

AN ABSTRACT OF THE THESIS OF

Anna C. Noson for the degree of Master of Science in Wildlife Science presented on March 13, 2002.

Title: Avian Communities in Relation to Habitat Influenced by Fire in a Sagebrush Steppe Landscape

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Abstract approved: _____

Richard A. Schmitz

Fire suppression in high-elevation sagebrush steppe over the last century has profoundly influenced the structure and complexity of vegetation communities. Although fire is the primary management tool used to restore these areas, the impact of this management practice on associated avian communities is poorly understood. We examined patterns of habitat use by breeding birds one year after a prescribed burn on Steens Mountain in southeastern Oregon. During the 2000 breeding season, we determined bird distribution and abundance using a fixed-radius point count method at 205 sites representing burned and unburned sagebrush, juniper, and aspen habitats. We developed resource selection models for individual species breeding in the sagebrush steppe, and predictive models of bird species richness and diversity (H') by combining bird and local vegetation data collected at the field sites with remotely-sensed landscape data. We used Akaike's Information Criterion (AIC_c) to select the best-approximating model from a suite of a priori candidate models.

Brewer's sparrows, sage thrashers, and green-tailed towhees had a positive relationship with increasing area of sagebrush, whereas vesper sparrows were negatively associated with area of sagebrush. Green-tailed towhee occurrence initially increased with increasing juniper within 1 km, but eventually declined as juniper continued to increase. All other species showed a strong negative relationship with increasing juniper. Brewer's sparrows, sage thrashers, and green-tailed towhees were also sensitive to sagebrush abundance within 1 km.

Bird species richness and diversity (H') were positively associated with increasing area of aspen and juniper density at the site. However, both bird community measures quickly reached a threshold at low values of either habitat type. Bird species richness increased with increasing habitat diversity (H') within 1 km, while bird diversity (H') increased with increasing habitat richness at the site.

The prescribed fire minimally impacted critical aspen habitat. Furthermore, our models indicate that even small aspen stands and the presence of a few juniper trees are adequate to sustain avian diversity in this landscape. These results suggest that, although fire has an immediate impact on some birds breeding in sagebrush steppe, in the long term, periodic fire enhances avian diversity and creates suitable habitat conditions for sagebrush obligates by maintaining aspen stands and limiting juniper.

Avian Communities in Relation to Habitat Influenced by Fire in a Sagebrush Steppe
Landscape

by
Anna C. Noson

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CONTRIBUTION OF AUTHORS

Dr. Richard A. Schmitz and Dr. Richard F. Miller were involved in the design, analysis, and writing of each manuscript.

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Avian Communities in Relation to Habitat Influenced by Fire in a Sagebrush Steppe Landscape

Chapter 1

Introduction

In the sagebrush steppe of western United States, the landscape has changed dramatically over the last century due to altered fire regimes. In high-elevation sites, overgrazing and fire suppression practices have reduced fire frequency, causing major changes in the structure of sagebrush (*Artemisia* spp.) communities, rapid juniper (*Juniperus* spp.) woodland expansion, and declines in aspen (*Populus tremuloides*) forest (Burkhardt and Tisdale 1976, Miller et al. 1994, Bartos and Campbell 1998, Miller and Rose 1999). Furthermore, landscape changes associated with the absence of fire in this ecosystem may result in significant losses of biological diversity and shifts in species distributions (Meffe and Carroll 1994, Christiensen 1988).

Maintaining a mix of ecological communities across the landscape by mimicking historic disturbance regimes is an increasingly popular approach to conservation of biological diversity (Noss 1983, Christiensen 1988, Kaufmann et al. 1994, Aplet and Keeton 1999). In fire-adapted ecosystems altered by human activities, prescribed burning is the primary tool used to mimic historic fires (Bunting 1987, Adams 1989, Clark and Starkey 1990). Yet prescribed fire remains

a controversial practice and information on the biological consequences of such coarse filter approaches to conservation are limited, particularly in non-forested ecosystems (Campa III et al. 1999).

Avian communities are especially sensitive to variability in habitat structure (MacArthur and MacArthur 1961, Cody 1985). Therefore, changes in fire frequency and behavior likely have important consequences for patterns of avian diversity in sagebrush steppe landscapes. Because sagebrush steppe covers over 40 million ha of the western United States (Miller et al. 1994), conservation of these areas is essential to maintaining avian diversity in the West. Furthermore, populations of many bird species associated with the sagebrush steppe are declining (Paige and Ritter 1999). The research presented in this thesis examines habitat associations of bird assemblages and individual species following prescribed fire in high-elevation sagebrush. A major criticism of coarse-filter approaches to conservation is that they are not species-specific, and therefore the habitat needs of native species may not be adequately met (Kaufmann et al. 1994, Haufler 1999). Therefore, we focused on individual bird species of conservation concern as well as bird diversity across the landscape. We examined bird response to habitat at two spatial scales—local and landscape. Understanding the spatial scale(s) at which fire influences avian communities is necessary to determine the scale of management that will benefit species of conservation concern (Noss 1983, Wiens et al. 1987, Campa III et al. 1999).

Fire disturbance has the potential to reduce availability of key habitats, such as sagebrush and aspen, that are critical to local avian diversity (Carothers 1974, Knopf et al. 1988, Knick and Rotenberry 1995). However, lack of fire disturbance may have an even greater impact on bird communities in fire-adapted sagebrush steppe communities. Life histories of many species are linked to the natural disturbance regime, and fire is often required to maintain suitable habitat conditions for these native species (Christiansen 1988, Agee 1993, Hutto 1995). Research in other systems have demonstrated that, in the absence of fire, woodland expansion and increases in forest edge can be detrimental to native bird populations, possibly introducing competing species as well as increasing predation and nest parasitism (Blair 1996, Coppedge et al. 2001). In mountain big sagebrush communities, encroaching juniper has also been associated with a rapid decline in shrub cover, which may further impact sagebrush obligate species (Miller et al. 2000). Therefore, we considered the importance of changes in habitat associated with fire relative to fire suppression.

This thesis contains an introduction, two chapters prepared as journal submissions, and summary conclusions. The chapters examine aspects of bird communities and habitat following prescribed fire, based on data collected on Steens Mountain, Oregon in 2000. In chapter 2, relationships between individual bird species and habitat influenced by prescribed fire and juniper encroachment are quantified. In Chapter 3, patterns of avian diversity across a landscape composed of burned and unburned habitats are determined, and the efficacy of a coarse filter

approach to conservation of biological diversity in the sagebrush steppe is evaluated based on predicted bird distributions.

Chapter 2

Influence of Fire and Juniper Encroachment on Birds in a Sagebrush Steppe Landscape

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ABSTRACT

We examined relationships between high-elevation sagebrush steppe habitats altered by prescribed fire and western juniper (*Juniperus occidentalis*) encroachment on breeding distributions of Brewer sparrows (*Spizella breweri*), vesper sparrows (*Pooecetes gramineus*), green-tailed towhees (*Pipilo chlorurus*), and sage thrashers (*Oreoscoptes montanus*) on Steens Mountain in southeastern Oregon. We conducted bird counts at 172 sites encompassing burned and unburned sagebrush (*Artemisia* spp.) habitat and a range of juniper densities in 2000. We developed resource selection models using local variables measured in the field and landscape variables derived from remotely-sensed data for each bird species. For each bird species, we used Akaike's Information Criterion (AIC_c) to select the best-approximating model from a suite of candidate models describing potential relationships with habitat. Brewer's sparrows, sage thrashers, and green-tailed towhees had a positive relationship with increasing area or largest patch of sagebrush, whereas vesper sparrows were negatively associated with area of sagebrush and positively related to increases in sagebrush patchiness. Green-tailed towhee occurrence increased with increasing area of juniper, but eventually declined when area of juniper exceeded 33%. All other species showed a strong negative relationship with area or density of juniper. With the exception of vesper sparrows, all species were associated with attributes measured at the landscape scale. Our results indicate that although fire has an immediate negative impact on

sagebrush birds, periodic fire is important for limiting juniper encroachment and maintaining suitable habitat conditions for sagebrush obligate birds.

