Studies in Avian Biology No. 25:130–140, 2002.

EFFECTS OF HABITAT FRAGMENTATION ON PASSERINE BIRDS BREEDING IN INTERMOUNTAIN SHRUBSTEPPE

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Abstract. Habitat fragmentation and loss strongly influence the distribution and abundance of passerine birds breeding in Intermountain shrubsteppe. Wildfires, human activities, and change in vegetation communities often are synergistic in these systems and can result in radical conversion from shrubland to grasslands dominated by exotic annuals at large temporal and spatial scales from which recovery to native conditions is unlikely. As a result, populations of 5 of the 12 species in our review of Intermountain shrubsteppe birds are undergoing significant declines; 5 species are listed as at-risk or as candidates for protection in at least one state. The process by which fragmentation affects bird distributions in these habitats remains unknown because most research has emphasized the detection of population trends and patterns of habitat associations at relatively large spatial scales. Our research indicates that the distribution of shrubland-obligate species, such as Brewer's Sparrows (*Spizella breweri*), Sage Sparrows (*Amphispiza belli*), and Sage Thrashers (*Oreoscoptes montanus*), was highly sensitive to fragmentation of shrublands at spatial scales larger than individual home ranges. In contrast, the underlying mechanisms for both habitat change and bird population dynamics may operate independently of habitat boundaries. We propose alternative, but not necessarily exclusive, mechanisms to explain the relationship between habitat fragmentation and bird distribution and abundance. Fragmentation might influence productivity through differences in breeding density, nesting success, or predation. However, local and landscape variables were not significant determinants either of success, number fledged, or probability of predation or parasitism (although our tests had relatively low statistical power). Alternatively, relative absence of natal philopatry and redistribution by individuals among habitats following fledging or post-migration could account for the pattern of distribution and abundance. Thus, boundary dynamics may be important in determining the distribution of shrubland-obligate species but insignificant relative to the mechanisms causing the pattern of habitat and bird distribution. Because of the dichotomy in responses, Intermountain shrubsteppe systems present a unique challenge in understanding how landscape composition, configuration, and change influence bird population dynamics.

Key Words: *Amphispiza belli*; *Eremophilus alpestris*; habitat fragmentation; landscape ecology; *Oreoscoptes montanus*; shrubsteppe; *Spizella breweri*; *Sturnella neglecta*.

The present rate of fragmentation in Intermountain shrubsteppe landscapes and subsequent conversion to unsuitable habitats is a critical management concern because of its effect on the associated avifauna (Braun et al. 1976, Knopf 1988, Saab and Rich 1997, Rotenberry 1998, Paige and Ritter 1999, Wisdom et al. 2000). Shrubsteppe regions in the Intermountain West, and particularly those at lower elevations in the Snake River Plain and interior Columbia River Basin, represent some of the most endangered ecosystems in North America (Noss and Peters 1995). Similarly, populations of bird species in grassland and shrubland groups have declined more than those in other bird groups during the last 30 years (Knopf 1994, Paige and Ritter 1999, Peterjohn and Sauer 1999). Despite significant habitat losses and declines in bird populations, we still do not adequately understand the mechanisms of bird responses to habitat fragmentation in Intermountain shrubsteppe or, more critically, how to reverse the loss of shrubsteppe habitats (Rotenberry 1998).

Intermountain shrubsteppe historically consisted of large expanses of sagebrush (*Artemisia* spp.), salt desert shrubs (primarily *Atriplex* spp.), and an understory of bunchgrasses interspersed with grassland patches (Hull and Hull 1974, Vale 1975; West 1979, 1983; Wright and Bailey 1982, Billings 1994, Young 1994, West and Young 2000). Shrubsteppe regions contained relatively little natural vegetative heterogeneity compared to other ecosystems in the Intermountain West (Kitchen et al. 1999) because of less pronounced gradients in elevation, moisture, and soil, and were highly susceptible to disturbance (Young and Sparks 1985). Similarly, avian diversity in shrubsteppe communities is low relative to other systems (Wiens and Rotenberry 1981, Wiens 1985a, Dobkin 1994, Rotenberry 1998).

Shrubsteppe birds live in habitats that now have a vastly different disturbance regime from that to which they were adapted. Wildfires, the primary disturbance that destroyed shrubs, historically were frequent but at small-scale, or large but relatively infrequent. Early explorers frequently reported fires in higher elevation, forested regions of the Intermountain West but few fires in the sparsely vegetated sagebrush valleys (Gruell 1985). Aboriginal burning, although common in higher elevation regions, was rare in plains habitats because of scarcity of wild game (Shinn 1980). Estimates of historical fire return intervals range from 20 to >100 years (Houston 1973, Young and Evans 1981, Wright and Bailey 1982). Sparse and patchily distributed fuels created incomplete burns. Thus, the disturbance regime was not severe enough to cause changes in vegetation composition at large scales (Wright 1985). Shrub renewal in disturbed areas was either by dispersal from remaining seed sources within the disturbed area or by regrowth from root crowns (Young and Evans 1978, 1989). The principal heterogeneity consisted of a mosaic of grasslands and different-aged patches of shrubland embedded within a larger shrub-dominated landscape (Young et al. 1979, West and Young 2000).

