success of shrubsteppe-obligate passerines was lower in landscapes fragmented by agriculture than in continuous shrubsteppe landscapes in eastern Washington State. The pattern of greater nest predation, lower seasonal fecundity, and greater parasitism rates in fragmented shrubsteppe was more similar to that from anthropogenically fragmented forest and grassland landscapes in the eastern and central United States than to naturally fragmented Western riparian forests (Tewksbury et al. 1998) and coastal sage scrub of California, where fragmentation is caused primarily by urban development (Bolger 2002, Morrison and Bolger 2002). Like forests and grasslands in the East and Midwest, Intermountain shrubsteppe historically was extensive on the landscape, and fragmentation by agriculture may have significantly altered the distribution of nest predators and parasites.

Predation typically is the greatest source of nest mortality for passerines (Ricklefs 1969, Martin 1992). Predator populations are likely to differ among vegetation communities and landscapes and these differences may partially explain the observed differences in nest survival (Chalfoun et al. 2002, Thompson et al. 2002).

TABLE 7. Size of completed clutches and number of fledglings from successful nests for birds in continuous (C) and fragmented (F) shrubsteppe landscapes in eastern Washington, 1996–1998.

Species	Landscape	Clutch size			No. fledglings		
		Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
Brewer's Sparrow	C	3.58	0.58	197	3.13	0.77	163
	F	3.54	0.55	179	3.08	0.86	129
Sage Thrasher	C	4.25	0.72	63	3.60	0.80	47
	F	4.13	0.66	38	3.88	0.62	16
Sage Sparrow	C	3.44	0.65	183	2.90	0.84	153
	F	3.46	0.73	52	2.95	0.97	41
Vesper Sparrow	C	3.44	0.86	34	3.06	0.97	17
	F	3.52	0.66	44	3.24	0.83	25

Note: Means exclude nests parasitized by cowbirds.

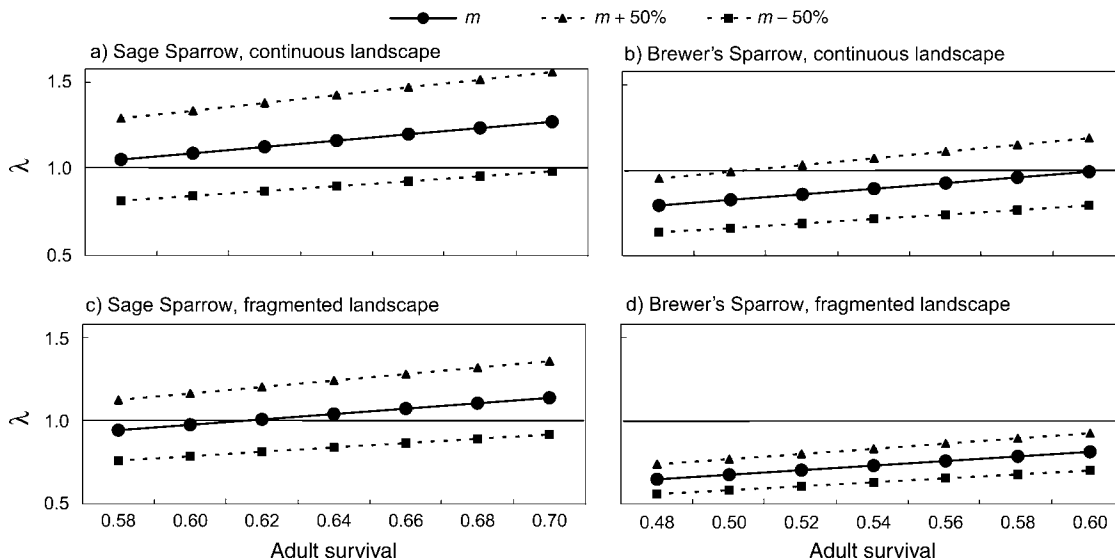


FIG. 6. Estimates of population growth rate λ at varying rates of adult annual survival and fecundity (m) in fragmented and continuous shrubsteppe landscapes in eastern Washington, where m was derived from landscape-specific empirical data and was varied 50% above ($m + 50\%$) and below ($m - 50\%$) the empirical estimate to examine sensitivity. Left-most survival values were derived from return rates of banded adult males and were set constant between landscapes. See *Methods* for model details.