INTRODUCTION

Disruption of natural disturbance regimes due to human activities has major consequences for the structure and function of ecosystems (Pickett and White 1985). In mountain big sagebrush communities (*Artemisia tridentata* subsp. *vaseyana*) of the sagebrush steppe, decreased fire frequency due to over-grazing by livestock and suppression practices has transformed mosaics of sagebrush and grassland into homogeneous stands of sagebrush, and contributed to the rapid expansion of juniper (*Juniperus occidentalis*) woodlands (Burkhardt and Tisdale 1976, Miller et al. 1994). Prior to settlement, fire typically occurred every 15-25 years across much of this cover type (Miller and Rose 1999), maintaining patches of native grassland and restricting juniper, a fire-intolerant species, to rocky outcrops and shallow-soil benchlands where fire was unlikely to spread (Burkhardt and Tisdale 1976, Miller and Wigand 1994). Today post-settlement juniper woodlands have invaded large areas of mountain big sagebrush and continue to encroach in the absence of fire (Burkhardt and Tisdale 1976, Miller and Rose 1999).

Many bird species associated with the sagebrush steppe are exhibiting population declines across their range due to habitat loss and fragmentation (Saab and Rich 1997, Paige and Ritter 1999). Fire influences habitat availability and

configuration at multiple scales, and has been documented to negatively effect sagebrush obligate birds (Tiagwad et al. 1982, Bock and Bock 1987, Knick and Rotenberry 1995). However, results among studies of bird-habitat relationships in sagebrush communities are inconsistent for many species, possibly due to differences in landscape context and local bird populations (Petersen and Best 1987, Knick and Rotenberry 1995). Variation among natural fire regimes associated with different sagebrush communities may also contribute to differences among previous studies. In low-elevation (usually less than 1500 m) sagebrush communities, (e.g. *A. tridentata* subsp. *wyomingensis*), fires were historically less frequent because low precipitation levels limited fuel accumulations (Whisenant 1990, Miller et al. 1998). At higher elevations, sagebrush communities dominated by mountain big sagebrush are typically more productive and hence burned more frequently (Miller et al. 1998). In addition, juniper encroachment is a concern primarily in higher elevations. The encroachment of juniper woodlands represents a major change in the structure of sagebrush habitat that has potential consequences for obligate species (Reinkensmeyer 2000, Rosenstock and Van Riper III 2001). Without periodic fire, juniper density increases, resulting in subsequent loss of sagebrush cover to <1 % (Miller et al. 2000). Furthermore, while mountain big sagebrush communities are adapted to frequent fire and recover quickly after disturbance, the permanence of juniper encroachment may inflict a more lasting impact on sagebrush birds. Once shrub cover declines, there is little fuel available

to carry fire and it becomes increasingly unlikely that the woodland will burn (Bunting 1987, Miller et al. 2000).

The purpose of this study was to examine avian responses to changes in habitat accompanying fire and fire suppression in sagebrush steppe communities. Recent research has focused on altered fire regimes in low-elevation sagebrush communities suffering rapid and potentially irreversible conversion to agriculture and exotic grasslands (Knick and Rotenberry 1995, Vander Haegen et al. 2000). These areas represent a major portion of the sagebrush steppe. However, high elevation sagebrush communities are still comparatively intact, and therefore represent vital breeding habitat for sagebrush obligates. Furthermore, there is evidence that the mountain big sagebrush cover type supports higher bird abundance and species richness than lower elevation sagebrush communities (Medin et al 2000). Prescribed fire is the primary management tool used to restore high-elevation sagebrush (Clark and Starkey 1990). Yet the influence of fire on avian communities across these sagebrush cover types has received little attention. Our objective was to quantify relationships between sagebrush-associated birds and habitats influenced by prescribed fire and lack of fire resulting in juniper invasion. We developed resource selection models for birds breeding in sagebrush steppe and considered species of high management concern (Manly et al. 1995). Our goal was to provide guidance for the use of fire in the management of high-elevation sagebrush bird communities.

STUDY AREA

The study was conducted on Steens Mountain, an isolated fault-block escarpment in southeastern Oregon. The climate in this region is cool and semi-arid (Hansen 1956). Annual precipitation ranges from 25 cm at the base to almost 36 cm at higher elevations and falls mainly during winter.

Mountain big sagebrush and low sagebrush (*A. arbuscula*) are the two dominant cover types on Steens Mountain. Isolated aspen (*Populus tremuloides*) stands form narrow bands along north-facing aspects, and western juniper woodlands stretch discontinuously between 1450 and 2100 m (Miller and Rose 1995). A few curleaf mountain-mahogany (*Cercocarpus ledifolius*) stands are also present. Western juniper has rapidly expanded into the more productive cover types on Steens Mountain, including mountain big sagebrush, aspen, and riparian. This pattern is similar to juniper woodland expansion throughout the western United States (Miller and Rose 1995, Miller and Rose 1999, Miller and Tausch 2001). The study area extended across 7,694 ha between 1,878 m to 2,319 m in elevation, and included a 2,464 ha prescribe burn conducted in the fall of 1999 by the Bureau of Land Management (BLM).

METHODS

Bird Surveys

Bird counts were conducted during the 2000 breeding season at 172 survey points that encompassed varying amounts and configurations of burned and unburned sagebrush steppe and juniper woodland. We generated a randomized, systematic grid of survey points in a Geographic Information System (GIS). Survey points were located 500-m apart to ensure independence of bird detections (Ralph et al. 1993). The grid was positioned using a random number generator to select coordinates for a point of origin within the study area. Unlike the mixed nature of juniper woodlands and sagebrush, aspen represents a distinct habitat type in the sagebrush steppe that supports a different bird community. To focus on sagebrush associated birds, we restricted our sampling and analyses to sagebrush and the sagebrush-juniper matrix, excluding all points that were located <100 m from aspen forest.

Each point was surveyed once from June 1 to 27 using fixed-radius point count methods (Ralph et al. 1993). After waiting at least 2 minutes upon arrival at a point, we recorded the presence of all birds seen or heard within 100 m during a 5-minute interval. Surveys were limited to the 4 hours following sunrise, on mornings with little wind (<15 km/h) and no precipitation.

Table 2.1. Local and landscape variables measured at sites and used to develop resource selection models for birds in sagebrush steppe on Steens Mountain, Oregon.

<i>Description</i>	<i>Variable</i>
Local scale (within 100 m)	
Percent area burned (%)	ABURN _{100m}
Percent area sagebrush (%)	ASAGE _{100m}
Density of juniper/mountain-mahogany trees (ha ⁻¹)	DJUNP _{100m}
Percent cover of shrubs within sagebrush area (%)	CSAGE _{100m}
Average height of sagebrush (cm)	HTSAGE _{100m}
Percent cover of grass (%)	CGRASS _{100m}
Index of sagebrush patchiness (no.)	PATCH _{100m}
Relative dominance of snowberry (1-5)	DOM _{100m}
Landscape scale (within 1 km)	
Percent area sagebrush within 1 km (%)	ASAGE _{1km}
Percent area juniper/mountain-mahogany trees within 1 km (%)	AJUNP _{1km}
Percent of area contained in largest patch sagebrush within 1 km (%)	LPI _{1km}
Edge density of sagebrush within 1 km (m/ha)	ED _{1km}