Exotic annuals, primarily cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kali*), and tumble mustards (*Descurainia* spp., *Sisymbrium* spp.), became established in the understory around the turn of the 20th century after ground surface disturbance caused by excessive grazing, failed agriculture, and intentional eradication of sagebrush (Vale 1974, Braun et al. 1976, Mack 1981, Yensen 1981). The synergistic pattern of ground disturbance, fire recurrence, and increased dominance by exotic vegetation have caused extensive fragmentation over large spatial scales and converted shrublands that once appeared endless to early settlers in the 1800s (Frémont 1845, Yensen 1982) into vast expanses of exotic annual grasslands (D'Antonio and Vitousek 1992, Young and Longland 1996, Hann et al. 1997, Knick and Rotenberry 1997). Parts of the Snake River Plain now burn every 3–5 years (Whisenant 1990). Using reported extremes for fire return intervals, fires that once impacted <1–5% of the historical landscape now burn 20–33% within some regions in an average year. In shrubland habitats within the Interior Columbia Basin ecosystem (eastern Oregon, eastern Washington, Idaho, northwestern Montana, and northeastern Nevada), the ratio of lethal to nonlethal fires in the current fire regime has increased greatly compared to the historical fire regime (Hann et al. 1997). Consequently, bird species that once experienced little if any habitat change within their home range and life span now live in a system that is undergoing rapid habitat fragmentation and loss (Knick and Rotenberry 2000). The large scale conversion of native shrubsteppe into grasslands dominated by exotic annual species may represent a degradation below a threshold from which recovery to native shrublands is unlikely (West and Young 2000).

In this paper, we discuss the effects of habitat fragmentation on birds living in shrubsteppe systems in the Intermountain West. The pattern of distribution and abundance of these birds is highly correlated at multiple scales with nonspatial measures of vegetative structure and floristics, and with spatial measures such as shrubland patch size, spatial texture, and shrubland-grassland perimeter (Rotenberry and Wiens 1980a, Wiens and Rotenberry 1981, Rotenberry 1985; Wiens 1985a,b; Wiens et al. 1987; Knick and Rotenberry 1995a, 1999, 2000). However, many of the underlying mechanisms of bird behavior and population dynamics that create the pattern of distribution remain unknown (Wiens et al. 1986a; Wiens 1989a,b; Rotenberry 1998, Rotenberry and Knick 1999).

Shrubsteppe systems present a unique challenge to understanding bird population responses to fragmentation. The pattern of distribution and abundance of shrubsteppe birds is highly related to the shrubland-grassland configuration of a region (Knick and Rotenberry 1995a, Vander Haegen et al. 2000). In contrast, mechanisms of disturbance that change habitat composition and configuration, such as fire or livestock grazing, readily cross shrubland-grassland boundaries. Similarly, the relatively slight structural differences between a shrubland patch and an adjacent grassland may have little influence on mechanisms that affect bird population dynamics, such as nest predation or parasitism, compared to boundaries between forest and nonforested habitats (Rotenberry 1998). Thus, fragmentation in shrubsteppe presents a dichotomy in response to habitat boundaries between bird distribution and the mechanisms that create the patterns in habitats and birds. In this review, we first describe the patterns of distribution and abundance of passerine birds in shrubsteppe regions of the Intermountain West. We then examine potential mechanisms by which fragmentation influences population change to produce those patterns.

We make two important assumptions in our review. First, and perhaps too pessimistically, we assume that shrubland fragmentation and loss in low elevation shrubsteppe, unlike other ecosystems in the Intermountain West, may result in degradation below a threshold to a permanent state of exotic annual grasslands from which recovery to a shrubland is not possible without extensive efforts for restoration (Westoby 1981, West and Young 2000). Second, we make untested assumptions about scaling up; that processes and patterns observed at the small spatial and temporal extent of individual studies are present at larger scales throughout the region (Wiens and Rotenberry 1981, Allen and Starr 1982, O'Neill 1989, Wiens 1989c, Levin 1992, Goodwin and Fahrig 1998, Rotenberry and Knick 1999).

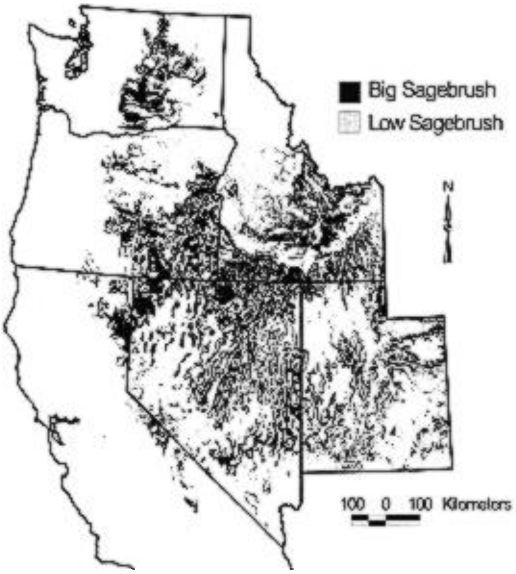

FIGURE 1. Distribution of Intermountain sagebrush steppe regions.

STUDY REGION AND SPECIES

We conducted our review for shrubsteppe regions of Idaho, Oregon, Nevada, Utah, and Washington and including portions of Wyoming and northeastern California (Fig. 1). The areal extent of potential natural vegetation in shrubsteppe habitats in this region, using Küchler's (1964) vegetation classes, is approximately 559,000 km^2 (Table 1). Within that region, long-term studies of shrubsteppe birds have been conducted in Oregon, Washington, and Idaho. We base much of our discussion on bird and fragmentation dynamics for shrubsteppe systems in the Snake River Plain of southern Idaho and the Interior Columbia Basin, Washington, because they contain studies that specifically addressed habitat fragmentation, and because habitat fragmentation and loss in these areas is most pronounced and may be a harbinger for other shrubsteppe regions of the Intermountain West. We recognize that some regions of the Great Basin, such as eastern Oregon, have the opposite problem of loss of fire, which has led to extensive stands of high density sagebrush. However, our emphasis was on the effects of fragmentation, which are most prevalent in regions currently undergoing high rates of severe disturbance.

TABLE 1. Total Area (km^2) in Potential Natural Vegetation for Shrubsteppe Classes in the Intermountain West (Küchler 1964)

Küchler's (1964) potential natural vegetation	Area (km^2)
38. Great Basin Sagebrush (*Artemisia*)	128,236
40. Saltbush-greasewood (*Atriplex-Sarcobatus*)	115,630
50. Fescue-wheatgrass (*Festuca-Agropyron*)	20,918
51. Wheatgrass-bluegrass (*Agropyron-Poa*)	36,377
55. Sagebrush steppe (*Artemisia-Agropyron*)	257,610
Total	558,771

Notes: Shrub dominated lands comprise 28–40% of the area within the conterminous western United States (McArther and Ott 1996). We summed estimates within vegetation classes (McArthur and Ott 1996) for Idaho, Utah, Oregon, Nevada, and Washington.