Cameras placed at artificial nests in shrubsteppe communities revealed corvids and small mammals as numerically dominant predators, with corvids visiting nests primarily in fragmented landscapes and small mammals common in both fragmented and continuous landscapes (Vander Haegen et al. 2002). As in other systems (Andr n 1992, Marzluff et al. 1994), corvids in shrubsteppe generally are associated with fragmentation and agricultural development. Point-count surveys of birds in the present study revealed significantly greater abundance of Black-billed Magpies (*Pica hudsonia*; the dominant corvid identified in the camera study) in fragmented landscapes (M. Vander Haegen, unpublished data). The deer mouse (*Peromyscus maniculatus*) and least chipmunk (*Tamias minimus*) were the dominant small mammals depredating nests in the camera study (Vander Haegen et al. 2002). Recent surveys for small mammals in eastern Washington revealed greater numbers of deer mice in shrubsteppe habitat fragmented by agriculture compared to continuous shrubsteppe, possibly a result of greater food supply in the surrounding agricultural matrix (R. Gitzen and S. West, unpublished data). Indeed, the grain fields that formed most of the agricultural matrix in these Washington studies represent a considerable potential resource for granivorous small mammals. Although several studies related to avian nest predation have failed to document increased numbers of small mammals with fragmentation, their focus was on edge effects in forests highly fragmented by agriculture and did not include continuous landscapes (Heske 1995, Marini et al. 1995, Chalfoun et al. 2002).

Snakes can be important predators of passerine nests in grasslands (Davison and Bollinger 2000) and shrublands (Morrison and Bolliger 2002), particularly during the nestling phase (James et al. 1983, Thompson et al. 1999). Snakes were observed depredating several nests in the present study and also were considered by Rotenberry and Wiens (1989) to be important nest predators in shrubsteppe habitats in Washington and Nevada. However, of the predator groups considered here, snakes may be the least likely to be contributing to lower nesting success in fragmented landscapes. Recent surveys for reptiles in fragmented and continuous shrubsteppe landscapes in eastern Washington indicate a greater abundance of snakes in continuous sites, perhaps related to availability of rocky sites for hibernacula (S. Germaine, unpublished data). Snakes also were found to be rare in fragments of coastal sage scrub in California (Morrison and Bolger 2002).

Seasonal productivity is a key parameter when considering reproductive success because it includes the contribution of repeated attempts at renesting (Powell et al. 1999, Murray 2000). Brewer's Sparrows clearly had lower nest survival in fragmented landscapes and this was reflected in lower seasonal productivity, as pairs were unable to make up for low nest survival through renesting effort. The pattern was less clear for Sage Sparrows, where seasonal reproductive success was depressed in fragmented landscapes yet we observed no difference in nest survival rates. This apparent contradiction may have resulted from methodological error on my part or from behavioral aspects of this area-sensitive species. Fewer pairs of Sage Sparrows in fragmented landscapes showed indications of nesting



PLATE 1. *Artemisia tridentate*–*Pseudoroegneria spicata*–*Poa secunda* community in south-central Washington State. Sagebrush communities historically were extensive on the landscape but now are fragmented by conversion to agriculture and other anthropogenic changes. Photo credit: M. Vander Haegen.

attempts, suggesting that either pairing status was erroneously assigned (i.e., some males thought to be paired actually were unpaired, a methodological error), or that nests were not surviving long enough to be located by searchers. In the latter case, pairs may have made fewer nesting attempts or the pair bond may have dissolved after early nest loss. In a study of Field Sparrows (*Spizella pusilla*), Best (1977) found that females frequently deserted males shortly after predation of a nest. The potential for abandoned male Sage Sparrows to attract a new mate may have been low in fragmented landscapes where the pool of available females was probably small. Sage Sparrows avoid fragmented landscapes and are most often associated with large expanses of unbroken shrubsteppe (Knick and Rotenberry 1995, Vander Haegen et al. 2000); in the present study they were found nesting in only the largest fragments (>1000 ha). Whether from low pairing success or low seasonal fecundity, males in fragmented habitats were at a reproductive disadvantage.