Local Habitat Measures

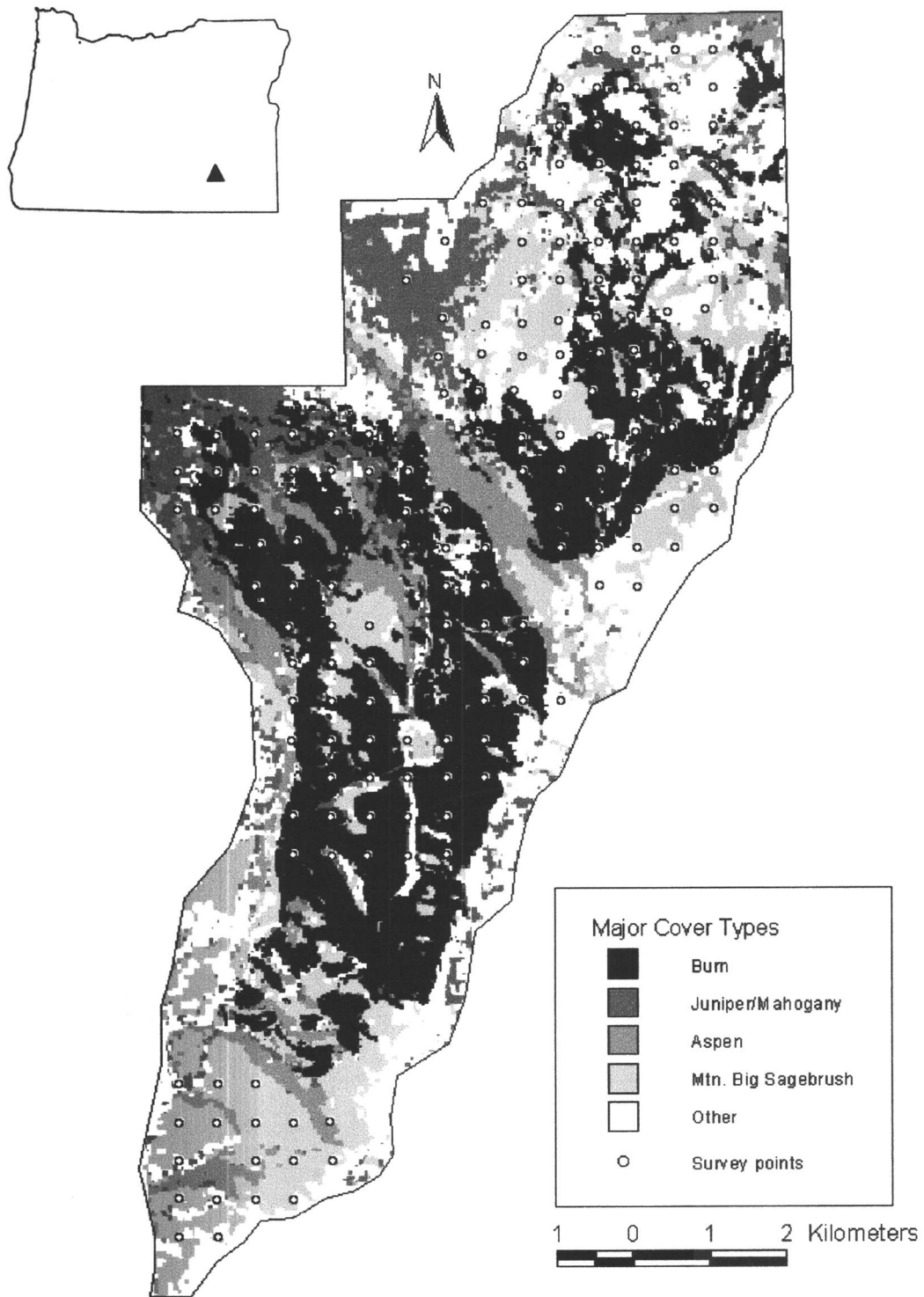
Local habitat characteristics were measured at each bird survey point from June-July 2000 (Table 2.1). Two parallel 200 m transects were positioned 25 m on either side of the point and were oriented on the same random compass bearing. We measured the proportion of each transect comprised of burn or mountain big sagebrush cover types. Percent cover of grass and percent cover of shrubs within the sagebrush cover type were calculated from ocular estimates taken along the transects. Prior to making ocular estimates, all surveyors calibrated their observations using the line-intercept method (Canfield 1941). For each transect, we also measured average sagebrush height and ranked shrub species dominance from 1-rare to 5-dominant. An index of sagebrush patchiness was measured as the

number of times the transects crossed from mountain big sagebrush to another cover type. Juniper and mountain-mahogany densities were obtained from counts of trees >1 m in height within 100-m radius of the point. Since mountain-mahogany occurred infrequently across the study area and was structurally similar to juniper, they were combined for analysis and will hereafter be referred to as juniper.

Landscape Habitat Measures

We used Landsat Thematic Mapper satellite images and aerial photographs to develop a GIS map of major cover types for the study area (Fig. 2.1). All images were spatially registered and corrected for geometric distortion (ERDAS 1999). Deciduous vegetation was classified from a satellite image taken 4 September 1999 using supervised classification methods and a maximum likelihood algorithm (ERDAS 1999). For classification of burned areas, we used the first satellite image available following the prescribed fire (20 October 1999), and digitized aerial photographs (scale 1:24,000) taken in August 2000. We combined vegetation and burn coverages to create a single map of major cover types that corresponded with our local scale habitat measures. Major cover types used in analysis were: (1) burn, (2) mountain big sagebrush, (3) juniper/mountain-mahogany woodland, (4) aspen forest, and (5) other. Resolution of the map was 25 m (resampled from 30 m pixel cells in the original Landsat TM images), therefore 25 m represented the smallest possible habitat patch. The Kappa coefficient for overall accuracy,

Figure 2.1. Location of Steens Mountain in Oregon, and map of major cover types in study area derived from satellite imagery and aerial photographs.



assessed with ground truth data not used for classification, was 80.16% (Congalton 1991).

Landscape metrics were calculated from the derived map of cover types within 1-km radius of each survey point using the spatial analysis program Patch Analyst (Elkie et al. 1999)(Table 2.1). Metrics at this scale were predictive of sagebrush bird occurrence in previous studies (Knick and Rotenberry 1995) and represented an area we felt was large enough to describe regional bird distributions.

Statistical Analysis

Resource selection models were developed for individual species from habitat characteristics measured at used and unused survey points (Design I/Sampling protocol C, Manly et al. 1995). Abundance of common species was modeled using Poisson regression (PROC GENMOD, SAS Institute 2000). When birds were rare, measures of abundance at points essentially described a binary response of present or absent. Therefore, we used logistic regression to model the probability of occurrence of less abundant species (PROC GENMOD, SAS Institute 2000). We measured relative abundance as the total number of detections of a given species at a point, and occurrence as one or more detections of that species at a point. The best-approximating model for each bird species was selected from a single suite of a priori models (Burnham and Anderson 1998).

Model Development

Prior to analyzing the data, we developed a suite of candidate models describing bird-habitat relationships that we deemed important based on existing biological information and our own experience. To account for possible multicollinearity, pairwise correlation was considered in the selection of variables. Models were developed for individual bird species from 12 variables at two spatial scales (local and landscape), and described: (1) amount burned, (2) amount of sagebrush, (3) characteristics of sagebrush (height, percent cover, etc.), (4) configuration of sagebrush, and (5) amount of juniper encroachment (Table 2.1). Fire influences the availability and structure of plant communities, which can in turn effect the distribution and abundance birds (MacArthur and MacArthur 1961, Cody 1985). The importance of sagebrush cover is well documented for sagebrush-obligate birds such as the Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus*) (Wiens and Rotenberry 1981, Knopf et al. 1990, Knick and Rotenberry 1995). Relationships with habitat characteristics, including shrub height and cover, have also been documented for bird species in the sagebrush steppe (Wiens and Rotenberry 1981, Knopf et al. 1990, Knick and Rotenberry 1995, Vander Haegen et al. 2000). Recent studies suggest many sagebrush obligates are also sensitive to decreases in size of sagebrush patches and increases in edge associated with fire (Knick and Rotenberry 1995, Vander Haegen et al. 2000). There is less information about how sagebrush birds respond to increasing juniper density. However, previous studies suggest sagebrush birds are

negatively impacted by juniper encroachment into sagebrush habitat (Reinkensmeyer 2000). We included contrasting models for species when habitat associations among previous studies were conflicting. For example, vesper sparrows (*Pooecetes gramineus*) are typically associated with grassland openings in sagebrush (Paige and Ritter 1999), but some studies have detected a positive relationship between vesper sparrows and increasing shrub cover (Wiens and Rotenberry 1981, Vander Haegen et al. 2000). We also considered alternative forms of variables (e.g. squared terms) for species with habitat associations suggesting a non-linear relationship with specific variables. In all, we developed 77 candidate models, including a null model with no variables and a global model (Appendix A). The best approximating model for each individual bird species was selected from this single suite of candidate models. For each species, the global model was tested for lack of fit using a drop-in-deviance chi-square test (Ramsey and Schafer 1997). The fit of Poisson models were also assessed graphically with normal probability plots and graphs of the residuals.

Model Selection

The candidate models were ranked by their ability to explain the data using Akaike's Information Criterion modified for small sample size (AIC_c) (Burnham and Anderson 1998).

$$AIC_c = -[2\log(L(\theta))] + 2K + \frac{2K(K+1)}{n-K-1}$$

Where $\log(L(\theta))$ is the natural logarithm of the likelihood function of the model parameters; K is the number of estimable parameters in the model; and n is the sample size. For species modeled using Poisson regression, a single variance inflation factor was estimated from the global model to correct for potential overdispersion (Burnham and Anderson 1998).

The model (i) with the minimum AIC_c value was selected as the best-approximating model to the data. Models with AIC_c values <2 units from the best-approximating model were considered competing models, and given equal importance, while those >4 were considered a marginal fit to the data (Burnham and Anderson 1998). We used Akaike weights (w) to assess selection uncertainty among competing models.