The primary species in this review include Horned Larks (*Eremophilus alpestris*), Sage Thrashers (*Oreoscoptes montanus*), Brewer's Sparrows (*Spizella breweri*), Sage Sparrows (*Amphispiza belli*), and Western Meadowlarks (*Sturnella neglecta*). Where available, we also include information on Rock Wrens (*Salpinctes obsoletus*), Loggerhead Shrikes (*Lanius ludovicianus*), Green-tailed Towhees (*Pipilo chlorurus*), Vesper Sparrows (*Pooecetes gramineus*), Grasshopper Sparrows (*Ammodramus savannarum*), Black-throated Sparrows (*Amphispiza bilineata*), and Lark Sparrows (*Chondestes grammacus*). Of these 12 species, 5 are classed by the Partners in Flight Western Working Group as requiring immediate conservation action in at least 1 state or province (Table 2). In addition, 5 of these species exhibit significant population declines in Breeding Bird Surveys conducted throughout the western region (Sauer et al. 1997; Table 2).

SHRUBSTEPPE HABITAT DYNAMICS

HABITAT FRAGMENTATION AND LOSS

Fragmentation and loss of shrubsteppe habitats has been widespread and relatively rapid throughout the Intermountain region largely because of human disturbance (Braun et al. 1976, D'Antonio and Vitousek 1992, Billings 1994, Young 1994, Hann et al. 1997, Mac 1998). More than 10% of the sagebrush steppe in the Intermountain region and 99% of the Palouse Prairie grasslands in eastern Washington, Oregon, and Idaho have been converted to agriculture (Noss et al. 1995). Livestock grazing is pervasive throughout the Intermountain West (Bock et al. 1993), and has influenced >99% of the shrublands and severely altered >30% (West 1996). The change in disturbance regime has facilitated the spread of invasive plants such as cheatgrass, and has altered both the form and function of shrubsteppe regions throughout the Intermountain West (Young 1994). Exotic annual vegetation may indirectly influence bird productivity,

TABLE 2. STATES AND PROVINCES IN WHICH CONSERVATION ACTION IS RECOMMENDED BY THE PARTNERS IN FLIGHT WESTERN WORKING GROUP AND WESTERN REGIONAL POPULATION TRENDS (% CHANGE/YEAR) IN BREEDING BIRD SURVEYS (SAUER ET AL. 1997) OF PASSERINE BIRDS BREEDING IN INTERMOUNTAIN SHRUBSTEPPE

Species	Conservation action	Population change		
		1966–1996	1966–1979	1980–1996
Horned Lark		−2.1*	−1.7*	−2.6*
Rock Wren		−0.9	1.8	−1.2
Sage Thrasher	BC, ID	0.6	2.7	0.1
Loggerhead Shrike	WA, BC, OR, ID	−4.1*	−8.1*	−1.6
Green-tailed Towhee		−0.1	−1.6	0.7
Brewer's Sparrow	BC, ID, UT	−3.5*	−1.8	−3.0*
Vesper Sparrow		0.0	−0.6	0.7
Lark Sparrow	WA	−1.1	0.9	−0.1
Black-throated Sparrow		−0.8	2.3	−1.2
Sage Sparrow	WA, OR, ID, UT	0.5	−4.9	1.9
Grasshopper Sparrow		0.5	−1.2	3.7
Western Meadowlark		−1.2*	−1.3	−1.5*

* Population trend is significant ($\alpha = 0.05$).

mortality, and population trends by increasing the severity of disturbance on the habitat and accelerating the rate of fragmentation and shrubland loss.

Fragmentation and loss of shrublands has been particularly pronounced in the Snake River Plain and Columbia River Basin (Whisenant 1990, Dobler et al. 1996). More than 99% of the basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) communities in southern Idaho have been converted to agriculture (Noss et al. 1995). Within the 200,000-ha region of the Snake River Birds of Prey National Conservation Area in southwestern Idaho, over 50% of the existing shrublands were destroyed by wildfires between 1979 and 1996 (Fig. 2). During that time, the total area in grasslands, primarily cheatgrass, increased from 17% to 53% (U.S. Dept. Interior 1996). Fire was the primary cause of shrubland loss, exacerbated by disturbance caused by livestock grazing and military training (U.S. Dept. Interior 1996, Knick and Rotenberry 1997). The average fire return interval in the National Conservation Area decreased from 80.5 yr between 1950 (the first year of fire records) to 1979, to 27.5 yr between 1980 to 1994. The fire return interval is as short as 3–5 years in other parts of the Snake River Plain (Whisenant 1990). By comparison, the fire return intervals in the historical disturbance regime, although difficult to reconstruct, were estimated at 60–125 years for nearby sagebrush systems at higher elevation (Wright and Bailey 1982).

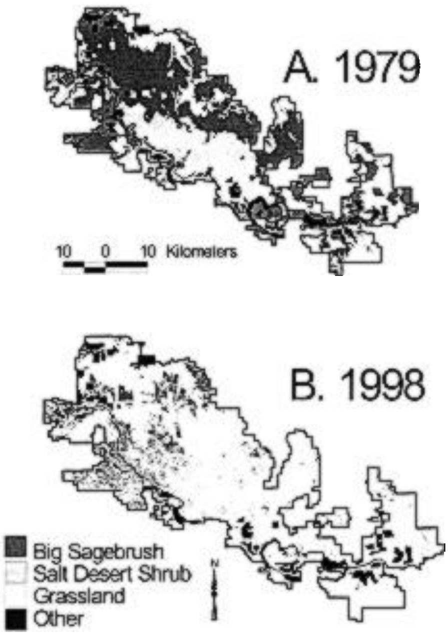

FIGURE 2. Shrubland loss from 1979 to 1994 in the Snake River Birds of Prey National Conservation Area, southwestern Idaho. The 1979 vegetation map was delineated from aerial photography. The 1994 vegetation map was classified from Landsat satellite imagery (Knick et al. 1997).