Although the banded males were tracked on a weekly basis, I could not be sure that all nests were found and that all nesting attempts were documented. However, my results for seasonal reproductive success were similar to those from two more intensive studies where all pairs on a smaller set of sites were followed through the breeding season. Fitzner (2000) documented the breeding effort of 52 Sage Sparrow pairs on the Hanford Site in south-central Washington during 1996–1997. Her research ran concurrent with the present study and portions of three sites (and data from nine males) were common to both studies. The percentage of pairs

fledging young on her sites (all were in continuous habitat) was similar to that on my continuous sites (87% in both studies); however, she reported a somewhat higher percentage of pairs fledging additional nests (38% vs. 25%). In a study in British Columbia, Canada (Mahony et al. 2002), investigators followed Brewer's Sparrow pairs on four sites in largely unfragmented habitat, documenting all nesting attempts of 176 color-banded pairs. Again, my results from continuous sites in Washington were similar to the British Columbia findings for percentage of pairs fledging young (79% vs. 70%), but somewhat lower for the percentage of pairs going on to fledge additional nests (7% vs. 18%). Regional variation in predator populations and effects of winter rainfall can influence reproductive success (Rotenberry and Wiens 1989) and rates of double brooding within a species also can vary regionally (Bourque and Villard 2001), possibly explaining some of this difference. From these comparisons, I conclude that the effort expended in tracking focal males in Washington was sufficient to document most nesting attempts, but may have missed some instances of multiple brooding.

Parasitism by Brown-headed Cowbirds typically is greater in landscapes where agriculture and livestock are common (Robinson 1999). For Brewer's Sparrows in my study, the strongest variables influencing parasitism rates were landscape and perennial grass cover, variables most strongly associated with the occurrence of cowbirds in eastern Washington (Vander Haegen et al. 2000). Parasitism of Sage Sparrow nests was most closely related to temporal variables: risk of parasitism

increased with day of the year. This relationship, along with the overall low parasitism rates in the present study, were probably due, in part, to timing of cowbird arrival on the study area. Cowbirds generally locate nests by observing the nest-building activities of hosts and parasitize nests during laying or early in incubation (Hann 1941). Cowbirds arrived on my study area in late April and early May, by which time the first nesting attempts for some potential hosts were well underway. Sage Sparrows, for example, initiated over 40% of their nesting attempts before cowbirds were observed laying on the study area (Vander Haegen and Walker 1999). Other factors that may influence the low rates of parasitism on the study area are the general lack of elevated observation perches (e.g., trees) that would facilitate cowbirds locating and tracking the progress of potential host nests, and the long distances between some of our sites and the nearest cowbird feeding areas. Further fragmentation of Washington's shrubsteppe, particularly by livestock farming and suburban development, could increase populations of cowbirds, leading to increased rates of brood parasitism for shrubsteppe obligates.

Conclusions and conservation implications

Fragmentation of the once-continuous shrubsteppe communities in Washington may be contributing to the decline of some shrubsteppe-obligate species by reducing annual reproductive success. In Brewer's Sparrows and Sage Thrashers, this lower reproductive success was manifested in lower rates of nest survival, largely a result of increased predation rates on nests. Fewer young fledging from parasitized nests further depressed reproductive success for Brewer's Sparrows in fragmented landscapes. Sage Sparrows also were less productive in fragmented landscapes, although the proximate cause may have been only partly related to nest predation and may have been linked to behavior associated with area sensitivity.