RESULTS

Prescribed Burn

The prescribed burn was approximately 7,695 ha in size, and covered 32% of the study area. The fire burned unevenly, creating a mosaic of burned and unburned sagebrush and a wide range of sagebrush patch sizes (Table 2.2). Within burned patches, almost all vegetation was consumed by fire. At survey points, average percent shrub cover in unburned sagebrush was 13.00% (S.D.=6.68), while

in burned areas average shrub cover was only 2.15% (S.D.=2.39). Most of the shrubs measured at the survey points were new growth following the fire.

Table 2.2. Summary statistics for local and landscape variables measured in 2000 at 172 survey points located on Steens Mountain, Oregon.

<i>Variables^a</i>	<i>Mean ± S.D.</i>
ABURN _{100m}	40.00 ± 37.80
ASAGE _{100m}	51.74 ± 34.15
DJUNP _{100m}	10.28 ± 26.63
CSAGE _{100m}	11.26 ± 7.24
HTSAGE _{100m}	60.29 ± 18.91
CGRASS _{100m}	5.35 ± 4.45
PATCH _{100m}	1.55 ± 1.10
DOM _{100m}	1.45 ± 1.22
ASAGE _{1km}	22.38 ± 14.07
AJUNP _{1km}	9.58 ± 12.12
LPI _{1km}	13.08 ± 14.46
ED _{1km}	66.60 ± 18.41

^a See Table 2.1 for descriptions of habitat measures.

Bird Occurrence

During the summer of 2000, observers recorded 1,525 individuals representing 49 species at the survey points. We concentrated our analysis on Brewer's sparrows, sage thrashers, green-tailed towhees (*Pipilo chlorurus*), and vesper sparrows. We selected these species because they breed in sagebrush steppe, are of management concern, and were detected at >10% of survey points. Brewer's sparrows and vesper sparrows were the two most common species and together made up over 50% of the total detections.

Resource Selection Models

Brewer's sparrows were detected at 154 survey points. The AIC_c -selected best model relating Brewer's sparrow abundance to habitat characteristics included both local and landscape-scale measures. Brewer's sparrow abundance increased with increasing area of sagebrush and sagebrush height at the site, and decreased with the amount of juniper within 1 km (Table 2.3; Fig. 2.2). Model {AJUNP_{1km} + ASAGE_{100m} + ED_{1km}} was a close competitor based on Akaike weights (Table 2.4), providing evidence that Brewer's sparrow abundance was also positively associated with the amount of sagebrush edge within 1 km.

Table 2.3. Coefficients in AIC_c -selected best approximating model fitted by Poisson (abundance) or logistic (occurrence) regression for birds in sagebrush habitats on Steens Mountain, Oregon.

<i>Variable</i>	<i>Parameter Estimate</i>	<i>S.E.</i>	<i>95% C.I.</i>
Brewer's sparrows (abundance)			
ASAGE _{100m}	0.007	0.001	0.005, 0.010
HTSAGE _{100m}	0.010	0.003	0.005, 0.015
AJUNP _{1km}	-0.043	0.006	-0.056, -0.031
Vesper sparrows (abundance)			
ASAGE _{100m}	-0.006	0.002	-0.010, -0.002
PATCH _{100m}	0.165	0.051	0.061, 0.262
DJUNP _{100m}	-0.020	0.005	-0.031, -0.010
Green-tailed towhees (occurrence)			
ASAGE _{1km}	0.064	0.017	0.032, 0.098
ED _{1km}	-0.025	0.013	-0.052, 0.000*
AJUNP _{1km}	0.212	0.052	0.052, 0.115
(AJUNP _{1km}) ²	-0.0034	0.001	-0.006, -0.001
Sage thrashers (occurrence)			
LPI _{1km}	0.049	0.014	0.023, 0.079
DJUNP _{100m}	-0.057	0.021	-0.11, -0.023

* 95% C.I. includes zero.

Table 2.4. Rankings based on AIC_c for a priori models used to relate bird abundance/occurrence to habitat features in sagebrush steppe on Steens Mountain, Oregon ($\Delta AIC_c < 4$ and global model shown).

<i>Model</i>	<i>AIC_c</i>	<i>K</i>	ΔAIC_c	<i>w</i>
Brewer's sparrow (abundance)				
AJUNP _{1km} + ASAGE _{100m} + HTSAGE _{100m}	-189.44	4	0.00	0.48
AJUNP _{1km} + ASAGE _{100m} + ED _{1km}	-188.80	4	0.64	0.35
AJUNP _{1km} + ASAGE _{100m} + CSAGE _{100m}	-187.17	4	2.27	0.15
Global model	-181.80	15	7.66	0.01
Vesper sparrow (abundance)				
DJUNP _{100m} + ASAGE _{100m} + PATCH _{100m}	206.98	4	0.00	0.31
DJUNP _{100m} + ASAGE _{100m} + PATCH _{100m} + HTSAGE _{100m}	208.36	5	1.38	0.16
DJUNP _{100m} + ASAGE _{100m} + PATCH _{100m} + CGRASS _{100m}	208.89	5	1.91	0.12
DJUNP _{100m} + ASAGE _{100m} + PATCH _{100m} + CSAGE _{100m}	209.08	5	2.11	0.11
Global model	219.88	15	12.90	0.0005
Green-tailed towhee (occurrence)				
AJUNP _{1km} + (AJUNP _{1km}) ² + ASAGE _{1km} + ED _{1km}	172.91	5	0.00	0.22
AJUNP _{1km} + (AJUNP _{1km}) ² + ASAGE _{1km}	174.29	4	1.38	0.11
AJUNP _{1km} + (AJUNP _{1km}) ² + ASAGE _{1km} + HTSAGE _{100m}	174.43	5	1.52	0.10
AJUNP _{1km} + (AJUNP _{1km}) ² + ASAGE _{1km} + DOM _{100m}	175.11	5	2.20	0.07
DJUNP _{100m} + (DJUNP _{100m}) ² + ASAGE _{1km}	175.15	4	2.24	0.07
DJUNP _{100m} + (DJUNP _{100m}) ² + ASAGE _{1km} + HTSAGE _{100m}	175.34	5	2.43	0.07
DJUNP _{100m} + (DJUNP _{100m}) ² + ASAGE _{1km} + ED _{1km}	175.41	5	2.50	0.06
AJUNP _{1km} + (AJUNP _{1km}) ² + ASAGE _{10m} + CSAGE _{100m}	176.20	5	3.29	0.04
DJUNP _{100m} + (DJUNP _{100m}) ² + ASAGE _{1km} + PATCH _{100m}	176.52	5	3.61	0.04
DJUNP _{100m} + (DJUNP _{100m}) ² + HTSAGE _{100m} + LPI _{1km}	176.74	5	3.83	0.03
Global Model	181.67	15	8.76	0.003
Sage thrasher (occurrence)				
DJUNP _{100m} + LPI _{1km}	201.73	3	0.00	0.38
DJUNP _{100m} + LPI _{1km} + ASAGE _{100m}	203.58	4	1.85	0.15
DJUNP _{100m} + LPI _{1km} + CSAGE _{100m}	203.78	4	2.04	0.14
DJUNP _{100m} + LPI _{1km} + HTSAGE _{100m}	203.83	4	2.10	0.13
Global model	213.09	15	11.36	0.001