Approximately 59% of the historical distribution of shrubsteppe landscapes and 35% of the sagebrush in Washington still exists (Dobler 1994, Dobler et al. 1996, MacDonald and Reese 1998), but more land continues to be converted each year (M. Vander Haegen, pers. comm.). With the exception of three large areas of shrubsteppe remaining in federal management (Yakima Training Center, Hanford Nuclear Site, Yakima Indian Nation), remaining shrubsteppe habitats are largely fragmented within a mosaic dominated by agriculture (Dobler et al. 1996). The primary cause of shrubland loss in the Columbia River Basin, Washington has been large-scale conversion of shrublands to agriculture, although fires also can be significant locally in destroying shrublands (Rickard and Vaughan 1988, Cadwell et al. 1996). Landscapes converted to agriculture are unlikely to be returned to shrublands in the foreseeable future (Dobler et al. 1996, Vander Haegen et al. 2000).

Current distribution compared to historical extent of habitats within the Interior Columbia Basin ecosystem had decreased 33% for big sagebrush, 34% for mountain big sagebrush, and 34% for salt desert shrubs, mostly due to agriculture (Hann et al. 1997). Similarly, areal extent of habitats used by Grasshopper Sparrows had decreased 15%, 19% for Vesper Sparrows, 20% for Western Meadowlarks, 19% for Lark Sparrows, 17% for Sage Thrashers, 15% for Brewer's Sparrows, 21% for Sage Sparrows, 15% for Black-throated Sparrows, and 9% for Loggerhead Shrikes (Wisdom et al. 2000).

HABITAT FRAGMENTATION AND SHRUBSTEPPE BIRDS

FRAGMENTATION AND DISTRIBUTION OF SHRUBSTEPPE BIRDS

Shrubsteppe birds in the Intermountain West are distributed along major gradients between extremes dominated by grassland and shrubland habitats (Rotenberry and Wiens 1980a,b; Wiens and Rotenberry 1981, Wiens et al. 1987, Wiens 1989a). Large scale conversion of shrublands to grassland habitats dominated by exotic annuals likely will result in loss of bird species richness, increased numbers of Horned Larks and Western Meadowlarks, and decreased numbers of shrubland-obligate species (Klebenow and Beall 1977, Rotenberry and Wiens 1978, Castrale 1982, Bock and Bock 1987, McAdoo et al. 1989, Shuler et al. 1993, Dobler 1994, Rotenberry et al. 1995, Bradford et al. 1998).

Few studies have related distribution and abundance of shrubland birds to the composition and configuration of large landscapes (km^2; Knick and Rotenberry 1995a, Vander Haegen et al. 2000). Alternatively, measures of spatial heterogeneity taken at small study sites (ha) have not correlated with species abundance or presence and may not reflect the scale at which birds respond to their environment (Wiens 1974a). In southwestern Idaho, we determined the distribution of species in a bird community in the Snake River Birds of Prey National Conservation Area relative to a gradient between shrub and grassland habitats. We used a canonical correspondence analysis (CANOCO; ter Braak 1986, 1988) of species abundances at 134 sites at which we measured local vegetation characteristics and landscape variables (Knick and Rotenberry 1995b). Canonical correspondence analysis is a multivariate direct gradient ordination of species variation relative to environmental variables. The ordination axes of bird species data are constrained to be linear combinations of the environmental variables, but the species are assumed to have a unimodal response to the environmental gradients (ter Braak and Prentice 1988). Shrubland-obligate species, such as Sage and Brewer's sparrows and Sage Thrashers, were associated with Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities and landscape variables of increasing shrub patch size and number of shrub cells in the 1-km radius surrounding the sample point (Fig. 3). In contrast, Horned Larks and Western Meadowlarks were associated with disturbed vegetation communities. Predictive maps of Sage Sparrow and Brewer's Sparrow presence, using a resource selection function based on landscape variables and the Mahalanobis distance statistic, again demonstrated the direct re-

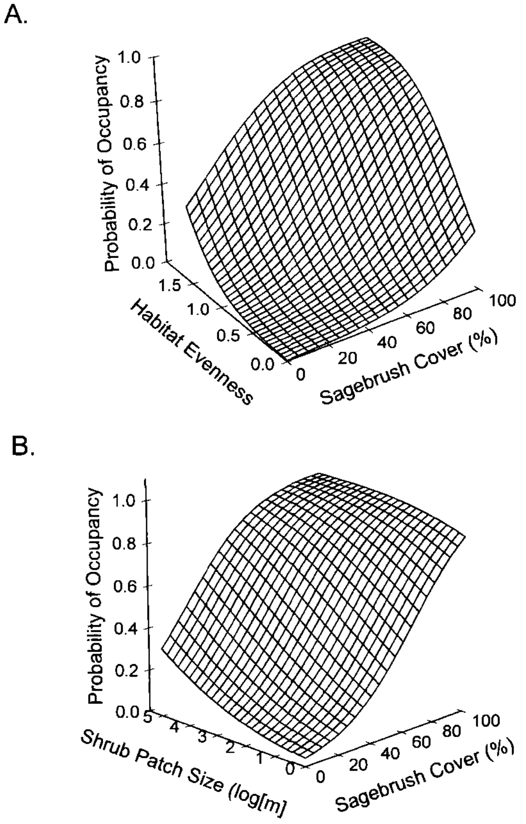

FIGURE 3. Relationship between local and landscape variables and probability of occurrence by Sage Thrashers (A) and Sage Sparrows (B) in southwestern Idaho (Knick and Rotenberry 1995a).