Documenting a negative effect of landscape characteristics on breeding birds is only a first step in assessing its ultimate impact on regional populations. My study was limited to three years and undoubtedly captured only part of the variability typically expressed in critical reproductive parameters, particularly in this "variable environment" (Rotenberry and Wiens 1991). However, simple models of population growth based on landscape-specific fecundity and estimates of adult and juvenile survival suggest that landscapes fragmented by agriculture may be functioning as sinks, at least in some years. This is supported by long-term declines documented for populations of Brewer's Sparrow (-3.19% per year) and Sage Thrasher (-1.08% per year) in the Columbia Plateau Province for the period 1968–2005 (Breeding Bird Survey; Sauer et al. 2005). If migratory bird populations are structured as metapopulations (sensu Pulliam 1988), as suggested by Donovan et al. (1995) for forest birds in the Midwest, the shrubsteppe

landscape in Washington may be providing a continuum of source-to-sink habitats along a gradient of fragmentation. Although sink habitats may have value in regional population dynamics (Pulliam 1988, Howe et al. 1991, Thompson et al. 2002), the continuing fragmentation and degradation of shrubsteppe communities may increase the proportion of sink habitats on the landscape and may magnify the observed declines in some species.

Fragmentation of shrubsteppe in eastern Washington largely is the result of exploitation of deep, fertile soils for crop production, a pattern that also has reduced and fragmented shrubsteppe communities throughout most of the Columbia Plateau as well as parts of Idaho, Utah, and Montana (Knick et al. 2003, Connelly et al. 2004). Over much of the shrubsteppe landscape in the West, the shrub component remains relatively intact and fragmentation takes the form of linear and point features such as roads, power lines, irrigation ditches, and well sites and related infrastructure associated with oil and gas extraction (Knick et al. 2003, Connelly et al. 2004). Roads may reduce the abundance of some shrubsteppe passerines (Ingelfinger and Anderson 2004) and the disturbance associated with energy extraction may adversely affect lek attendance, nesting, and survival of Greater Sage-Grouse, *Centrocercus urophasianus* (Braun et al. 2002, Holloran 2005). The corvid predators and parasitic cowbirds responsible for lower reproductive success in eastern Washington were largely associated with fragmentation of the landscape by cropland; it remains to be tested whether fragmentation by factors other than agriculture will result in similar reductions in productivity.

Continued research on avian ecology in shrubsteppe communities should be a high priority. There is an obvious need for accurate estimates of adult and juvenile survival to improve our ability to model population growth for these and other birds. There also is a clear and pressing need for additional demographic data collected over a range of landscapes and habitat conditions if we are to understand the effects of landscape change on regional populations of shrubsteppe birds (Knick et al. 2003). Immediate conservation needs include halting further fragmentation of shrubsteppe by agriculture and restoring low-productivity agricultural lands and annual grasslands to shrubsteppe where possible. Reversing the current trend of increased fragmentation and degradation of shrubsteppe communities will take the concerted effort of federal and state agencies and local conservation organizations, as well as an effective plan to convince the public of the intrinsic value of these imperiled ecosystems (Knick et al. 2003).

ACKNOWLEDGMENTS

Support for this project was provided by the National Fish and Wildlife Foundation, Washington Department of Fish and Wildlife (WDFW), Washington Department of Natural Resources, U.S. Department of Energy, and Battelle-Pacific Northwest Laboratory. I am grateful to Larry Cadwell for

helping to coordinate activities on the Hanford Site and to Frank Thompson and Terry Shaffer for advice on analysis of nesting data. John Pierce, Frank Thompson, Geraldine Vander Haegen, and Peter Vickery provided helpful reviews of the manuscript. I thank Lisa Fitzner for her contributions to the field effort. I also am indebted to Fred Dobler, John Pierce, Tom Juelson, and other professionals within WDFW who, early on, recognized the critical threats to the shrubsteppe ecosystem and the need for long-term, applied research to address them. This project would not have been possible without the hard work of many dedicated field assistants and the private landowners who granted access to their lands.