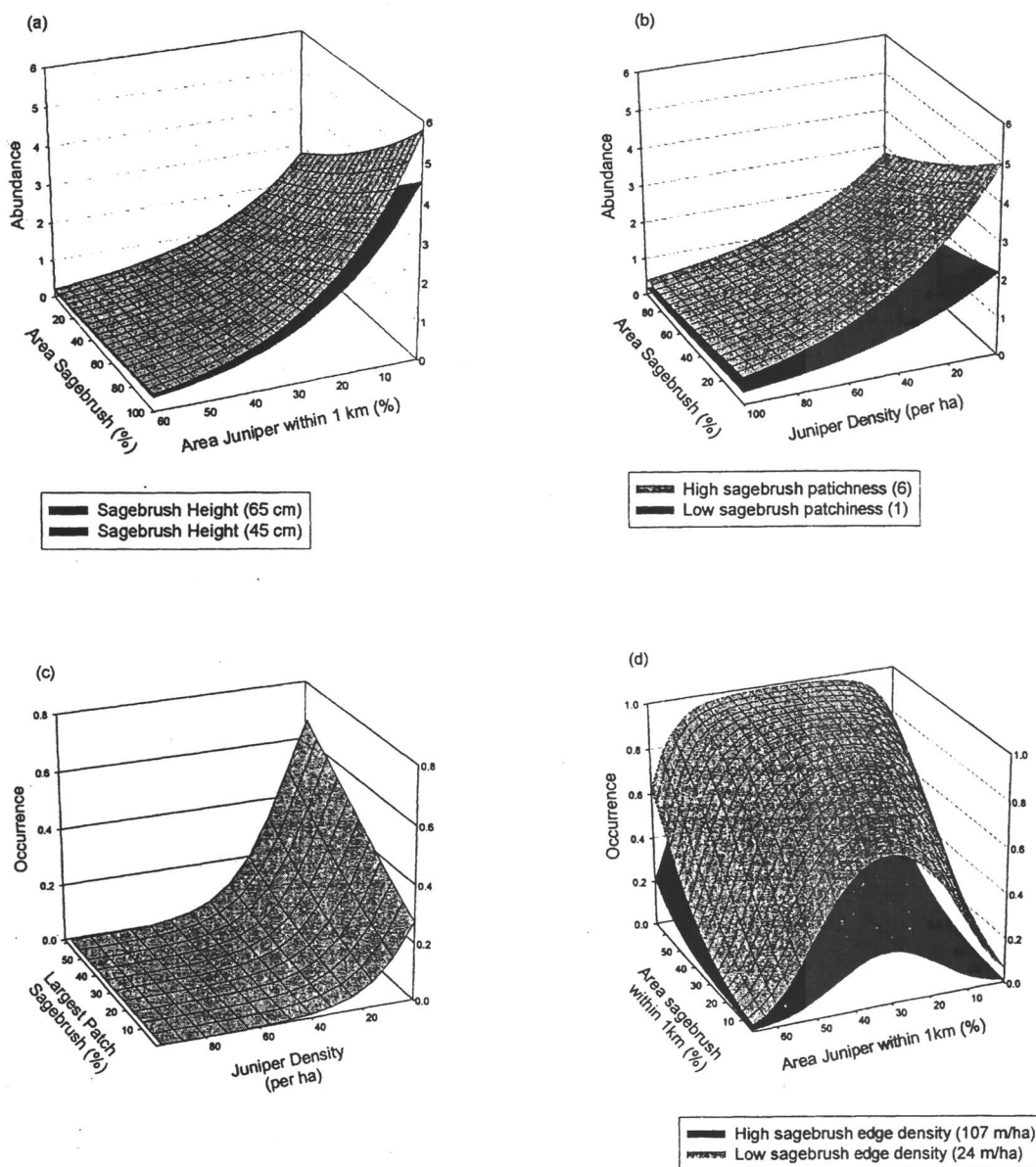
We observed vesper sparrows at 126 survey points. There were four competing models explaining vesper sparrow abundance (Table 2.4), all of which contained only local scale variables. We retained the AIC_c -selected best model {DJUNP_{100m} + ASAGE_{100m} + PATCH_{100m}} based on Akaike weights indicating that this

model was twice as likely to be the best-fitting model as the next ranked model.

The best-approximating model predicted vesper sparrow abundance was negatively associated with tree density and sagebrush area, and positively associated with sagebrush patchiness (Table 2.3; Fig. 2.2). However, the competing models also suggest an association with decreasing sagebrush height and shrub cover, and/or increasing grass cover.

Green-tailed towhees were observed at 44 points. We analyzed 109 models that included the 66 a priori models and 43 models with a quadratic form for $DJUNP_{100m}$ and $AJUNP_{1km}$. We included the quadratic form based on findings from previous studies and the fit of the global model (Knopf et al. 1990, Franklin et al. 2000). The best approximating model for green-tailed towhee occurrence was $\{AJUNP_{1km} + (AJUNP_{1km})^2 + ASAGE_{1km} + ED_{1km}\}$ based on AIC_c . The model indicates that the probability of green-tailed towhee occurrence increased as area of sagebrush increased and sagebrush edge density decreased. The model also shows a curve-linear relationship with area of juniper within 1 km, such that the probability of occurrence peaked at approximately 33% and then declined with increasing juniper (Table 2.3; Fig. 2.2). When the density of sagebrush edge was high, no green-tailed towhees were predicted to occur at any range of the other two variables. No single model had strong support based on Akaike weights (Table 2.4). However, there was a distinct pattern in the model ranking, such that the first four models all included landscape scale measures of area juniper and area of sagebrush, varying only in the addition of edge density, sagebrush height, or

Figure 2.2. Influence of habitat characteristics on predicted abundance of (a) Brewer's sparrows and (b) vesper sparrows, and occurrence of (c) sage thrashers and (d) green-tailed towhees. Estimates based on AIC_c-selected best model for each species. (Note: maximum and minimum recorded values are shown as separate surfaces for models containing 3 variables).



snowberry (*Symphoricarpos albus*) dominance to the model. The next three models were identical except that the landscape measure of area of juniper was replaced with juniper density within 100 m. All models containing a quadratic form for juniper were an improvement over the linear model based on minimum AIC_c values.

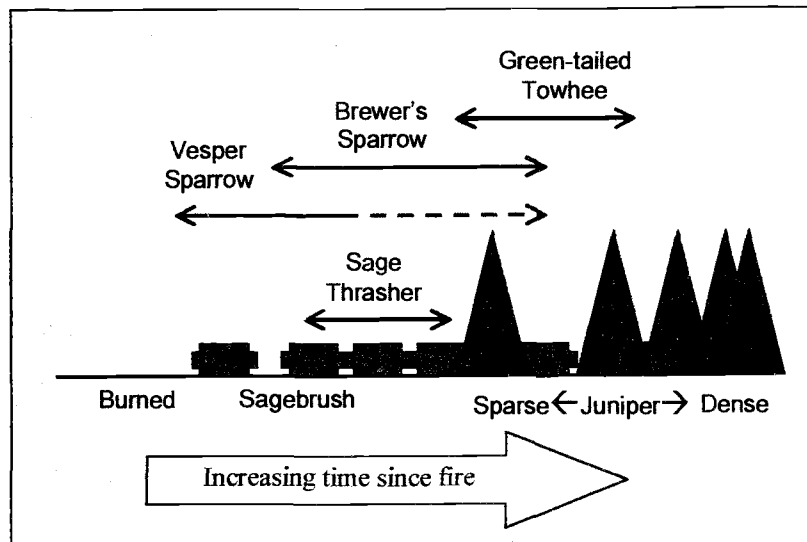
We detected sage thrashers at 48 survey points. All best models included local juniper density and the largest sagebrush patch within 1km (Table 2.4). Local area of sagebrush, shrub cover, and sagebrush height explained additional variation in sage thrasher occurrence. The best approximating model {DJUNP_{100m} + LPI_{1km}} indicated a sharp decrease in the probability of sage thrasher occurrence with increasing juniper density and an additional decline in occurrence with decreasing sagebrush patch size within 1 km (Table 2.3; Fig. 2.2).

DISCUSSION

The bird species we examined had distinct relationships with vegetation structure and composition. Vesper sparrows were most abundant in patchy, open sagebrush stands, while Brewer's sparrow numbers were greater in areas with more sagebrush habitat and sage thrashers favored large patches of sagebrush. Green-tailed towhees occurred most often in areas of mixed sagebrush and juniper. This study provides a snapshot of bird species relationships with habitat characteristics at a static point in time. However, ecological processes occurring through time shape variation in habitats present in the landscape. Areas with low-density

juniper represent an early stage in the process of juniper encroachment, while areas with high juniper density represent late-successional woodlands. Furthermore, burns, sagebrush, and juniper woodlands represent habitats along a trajectory from recently burned to increasing time since fire, and individual bird species were associated with habitat conditions at different points along this trajectory (Fig. 2.3).

Fig. 2.3. Habitat associations of sagebrush birds along a trajectory from recently burned on the left to increasing time since fire on the right. Arrows represent approximate ranges of suitable habitat (dashed line indicates that vesper sparrows were associated with patchy sagebrush but were not highly sensitive to low densities of juniper).



Because fire in this system reduces and fragments sagebrush habitat, our results suggest that fire has an immediate negative impact on many birds in a high-elevation sagebrush community. Yet, our models demonstrate that the species we considered are also dependent on habitat maintained by periodic burning. Unlike

low-elevation areas, where fire frequency has been elevated through conversion to introduced annual grasses over the last century (Young and Evans 1978, Rotenberry 1998), the absence of fire has changed the structure and function of more productive high-elevation sagebrush communities adapted to frequent disturbance (Miller and Rose 1999). Perhaps the greatest change associated with fire suppression in these sagebrush communities is the encroachment of fire-intolerant juniper species. Our models quantify the sensitivity of sagebrush obligate birds to increases in juniper, and define previously unidentified upper limits of habitat suitability for green-tailed towhees. Moreover, our findings demonstrate that juniper and sagebrush characteristics are equally important, even for sagebrush obligates like Brewer's sparrows and sage thrashers.