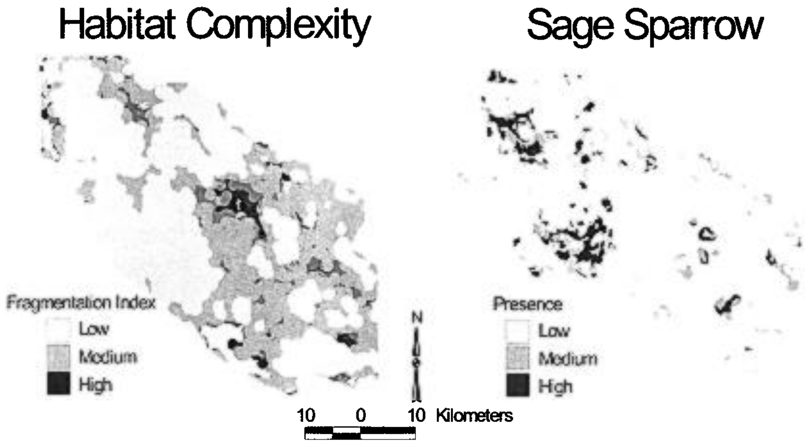

FIGURE 4. Habitat fragmentation within a 5-km radius (average perimeter/area of shrub patches) (top) and probability of Sage Sparrow presence (bottom) in a 200,000-ha shrubsteppe region in southwestern Idaho.

lationship between species presence and large shrubland patches (Fig. 4; Knick and Rotenberry 1999).

The interaction between local vegetation characteristics and landscape measures of fragmentation that determine the probability of bird occupancy carries important implications for our understanding of habitat selection and management. Equal probabilities of occupancy were possible with different combinations of ground cover of sagebrush and patch size (Fig. 3). Moreover, the shape of the selection function changed relative to differences in value of a habitat variable (Rotenberry and Knick 1999). Thus, management questions of minimum areas required by a species may be best answered by a probability of occupancy produced by multiple patch sizes and characteristics. The low probability of occupancy also implies that only a portion of available patches may be occupied, even though the patch may be of sufficient size to encompass multiple territories of individuals (Robbins et al. 1989a).

MECHANISMS UNDERLYING THE DISTRIBUTION PATTERNS

Landscapes generate patterns of species distribution by influencing productivity, mortality, or movements among habitats (Wiens 1976, 1994; Urban and Shugart 1986, Danielson 1992, Pulliam et al. 1992). Many species of birds exhibit a meta-population structure composed of source or sink populations within a region (Pulliam 1988, Hanski 1991, Opdam 1991, Pulliam and Danielson 1991, McCullough 1996). We expected that fragmentation of shrublands facilitated mechanisms that would decrease productivity or increase mortality and thus lower the number and individual contribution of source populations by decreasing and isolating the area of suitable resources, and increasing the amount of edge (Fahrig and Merriam 1994, Wiens 1996). We reviewed studies for evidence that fragmentation resulted in lower nest success or productivity, increased mortality due to predation or parasitism, or influenced movements among habitats.

Productivity

Productivity might be related to fragmentation of shrublands and landscape configuration by differences in breeding density, nest success, or number of young produced. Measures of productivity, as well as microhabitat characteristics of nest placement have been reported for numerous shrubsteppe species (Rich 1980a,b; Reynolds 1981; Petersen and Best 1985a,b; Winter and Best 1985; Rotenberry and Wiens 1980b, 1991). However, few studies have related productivity to large scale measures of spatial characteristics in Intermountain shrubsteppe systems (Knick and Rotenberry 1995b, 1996; Vander Haegen et al. 2000). Of these, only nest success relative to landscape configuration has been measured.

Young were successfully fledged at 11 of 13 Sage Sparrow nests, 27 of 36 Brewer's Sparrow nests, and 8 of 37 Sage Thrasher nests during 1994 and 1995 in southwestern Idaho (Knick and Rotenberry 1996). Local or landscape variables were not associated ($P > 0.05$) with nesting success of Sage Sparrows. For Brewer's Sparrows, increased nest success was marginally related to increasing landscape heterogeneity ($P = 0.098$), a trend that was contrary to expectation. Sage Thrasher nests were more successful

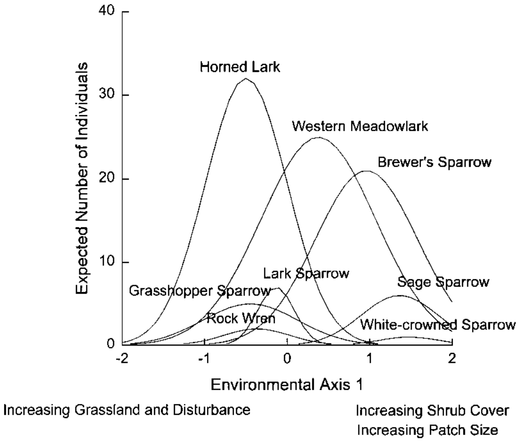

FIGURE 5. Gaussian response curves of bird species along the first environmental axis of a canonical correspondence analysis of bird species and environmenatal variables. The species response curve was a function of the maximum number of observations (y_o) at a site for the species in the sample, the modal score on the environmental axis (m), and the dispersion (s) along the axis in units of standard deviation. The expected value ($\hat{y}$) then is: $\hat{y} = y_o \cdot \exp\{[-(1/2)\cdot(x - m)^2]/s^2\}$ for any point x of the environmental axis (ter Braak and Looman 1986). Environmental variables were percent ground cover of sagebrush, winterfat, shadscale, and grasslands, and the area, amount of perimeter, and thickness of shrub patches within 1 km of the sampling point.

with increasing shrub patch size ($P = 0.064$). In Washington, Sage Thrashers, Brewers Sparrows, and Lark Sparrows had lower nest success in fragmented compared to unfragmented regions (M. Vander Haegen, unpubl. data). In eastern Idaho, clutch size and nest success did not differ between an experimentally burned area that reduced sagebrush cover by 50% and control plots, but no spatial characteristics of the landscape were measured (Petersen and Best 1987).