LITERATURE CITED

- Allison, P. D. 1999. Logistic regression using the SAS system: theory and applications. SAS Institute, Cary, North Carolina, USA.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73: 794–804.
- Best, L. B. 1977. Territory quality and mating success in the field sparrow (*Spizella pusilla*). *Condor* 79:192–204.
- Bolger, D. T. 2002. Habitat fragmentation effects on birds in southern California: contrast to the “top-down” paradigm. *Studies in Avian Biology* 25:141–157.
- Bourque, J., and M.-A. Villard. 2001. Effects of selection cutting and landscape-scale harvesting on the reproductive success of two neotropical migrant bird species. *Conservation Biology* 15:184–195.
- Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. *Wilson Bulletin* 88:165–171.
- Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage-grouse. *Transactions of the North American Wildlife and Natural Resources Conference* 67:337–349.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39: 386–394.
- Cavitt, J. F., and T. E. Martin. 2002. Effects of forest fragmentation on brood parasitism and nest predation in eastern and western landscapes. *Studies in Avian Biology* 25: 73–80.
- Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson III. 2002. Songbird nest predators in forest–pasture edge and forest interior in a fragmented landscape. *Ecological Applications* 12:858–867.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Unpublished report. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
- Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:43–64.
- Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62. Washington State University, Pullman, Washington, USA.
- Davison, W. B., and E. Bollinger. 2000. Predation rates on real and artificial nests of grassland birds. *Auk* 117:147–153.
- Dobkin, D. S., and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy: distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. Report, High Desert Ecological Research Institute, Bend, Oregon, USA.
- Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* 12:364–374.
- Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11: 871–882.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380–1395.
- ESRI. 2004. ArcGIS Version 9.1. ESRI, Redlands, California, USA.
- Fitzner, L. E. 2000. Reproductive ecology of the sage sparrow (*Amphispiza belli*) and its relationship to the characteristics of native and cheatgrass (*Bromus tectorum*) dominated habitats. Thesis. Washington State University, Pullman, Washington, USA.
- Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. *Conservation Biology* 4:193–196.
- Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493–504 in A. Keast and E. S. Morton, editors. *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, D.C., USA.
- Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* 10:188–202.
- Hann, H. W. 1941. The cowbird at the nest. *Wilson Bulletin* 53: 211–221.
- Herkert, J. R., et al. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology* 17:587–594.
- Heske, E. J. 1995. Mammalian abundances on forest–farm edges versus forest interiors in Southern Illinois: Is there an edge effect? *Journal of Mammalogy* 76:562–568.
- Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation. University of Wyoming, Laramie, Wyoming, USA.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley, New York, New York, USA.
- Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of sink populations. *Biological Conservation* 57:239–256.
- Ingelfinger, F., and S. Anderson. 2004. Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. *Western North American Naturalist* 64:385–395.
- Jacobson, J. E., and M. C. Snyder. 2000. Shrubsteppe mapping of eastern Washington using Landsat satellite thematic mapper data. Research Report, Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- James, D. K., L. Petronovich, and T. L. Patterson. 1983. Predation of White-crowned Sparrow nestlings by the western terrestrial garter snake in San Francisco, California. *Copeia* 2:511–513.
- Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106–111.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conservation Biology* 9:1059–1071.
- Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247–257.

- Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. *Conservation Biology* 19:1537–1546.
- Mahony, N. A., W. M. Vander Haegen, B. L. Walker, and P. G. Krannitz. 2002. Male incubation and multiple brooding in Sagebrush Brewer's Sparrows. *Wilson Bulletin* 113:441–444.
- Marini, M. A., S. K. Robinson, and E. J. Heske. 1995. Edge effects of nest predation in the Shawnee National Forest, southern Illinois. *Biological Conservation* 74:203–213.
- Martin, J. W., and B. A. Carlson. 1998. Sage Sparrow (*Amphispiza belli*). In A. Poole and F. Gill, editors. *The birds of North America*. Number 326. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.
- Martin, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 in J. M. Hagan and D. W. Johnson, editors. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C., USA.
- Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141:897–913.
- Marzluff, J. M., R. B. Boone, and G. W. Cox. 1994. Historical changes in populations and perceptions of native pest bird species in the West. *Studies in Avian Biology* 15:202–220.
- McDonald, M. W., and K. P. Reese. 1998. Landscape changes within the historical distribution of Columbian Sharp-tailed Grouse in eastern Washington: Is there hope? *Northwest Science* 72:34–41.
- Morrison, S. A., and D. T. Bolger. 2002. Lack of an urban edge effect on reproduction in a fragmentation-sensitive sparrow. *Ecological Applications* 12:398–411.
- Murray, B. G. Jr. 2000. Measuring annual reproductive success in birds. *Condor* 102:470–473.
- National Research Council. 1995. *Upstream: salmon and society in the Pacific Northwest*. National Academy Press, Washington, D.C., USA.
- Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441–464 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Applied Science, London, UK.
- Paige, C., and S. A. Ritter. 1999. *Birds in a sagebrush sea: managing sagebrush habitats for bird communities*. Report, Partners in Flight Western Working Group, Boise, Idaho, USA.
- Powell, L. A., M. J. Conroy, D. G. Krementz, and J. D. Lang. 1999. A model to predict breeding-season productivity for multibrooded songbirds. *Auk* 116:1001–1008.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Quigley, T. M., and S. J. Arbelbide. 1997. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins. General Technical Report PNW-GTR-405. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* 9:1–48.
- Robinson, S. K. 1999. Cowbird ecology: factors affecting the abundance and distribution of cowbirds. *Studies in Avian Biology* 18:4–9.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Rotenberry, J. T., M. A. Patten, and K. L. Preston. 1999. Brewer's Sparrow (*Spizella breweri*). In A. Poole and F. Gill, editors. *The birds of North America*. Number 390. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.
- Rotenberry, J. T., and J. A. Wiens. 1989. Reproductive biology of shrubsteppe passerine birds: geographical and temporal variation in clutch size, brood size, and fledging success. *Condor* 91:1–14.
- Rotenberry, J. T., and J. A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology* 72:1325–1335.
- Saab, V. A., and T. D. Rich. 1997. Large-scale conservation assessment for Neotropical migratory land birds in the interior Columbia River Basin. General Technical Report PNW-GTR-399. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2005. *The North American Breeding Bird Survey, results and analysis 1966–2005*. Version 6.2.2006. USGS Patuxent Wildlife Center, Laurel, Maryland, USA. (<http://www.mbr-pwrc.usgs.gov/bbs/>)
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- Skagen, S. K., A. M. Y. Adams, and R. D. Adams. 2005. Nest survival relative to patch size in a highly fragmented shortgrass prairie landscape. *Wilson Bulletin* 117:23–34.
- Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- Tewksbury, J. J., S. J. Heil, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a Western landscape. *Ecology* 79:2890–2903.
- Thompson, F. R. III, W. Dijk, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116:259–264.
- Thompson, F. R. III, T. M. Donovan, R. M. DeGraaf, J. Faaborg, and S. K. Robinson. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Studies in Avian Biology* 25:8–19.
- Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, USA. *Conservation Biology* 14:1145–1160.
- Vander Haegen, W. M., M. A. Schroeder, and R. M. DeGraaf. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. *Condor* 104:496–506.
- Vander Haegen, W. M., and B. Walker. 1999. Parasitism by brown-headed cowbirds in the shrubsteppe of eastern Washington. *Studies in Avian Biology* 18:34–40.
- Vickery, P. D., M. L. Hunter Jr., and J. V. Wells. 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. *Auk* 109:697–705.
- Vickery, P. D., P. L. Tubaro, J. M. Cardoso Da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. Conservation of grassland birds in the Western Hemisphere. *Studies in Avian Biology* 19:2–26.
- Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110:759–768.
- Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* 13:1424–1436.
- Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *Condor* 102:256–266.