Effects of Juniper Encroachment

Juniper had a consistently strong influence on the sagebrush birds in our study. Perhaps most striking was the sharp decline in sage thrasher occurrence predicted at low juniper densities. Juniper encroachment decreases sagebrush cover at high densities (Bunting 1987, Miller et al. 2000), which may explain the eventual decline in green-tailed towhees, as sagebrush habitat disappears. The sensitivity of the other species, such as the sage thrasher, to low densities of juniper suggests that even the presence of juniper decrease habitat suitability for these birds. Juniper support avifauna that may compete with sagebrush birds (Blair 1996). In addition, predators and brood parasites often increase along woodland

edges (Johnson and Temple 1990). In central Oregon, Reinkensmeyer (2000) detected significantly more brown-headed cowbirds in areas with western juniper than sagebrush communities without juniper. Similar to our findings, in previous studies fewer shrub-nesting birds were detected in sagebrush with juniper than without juniper (Maser et al. 1984, Rosenstock and Van Riper 2001). Reinkensmeyer (2000) detected significantly higher Brewer's sparrow and sage thrasher densities in sagebrush than in mid- and late-successional juniper woodlands. However, the relationship between green-tailed towhees and juniper is not consistent across previous studies. Reinkensmeyer (2000) detected more green-tailed towhees in grasslands with no juniper than other cover types. Whereas, a regional study conducted by Knopf et al. (1990) indicated that green-tailed towhees most often occur at ecotones between sagebrush and other large shrub or tree communities.

In addition, juniper woodlands within 1 km influenced landscape scale distributions for two species, the green-tailed towhee and Brewer's sparrow. The stronger relationship between sage thrasher occurrence and local tree density may be more attributable to the species' high degree of sensitivity to the presence of low-density juniper, which were not measured at the coarse resolution of the landscape analysis, than a relationship with scale.

Response to Sagebrush Habitat

While the amount of burned habitat poorly described sagebrush bird populations, the amount of unburned sagebrush was included in the best models for every species we considered. The importance of sagebrush to these species is consistent with findings documented in previous studies (Wiens and Rotenberry 1981, Knopf et al. 1990, Knick and Rotenberry 1995). Brewer's sparrows and sage thrashers are considered sagebrush-obligates (Wiens and Rotenberry 1981) and green-tailed towhees have been termed a near-obligate (Braun et al. 1976). Because fire typically removes most of the shrub layer in this ecosystem, our results indicate that recent burns will negatively impact these bird species. In contrast, vesper sparrows, often considered a grassland species, were more abundant in areas with patchy sagebrush and less total sagebrush area—conditions created by fire. High vesper sparrow densities have been recorded in recent burns (Petersen and Best 1987, Reinkensmeyer 2000), however others have found positive associations between vesper sparrow abundance and shrub cover (Wiens and Rotenberry 1981, Vander Haegen 2000).

Importance of Landscape Pattern

Sagebrush birds also showed sensitivity to the configuration of sagebrush habitat in the surrounding landscape. Sage thrashers selected habitats with larger patches of intact sagebrush. Similarly, in a study conducted in southeastern Idaho, sage thrashers occurred more often in areas with higher spatial similarity of habitat

within 1 km (Knick and Rotenberry 1995). In contrast, Vander Haegen et al. (2000) found a negative relationship between sage thrashers and increasing sagebrush within 5-km. Green-tailed towhees occurred in areas with less sagebrush edge density, describing areas of sagebrush less fragmented by other cover types. Interestingly, Brewer's sparrow abundance, while positively associated with the amount of sagebrush at a local scale, showed some evidence of a positive relationship with sagebrush edge density in the surrounding landscape. This is difficult to explain in a sagebrush obligate species, and contrary to the findings of Knick and Rotenberry (1995) who reported Brewer's sparrows occurring more often in larger sagebrush patches. Vesper sparrows were the only species we examined without evidence of association with habitat at the landscape scale. Although sagebrush birds are subject to predation and nest parasitism (Reynolds 1981, Vander Haegen and Walker 1999), the mechanisms that drive sagebrush bird sensitivity to landscape configuration and composition are not clear (Knick and Rotenberry 1995). It is unlikely that the generalist predator species associated with shrublands (corvids, snakes, small mammals) are limited to edge habitat as is known to occur in forest habitats (Rotenberry 1998).

MANAGEMENT IMPLICATIONS

Any management action that reduces available sagebrush habitat for sagebrush obligate birds threatened by widespread habitat loss in lower elevation

sagebrush communities is controversial. However, our results indicate that these species depend on periodic fire to maintain favorable habitat conditions in high-elevation sagebrush landscapes. Even minimal juniper encroachment has major consequences for sagebrush birds. Furthermore, the effects of juniper expansion are potentially permanent. As woodlands develop, sagebrush cover declines until a threshold is crossed and the probability of a fire of sufficient intensity to remove juniper becomes unlikely (Bunting 1987, Miller et al. 2000). Therefore juniper control should be a management priority in these areas. There are alternative methods for controlling juniper, such as chaining or cutting, but it is widely accepted that the best long-term approach to ecosystem maintenance is restoring natural ecosystem processes such as fire (Pickett and White 1985, Miller et al. 2000).

The negative effects of burning may be minimized through incomplete burning that resembles the naturally spotty fires that occurred historically and retain residual unburned sagebrush within burns. For example, Brewer's sparrows occurred in areas with even a few remaining unburned shrubs, and other species like the vesper sparrow may benefit from patchy sagebrush. Previous studies have also documented minimal changes in sagebrush obligate communities with incomplete removal of sagebrush from a site (Tiagwad et al. 1982, Wiens and Rotenberry 1985, Petersen and Best 1987). Unburned islands of sagebrush act as refugia, providing a source of sagebrush seeds and harboring habitat characteristics necessary for associated birds (Smith 2000). Prescribed burning can be conducted

under weather conditions that increase the patchiness of burns, whereas wildfires tend to occur under severe conditions that, due to the long interval without fire in this system, usually result in a more complete burn. Therefore, prescribed fire is preferable to a hands-off approach until the natural heterogeneity of the system is restored. Features at multiple scales influence habitat use by sagebrush birds, and some species like the sage thrasher are sensitive to sagebrush fragmentation. Hence, it is also important to reserve larger tracts of unburned sagebrush. Long-term response by bird communities to burning is still unknown. Information on the suitability of older burns as habitat will be necessary to further guide management in the use of fire in these systems. Because bird occurrence and abundance are not always indicators of habitat quality (Van Horne 1983), the influence of fire on survival and reproductive success of sagebrush birds needs research attention.

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Chapter 3

Relationships Between Fire and Avian Diversity in a Sagebrush Steppe Landscape

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ABSTRACT

We examined patterns of bird diversity in a high elevation sagebrush steppe landscape one year following prescribed fire on Steens Mountain in southeastern Oregon. During the 2000 breeding season, we conducted point counts of songbirds at 205 sites across a mosaic of burned and unburned habitat types including sagebrush (*Artemisia* spp.), aspen (*Populus tremuloides*) forest, and Western juniper (*Juniperus occidentalis*) woodland. Bird and habitat data collected at the field sites were combined with landscape data derived from satellite imagery and aerial photographs to identify important predictors of bird species richness and diversity (H'). We used Akaike's Information Criterion (AIC_c) to select the best-approximating model for each bird diversity measure from a single suite of a priori candidate models. Both measures of bird diversity were predicted to have an asymptotic relationship with increasing area aspen and juniper density, such that most gains in diversity were made at low levels of aspen and juniper. A positive relationship with increasing habitat heterogeneity was also predicted for bird species richness and diversity (H') as measured by landscape habitat diversity (H') and local habitat richness, respectively. Within the study area, habitats most critical for supporting avian diversity were among those least impacted by prescribed fire (less than 10% of aspen forest was burned following prescribed fire, while over 50% of sagebrush burned). Furthermore, our models indicate that most bird diversity in this system is maintained by small patches of aspen and the presence of even a few juniper. Our results suggest that prescribed fire had little

negative influence on avian diversity, and in the long-term periodic fire may support avian diversity by increasing habitat heterogeneity and maintaining critical aspen habitat.