The pattern of species presence along a habitat gradient of decreasing grassland cover and disturbance to increased shrub cover and patch size of shrublands changed from grassland species, such as Grasshopper Sparrows and Horned Larks to shrubland obligates, such as Brewer's and Sage sparrows (Fig. 5). The density of singing males was greatest in unfragmented shrubland habitats for Sage Thrashers, and Brewer's and Sage sparrows (Knick and Rotenberry 1995, 1999). Large-scale habitat changes in southwestern Idaho that increased fragmentation and habitat richness in the landscape were associated with lower densities of Horned Larks, Western Meadowlarks, and Brewer's Sparrows (Knick and Rotenberry 2000). However, bird response was not strongly associated with habitat changes at small spatial or temporal scales. Densities of Sage and Brewer's sparrows did not differ consistently between plots in controlled fire and unburned areas in eastern Idaho and densities of Sage Thrashers did not change (Petersen and Best 1987, 1999). In Montana, a 50% reduction of sagebrush cover by herbicidal spraying did not affect numbers of breeding pairs of Brewer's Sparrows or Vesper Sparrows the following year, but Brewer's Sparrows declined in the total-kill sagebrush plot (Best 1972). Similarly, prediction of densities of Sage Sparrows and Brewer's Sparrows did not track local habitat changes in eastern Oregon (Wiens and Rotenberry 1985, Wiens et al. 1986b, Rotenberry 1986, Rotenberry and Knick 1999).

Food resources may not limit productivity in shrubsteppe regions except during "ecological crunch" periods (Wiens 1974b, 1989a,b). However, no studies have related food resources in fragmented and unfragmented habitats to differences in nesting success or clutch size. Reduction of arthropod abundance and biomass did not adversely affect productivity of Brewer's Sparrows or Sage Thrashers in Idaho (Howe et al. 1996). Similarly, available biomass of arthropods was >2 orders of magnitude greater than required for bioenergetic demands of a community of shrubsteppe birds breeding in Oregon (Rotenberry 1980).

Predation and parasitism

Edge-related processes that increase predation or parasitism associated with increased fragmentation and decreased patch size can reduce productivity in fragmented habitats relative to larger patches (Urban and Shugart 1986, Wiens et al. 1986a, Temple and Cary 1988, Porneluzi et al. 1993, Paton 1994). Nest predation ranged from 11–100% of the causes of nest failure in Brewer's Sparrows (Reynolds 1979, 1981; Petersen and Best 1987, Rotenberry and Wiens 1989, Rotenberry et al. 1999). Predators included Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica pica*), Loggerhead Shrikes, snakes, long-tailed weasels (*Mustela frenata*), chipmunks (*Tamias* spp.), and ground squirrels (*Spermophilus* spp.). However, no studies have related predation rates to fragmentation in shrubsteppe habitats.

Brown-headed Cowbirds (*Molothrus ater*) parasitize nests of Brewer's and Sage sparrows (Rich 1978, Reynolds 1981, Biermann et al. 1987), but few data exist on the probability of parasitism by cowbirds relative to degree of fragmentation in shrublands. The extent to which cowbirds also may attempt to parasitize Sage Thrasher nests is unknown because Sage

Thrashers reject cowbird eggs (Rich and Rothstein 1985, Reynolds et al. 1999).

The overall parasitism rate on Brewer's and Sage sparrows in the Columbia River Basin, Washington, was <10% (Vander Haegen and Walker 1999), because most nesting attempts by host species were started before cowbirds arrived on the study areas. In addition, the relatively long distance from agriculture developments and cattle feedlots, which provide feeding areas for cowbirds, to shrubsteppe areas in Washington may have accounted for the low parasitism rates (Vander Haegen and Walker 1999). The rate of parasitism in Idaho and Oregon also was low (0–13%) and may reflect the relatively low presence of cowbirds (Rich 1978, Rotenberry and Wiens 1989, Rotenberry et al. 1999). In contrast, cowbirds parasitized 52% of Brewer's sparrow nests in southeastern Alberta (Biermann et al. 1987). Therefore, parasitism by cowbirds increases when shrublands are converted to agriculture or cattle feedlots, providing feeding sites for Brown-Headed Cowbirds from which they can travel into surrounding areas to parasitize nests.

The structural difference between shrubland and grassland to predators or cowbirds may be less significant in producing an edge effect than boundaries between forest and nonforested habitats (Rotenberry 1998). As such, the function of fragmentation may be indirect, by providing homesites, feeding or watering sites, or different plant assemblages in unsuitable fragments that increase the presence or proximity of potential predators or cowbirds (Coker and Capen 1995, Robinson et al. 1995a, Knight et al. 1998).

Redistribution and individual movements

In the absence of habitat-specific differences in productivity or survival to create differences in species abundance relative to habitat fragmentation, the pattern of a species distribution also could result from individuals moving among habitats (Dunning et al. 1992). We expect that adults might exhibit strong site tenacity (Wiens 1985a, Wiens and Rotenberry 1985, Knick and Rotenberry 2000) and return after migration to the same breeding territory as the previous year regardless of any habitat alternation (Rotenberry and Knick 1999; M. Vander Haegen, pers. comm.). In contrast, young birds that previously have not established successful territories may seek new areas either following fledging or upon returning from migration. We do not know if dispersal and migration characteristics, or habitats selected by juveniles differ between those hatched in fragmented or unfragmented shrublands.

Redistribution by individuals following migration and return to the breeding grounds also could account for the pattern of distribution and abundance relative to fragmentation. Many species of shrubsteppe birds migrate seasonally, breeding in the northern Great Basin, and wintering in the southwestern U.S. or northern Mexico. Unfortunately, the considerable majority of detailed research occurs only during the breeding season. There are ample theoretical reasons to expect that events that occur in migration or during winter may play an equal or even greater role in determining population dynamics on the breeding grounds (Dunning and Brown 1982, Knopf 1994, Sherry and Holmes 1995, Herkert and Knopf 1998). Most importantly, the linkage between any specific breeding area and any specific wintering area is unknown for virtually all populations. In essence, then, the breeding grounds of these species represent "open" systems, systems whose properties are affected by events that lie outside the domain of study and, hence, cannot be completely understood without expanding the scale of study.

Linkages within a meta-population are driven by the movements of individual animals, particularly those movements associated with natal dispersal (although post-breeding dispersal may also play a role in some species). Unfortunately, empirical data relating to dispersal are usually lacking, which severely constrains our ability to understand and to adequately model population dynamics in most species. Because many species in fragmented landscapes are potentially threatened, conservation efforts are hampered by the lack of reliable information on dispersal. Patterns of natal dispersal also are relevant to issues of genetic structure and differentiation in populations, which also may have conservation-related consequences. Furthermore, most meta-population models deal only with resident species; little is known about linkages of migrant populations breeding in a fragmented landscape, or whether they even show meta-population structure.

DISCUSSION

The effect of habitat fragmentation and the increased intensity of land use on the biota and its diversity are important considerations in the conservation of the earth's resources (Wilson 1988, Saunders et al. 1991). Increasingly, birds and other animals are forced to live in habitats that have become fragmented in space by the direct or indirect actions of humans. Our understanding of habitat fragmentation and its consequences for bird populations have primarily been developed from forested (Robbins et al. 1989a, Rolstad 1991, Freemark and Collins 1992, Robinson 1992, Robinson et al. 1995a) or grassland regions (Johnson and Temple 1986, Herkert 1994). Yet, fragmentation of shrubsteppe from disturbances such as wildfires, agriculture, or other human-caused land use is equally dynamic and has significant consequences for shrubsteppe birds as well as other taxa (Braun et al. 1976, Knick 1999). Unlike other ecosystems, loss of shrubsteppe may be irreversible once cheatgrass dominates the system because of loss of seed sources, changes in soils, and the increased fire frequency (Westoby 1981, D'Antonio and Vitousek 1992, West and Young 2000).

Populations of shrubsteppe birds are of conservation concern in Intermountain states because of declines over part or most of the Great Basin and Intermountain shrubsteppe regions. In addition to passerines, population declines of Sage Grouse (*Centrocercus urophasianus*) and Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus* ssp. *columbianus*) are linked directly to fragmentation and habitat loss (Swensen et al. 1987, Dobkin 1995, Connelly and Braun 1997, MacDonald and Reese 1998; M. Schroeder et al., unpubl. manuscript). Sage Grouse have recently been petitioned for listing under the Endangered Species Act because of concerns over rangewide declines in numbers, and Columbian Sharp-tailed grouse currently are under status review.

Landscape analyses in shrubsteppe and other arid ecosystems have not been as prevalent as in other major ecosystems largely because mapping and describing habitats over large extents, particularly from satellite imagery, pose difficult technological challenges (Knick et al. 1997). Mapping habitat change by standard remote sensing techniques (Singh 1989, Dunn et al. 1991) also is problematic because of inability of satellite sensors to detect vegetation in sparsely covered shrublands. Appropriate measurement metrics to quantify fragmentation in shrublands are more difficult compared to agricultural and forested systems because of the complex patterns produced by fires (Knick and Rotenberry 1997). Thus, few studies have quantified spatial attributes of composition and configuration of landscapes relative to bird population dynamics in shrubsteppe compared to forested systems.

The process of fragmentation operates at multiple scales of space and time. At large spatial scales in shrublands, fragmentation was associated with distribution and abundance of populations of shrubland species. Declines in populations of Brewer's Sparrows, Western Meadowlarks, and Horned Larks also may be directly related to large-scale fragmentation in Intermountain shrubsteppe. Large-scale fragmentation may influence nesting success or facilitate cowbird movements into previously unsuitable habitats. At smaller scales, we expected that fragmentation would affect individuals within the population to produce the larger pattern. Presence of shrubland birds was influenced by local vegetation characteristics in combination with landscape measures at spatial extents much larger than individual home ranges. However, we did not find convincing evidence that individual productivity or probability of predation was directly related to fragmentation. Thus, the larger regional context in which shrubsteppe birds establish their territories may be more important in determining range-wide patterns than dynamics within that territory once established (Rotenberry and Knick 1999). Cross-scale research is needed to determine appropriate scales at which birds respond to the system (Wiens 1974a, Wiens and Rotenberry 1980, Holling 1992).

Interaction of local and landscape variables in predicting species presence emphasized the difficulty in defining habitat fragmentation in shrubsteppe systems. If fragmentation is defined relative to a species-specific probability of presence, then multiple combinations of local and landscape variables might yield similar probabilities of occupancy by individuals. Similar to defining minimum patch requirements, our understanding of fragmentation must be done in the context of multiple gradients of patch size, perimeter, and the degree of isolation of the patch (Fahrig and Merriam 1994; Wiens 1994, 1996).

The declining populations of Horned Larks and Western Meadowlarks, determined from the North American Breeding Bird Surveys (Sauer et al. 1997), are contrary to our expectations from habitat changes throughout the Intermountain shrubsteppe region. Horned Larks and Western Meadowlarks are grassland species that are common after disturbance and we would predict increases in populations of these two species. However, the exotic-dominated grasslands that result from loss of shrublands throughout much of the Intermountain region are very different from the native grasslands to which Horned Larks and Western Meadowlarks are adapted. Declines in populations of Horned Lark and Western Meadowlark populations indicate that exotic annual grasslands are not ecologically equivalent to native grasslands. Numbers of Western Meadowlarks were lower but those of Horned Larks were higher on transects in cheatgrass compared to sagebrush communities in southcentral Washington (Rogers et al. 1988).

In another apparent discrepancy between species population and habitat trends, numbers of Sage Sparrows observed on Breeding Bird Surveys were increasing, although the trend was statistically insignificant. Possibly, the Breeding Bird Surveys may not be sampling the available habitats, or tracking the habitat changes. We also suggest that for all of these species, dynamics on the wintering grounds may be equally, or even more important in driving population trends than habitat changes on the breeding grounds.