INTRODUCTION

The importance of natural disturbance regimes to the maintenance of biological diversity has received recent attention by conservation scientists (Pickett & White 1985; Meffe & Carroll 1994; Noss & Cooperrider 1994; Baydack et al. 1999). Empirical evidence increasingly supports the premise that natural disturbance, and the spatial heterogeneity it creates, allows species with different life histories to more precisely subdivide resources (Christensen 1988; Petraitis et al. 1989; Reice 1994). Furthermore, recurring natural disturbances maintain landscape conditions that species have adapted to over evolutionary time (Agee 1993; Perry & Amaranthus 1997). Given the close relationship of species and their habitat to natural disturbance regimes, management objectives aimed at maintaining ecosystem integrity may be the best long-term approach to conserving biodiversity (Noss 1983; Walker 1992; Aplet & Keeton 1999). This coarse-filter approach assumes that providing the appropriate mix of ecological communities based on an understanding of historic disturbance regimes will maintain biodiversity without requiring management for individual species (Kaufmann et al. 1994; Aplet & Keeton 1999). However, the biological implications of this strategy are yet to be adequately determined (Campa III et al. 1999).

Fire prone landscapes, such as the sagebrush steppe of western United States, represent a particular challenge to land managers attempting to enhance biodiversity by restoring historic disturbance regimes (DellaSala et al. 1996). Reintroducing fire risks destruction of critical habitats in areas already suffering habitat loss and degradation due to anthropogenic disturbances like agricultural conversion and livestock grazing (Paige & Ritter 1999). Yet, the continued absence of fire may result in even greater long-term harm to native plant and animal species adapted to the natural disturbance regime (Reice 1994).

Fire frequency and behavior is influenced by topography and climate, and is highly variable across sagebrush communities (Christiensen 1992). In landscapes dominated by relatively productive mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) communities, fires were historically frequent (every 15-25 years) but patchy in distribution, creating a shifting mosaic of habitats at different stages of recovery following fire (Miller & Rose 1999). Human activities over the last century have exerted a profound influence on the region's fire regimes, particularly in mountain big sagebrush communities, where overgrazing of livestock and suppression practices have virtually eliminated fire from the system (Burkhardt & Tisdale 1976; Miller et al. 1994). In the absence of fire, early-successional grasslands and aspen forests (*Populus tremuloides*) have declined (Miller et al. 1994; Wall et al. 2001), while fire-intolerant juniper (*Juniperus* spp.) woodlands have increased in density and expanded into surrounding habitats (Burkhardt & Tisdale 1976; Miller & Rose 1995, 1999; Wall et al. 2001).

Prescribed fire is the primary tool used to restore natural disturbance processes to sagebrush steppe altered by fire suppression.

Changes in the structure and availability of habitats due to fire have potentially important consequences for avian diversity in sagebrush steppe landscapes. There is growing concern over losses of avian diversity across the continent (Martin & Finch 1993), and many species breeding in the sagebrush steppe appear especially threatened due to widespread habitat loss and degradation (Paige & Ritter 1999). In this shrub-dominated region, less common woody habitats, such as riparian vegetation and aspen forest, may also provide critically important habitat for birds (Carothers 1974; Knopf et al. 1988; Saab et al. 1995). Although riparian and aspen habitats make up <1% of land area in the semi-arid West, together they contain the highest number of bird species (Winternitz 1980; Knopf et al. 1988).

The purpose of this study was to examine relationships between bird diversity and habitat characteristics in an ecosystem adapted to frequent fire disturbance. In particular, we sought to determine which habitat types were critical to bird species richness and diversity, and how the availability and configuration of these habitats across the landscape influenced patterns of avian diversity.

STUDY AREA

The study was conducted on Steens Mountain, an isolated fault-block escarpment in southeastern Oregon. The study area extends from 1,878 m to 2,319

m in elevation and includes a prescribed burn conducted in the fall of 1999 by the Bureau of Land Management (BLM). The climate in this region is cool and semi-arid (Hansen 1956; Miller et al. 1994). Annual precipitation ranges from 25 cm at the base to almost 36 cm at higher elevations and falls mainly during winter.

Indicative of high-elevation areas in the Great Basin, the landscape is comprised of diverse vegetation communities. Mountain big sagebrush dominates, with low sagebrush (*A. arbuscula*) occurring in shallow soils. Isolated aspen stands form narrow bands along north-facing aspects, while western juniper (*J. occidentalis*) woodlands stretch discontinuously between 1450 and 2100 m (Miller & Rose 1995). Scattered stands of curleaf mountain-mahogany (*Cercocarpus ledifolius*) are also present. Riparian habitats include willow-dominated (*Salix* spp.) vegetation along perennial creeks and scattered wet meadows.

METHODS

Avian Community Sampling

We conducted fixed-radius point count surveys (Ralph et al. 1993) during the 2000 breeding season across a range in composition and configurations of burned and unburned habitat types. Using a Geographic Information System (GIS), we generated a randomized, systematic grid of 205 survey sites that extended across the study area in an effort to sample all habitats in proportion to their availability in the landscape. The grid was positioned using a random number

generator to select coordinates for a site of origin within the study area. Survey sites were located 500-m apart to ensure independence of bird detections (Ralph et al. 1993). Each site was surveyed once from June 1 to 27 during the 4 hours following sunrise on mornings with little wind (<15 km/h) and no precipitation. Observers waited > 2 min to reduce disturbance before recording the presence of all birds seen or heard during a 5 min interval within 100 m of the survey site (Ralph et al. 1993).

Habitat Measures

Management of ecological processes at appropriate scales is essential for maintaining biodiversity in disturbance-adapted ecosystems (Noss 1983; Campa III et al. 1999). Furthermore, habitat features at more than one spatial scale may influence bird assemblages (Wiens et al. 1987). At the local scale, fire can significantly alter habitat suitability by changing resource availability and the physical environment (Agee 1993). At broad scales, fire produces a mosaic of disturbance patches across the landscape (Pickett & White 1985), and the spatial patterns of these patches may exert a strong influence on the abundance and distribution of bird populations (Dunning et al. 1992; Freemark et al. 1995). Therefore we examined avian relationships with habitat at both local and landscape scales.

Table 3.1. Local and landscape variables used in a priori models relating bird species richness and diversity to habitat characteristics on Steens Mountain, Oregon.

<i>Description</i>	<i>Variable</i>
Local scale (within 100 m)	
Percent area burned (%)	ABURN _{100m}
Percent area sagebrush (%)	ASAGE _{100m}
Percent area aspen (%)	APOTR _{100m}
Density of juniper/mountain-mahogany trees (ha ⁻¹)	DJUNP _{100m}
Average height of sagebrush (cm)	HTSAGE _{100m}
Average height of primary aspen canopy (m)	HTPOTR _{100m}
Percent cover of shrubs within sagebrush area (%)	CSAGE _{100m}
Number of cover types	RICH _{100m}
Landscape scale (within 1 km)	
Percent area burned within 1 km (%)	ABURN _{1km}
Percent area sagebrush within 1 km (%)	ASAGE _{1km}
Percent area aspen within 1 km (%)	APOTR _{1km}
Percent area juniper/mountain-mahogany within 1 km (%)	AJUNP _{1km}
Sagebrush edge density within 1 km (m/ha)	ED _{1km}
Cover type diversity (Shannon's Index)	SDI _{1km}