COMPARISON TO MIDWESTERN SHRUBLAND AND GRASSLAND SYSTEMS

Birds living in grassland systems are experiencing a more extreme scenario of habitat fragmentation and loss than birds in shrubland systems. Conversion to agricultural cropland, livestock grazing, and urbanization have altered most of the grassland ecosystems in North America (Knopf 1994, Herkert 1995, Noss et al. 1995, Vickery and Herkert 1999). Habitat loss exceeds 80% of the original distribution of prairie grasslands and is almost complete in areas suitable for agricultural croplands (Samson and Knopf 1994). Other more subtle changes in grassland habitats have resulted from differences in the grazing regime by large herbivores and alteration of historical fire frequencies (Saab et al. 1995). In grasslands, as well as shrublands, restoration of native species and processes remains a significant challenge (Bock et al. 1993, Rotenberry 1998, Vickery et al. 1999).

Fire, grazing, and climate were significant influences in native grasslands but varied in their impact on system processes relative to geographic location. In Great Plains and eastern tallgrass prairies, natural and aboriginal-caused fires were large scale, intense, and frequent (5–30 year return interval), and combined with periodic drought to maintain grasslands and prevent shrub or tree growth (Wright and Bailey 1982, Sims and Risser 2000). Grazing by large herds of bison (*Bison bison*) was locally intensive but highly variable in space and time. In contrast, fire was the dominant disturbance in western grasslands and shrublands because large grazers have been absent since approximately 12,000 years presettlement (Mack and Thompson 1982, West and Young 2000). In all grassland and shrubland systems, fire suppression and control, either by direct intervention or indirectly by human-created fire-breaks, have disrupted successional and cyclic pathways. Similarly, effects of grazing have changed significantly because of reduced native ungulate herds and increased domestic livestock use, often resulting in a more intensive disturbance that is spatially and temporally uniform in the landscape (Bock et al. 1993).

Population trends of grassland birds, as a group, decreased throughout North America from 1966–1996; 13 of 25 species had significant declines and 3 had significant increases during this period (Peterjohn and Sauer 1999). Populations of grassland species also have declined over the past 100 years corresponding to the long-term loss of grasslands (DeSante and George 1994). However, as in shrubland systems, range-wide population changes detected in Breeding Bird Surveys were not well supported by studies at local scales (Herkert and Knopf 1998). In addition, the pattern of distribution and abundance of grassland birds was sensitive to landscape measures, but the mechanisms producing those patterns remain unclear (Herkert and Knopf 1998).

The winter ecology of grassland and shrubland birds is largely unknown, despite potentially having a large influence on sizes of breeding populations (Dunning and Brown 1982). Most western grassland and shrubland bird species are short-distance migrants to southern and southwestern United States and northern Mexico (DeSante and George 1994, Rotenberry 1998, Vickery et al. 1999). Therefore, influences on populations of these species are largely North American processes (Knopf 1994, Herkert 1995, Rotenberry 1998).

The effects of fragmentation in shrubland or grassland systems may be most pronounced when the severity of disturbance results in a highly contrasting mosaic of suitable and unsuitable habitats derived from a previously homogeneous landscape. The structural difference between shrublands and grasslands, or between grasslands and agriculture or urban areas, although slight relative to forest and nonforest boundaries, nonetheless is a significant component to bird distribution and abundance. Where shrublands or grasslands have been fragmented into unsuitable areas, numbers of area-sensitive bird species decline (Johnson and Temple 1986, Herkert 1994, Vickery et al. 1994, Bock et al. 1999, O'Connor et al. 1999, Walk and Warner 1999). Conversely, habitat fragmentation may not be a significant factor in bird dynamics in areas in which habitats remain largely unchanged because the relative severity of disturbance is minimal or infrequent, or in landscapes in which natural heterogeneity of habitats is high. In Colorado foothills containing a high degree of natural heterogeneity, shrubland birds were not sensitive to landscape characteristics (Berry and Bock 1998).

The answer may lie in behavioral mechanisms of habitat selection, particularly the recognition of a suitable place in which to settle for the first time. Prior to the onset of anthropogenically-induced fragmentation, most of the species in this review occurred in (and presumably were adapted to) landscapes dominated by shrublands that were homogeneous over large spatial scales. Perhaps reduction of these vast tracts of shrublands below some minimum, but currently unknown, size to current fragmented landscapes simply represents a poor fit to the habitat template of these birds.

CONCLUSIONS

The distribution of shrubsteppe birds was significantly related to large-scale habitat fragmentation. However, differences in productivity, predation, or parasitism associated with fragmentation of shrublands were either unreported or largely lacking. We suggest that individuals select location of home ranges within a hierarchy of landscape and local vegetation characteristics to produce the range-wide patterns of distribution. However, habitat structure may not be important in influencing mechanisms that affect productivity and mortality among individuals. Thus, patterns of species distribution are the result of individual movements among habitats either post dispersal or after migration. A lag effect due to site tenacity is evident in bird population responses to habitats (Wiens and Rotenberry 1985; Peterson and Best 1987, 1999; Rotenberry and Knick 1999, Knick and Rotenberry 2000). Ultimately, populations of shrubland obligates may not persist in landscapes of increasingly fragmented patches after disturbance (Braun et al. 1976, Rotenberry and Wiens 1980a).

ACKNOWLEDGMENTS

The USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, US Department of Interior Global Climate Change Program, University of California, Riverside, and the Bureau of Land Management Challenge Cost Share Program have supported our work on shrubsteppe habitats and passerine birds. We thank F. Howe (Utah Dept. of Wildlife), M. Vander Haegen (Washington Dept. of Fish and Wildlife), and T. Rich (US Bureau of Land Management) for their discussions on shrubsteppe birds, and R. Rosentreter (US Bureau of Land Management), N. West (Utah State University), and J. Young (USDA Agricultural Research Services) for insights into presettlement conditions of shrubsteppe regions. We appreciate reviews of the manuscript by D. Dobkin, T. Rich, and P. Vickery.