Local Measures

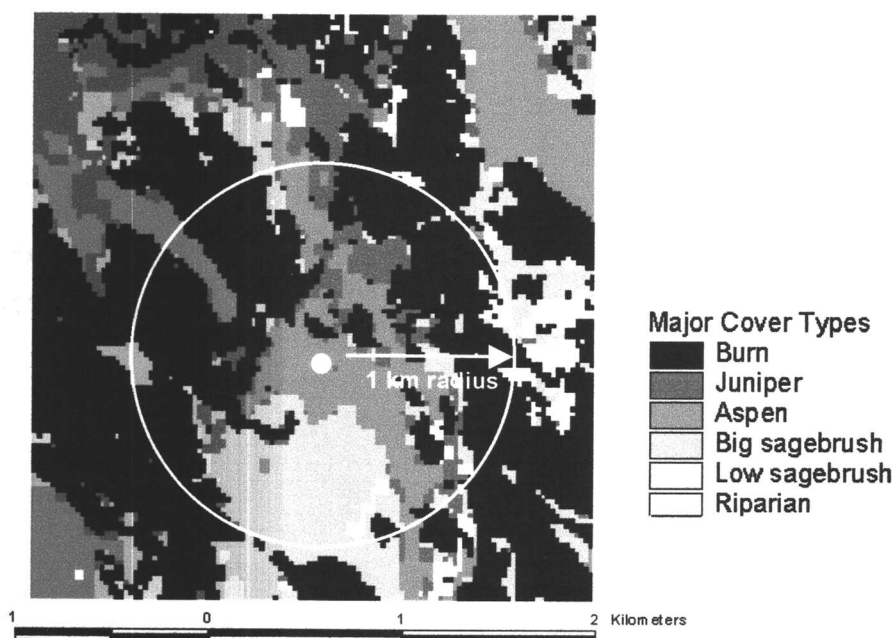
Local habitat characteristics were measured at each bird survey site from June-July 2000 (Table 3.1). Two parallel 200 m transects were positioned 25 m on either side of the site and were oriented on the same random compass bearing. We measured the proportion of each transect comprised of major habitat types including burn, sagebrush, riparian, and aspen. The average height of sagebrush and aspen were also recorded along the transects. Following calibration using the line-intercept method, observers made ocular estimates of shrub cover along the transects (Canfield 1941). Juniper and mountain-mahogany densities were calculated using counts of trees >1 m in height within 100-m radius of the survey

site. Since mountain-mahogany occurred infrequently across the study area and was structurally similar to juniper, they were combined for analysis and will hereafter be referred to as juniper.

Landscape Measures

We derived a digital map of major cover types from Landsat Thematic Mapper satellite imagery and aerial photography (Noson 2002). Deciduous vegetation was classified from a satellite image taken 4 September 1999 (ERDAS 1999). For classification of burned areas, we used the first satellite image available following the prescribed fire (20 October 1999), and digitized aerial photographs (scale 1:24,000) taken in August 2000. We then combined vegetation and burn coverages to create a single digital map consisting of 7 major cover types (Fig. 3.1): (1) burn, (2) mountain big sagebrush, (3) low sagebrush, (4) riparian/wet meadow, (5) aspen forest, (6) juniper woodland, and (7) other. Classification accuracy of the cover types was 80.16% (Kappa coefficient). Resolution of the map was 25 m (resampled from 30 m pixel cells in the original Landsat TM images).

Figure 3.1. Example of cover types derived from satellite imagery and aerial photography on Steens Mountain, Oregon. The small circle is centered on a survey site and represents local scale sampling within 100 m; the large circle shows the 1-km radius within which landscape metrics were calculated.



Measures of landscape pattern were calculated from the GIS map of cover types using the spatial analysis program Patch Analyst (Elkie et al. 1999). Landscape metrics were measured within a 1-km radius area centered at each survey site to encompass surrounding landscape features likely to affect regional bird distributions, and because the 1-km scale was associated with bird occurrence in sagebrush steppe habitats in Idaho (Knick & Rotenberry 1995). We calculated area of burn, big sagebrush, juniper, and aspen, the Shannon's diversity index for all cover types, and sagebrush edge density (Table 3.1).

Statistical Analysis

We fit statistical models to two measures of bird assemblage diversity: species richness (the total number of species detected at each site), and a combined measure of species richness and evenness (Shannon's diversity index H'). We modeled the relationship between species richness and habitat characteristics using Poisson regression (PROC GENMOD, SAS Institute 2000). Calculated diversity (H') was modeled using multiple linear regression (PROC REG, SAS Institute 2000). The best-approximating model for each measure of bird diversity was selected from a single suite of candidate models developed prior to data analysis (Burnham & Anderson 1998).

Model Development

We developed 67 a priori models relating bird diversity to habitat characteristics based on existing literature and our own experience (Appendix B). Models were comprised of combinations of 14 habitat variables and described alternative hypotheses for relationships between bird diversity and habitat. To account for possible multicollinearity, pairwise correlation was considered in the selection of variables. We hypothesized that the most important predictors of diversity across the landscape would be: (1) amount of fire disturbance, (2) availability of one or a few key habitat types, (3) quality of key habitats as measured by vegetation structure and composition, (4) diversity of habitat types, (5) degree of habitat fragmentation/mixing, or (6) a combination of these. Previous

studies in sagebrush-dominated regions have documented increases in bird species richness and shifts in species abundances following prescribed fire (Tiagwad et al. 1982; Petersen & Best 1987). We predicted that the dominant cover type, mountain big sagebrush, would be important to maintaining bird diversity in the system. However, woody habitats with high structural complexity, such as riparian and aspen habitats, contain the highest biodiversity in semi-arid habitats (Knopf et al. 1988), so we expected the presence of these habitat types were also important. Since riparian habitats with vertical woody structure were rare, we focused our analysis on aspen as the habitat most likely to contain the most bird species. We also selected measures of sagebrush and aspen habitat that described local scale vegetation composition and structure, since high avian diversity has been found in areas with high structural complexity, and many bird species have affinities for specific structural characteristics influenced by fire (MacArthur & MacArthur 1961). Periodic fire increases habitat heterogeneity, which is associated with high species diversity in birds (Freemark & Merriam 1986), but also increases habitat fragmentation. The negative effects of habitat fragmentation on avian populations has been documented in many ecosystems, including sagebrush steppe in Idaho (Knick & Rotenberry 1995; Vander Haegen et al. 2000). Yet, birds may respond differently to habitats fragmented by natural disturbances to which they are adapted (Strong & Bock 1990). Therefore, we included measures of habitat diversity as well as habitat fragmentation in the suite of a priori models.

We incorporated alternative model forms into the analysis for habitat area variables, representing potential non-linear relationships between bird species richness/diversity and amount of habitat (Franklin et al. 2000). A pseudothreshold form was approximated using logarithmic (\ln) transformation of variables to describe a situation where bird measures increase or decrease to some threshold area and then level. We tested for lack-of-fit of the global model using an extra-sum-of-squares F-test for species diversity and a drop-in-deviance chi-square test for species richness (Ramsey & Schafer 1997).

Model Selection

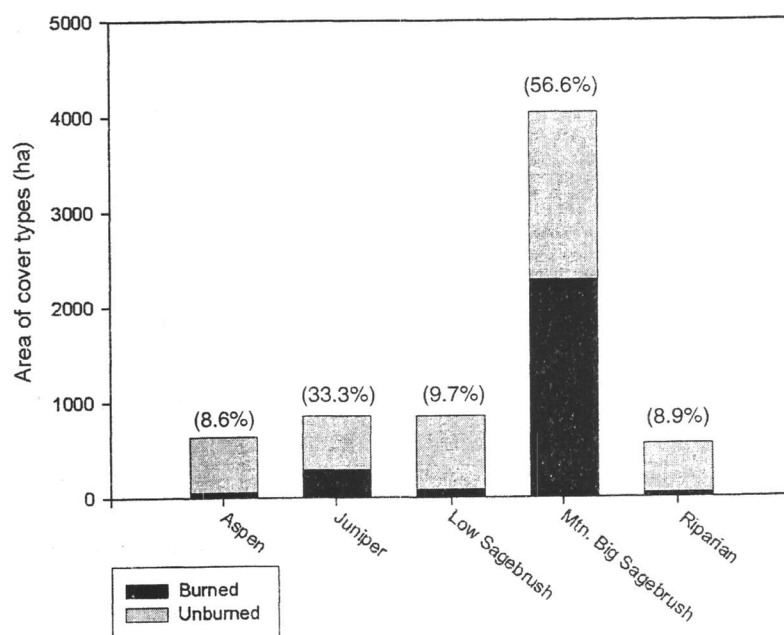
The candidate models were ranked in terms of their ability to explain the data using Akaike's Information Criterion modified for small sample size (AIC_c) (Burnham and Anderson 1998). We selected the model with the minimum AIC_c value as the best-approximating model to the data, but all models with ΔAIC_c values (the difference between model AIC_c and the minimum AIC_c value) < 2 were also considered as competing models. We used Akaike weights (w) to assess selection uncertainty among these competing models. Models with a $\Delta AIC_c > 4$ are considered marginal and $\Delta AIC_c > 10$ are a poor fit to the data (Burnham & Anderson 1998). Only the best-fitting form of each model was considered (e.g. linear or pseudothreshold). Graphs of residuals and normal probability plots were examined to assess whether the model assumptions of equal variance and normality were adequately met for the selected model forms.

RESULTS

Pattern of Prescribed Burn

An estimated 32% of the study area burned. The fire burned differentially among cover types, such that some types were more impacted than others (χ^2 p-value <0.0001; based on estimates from a comparison of GIS cover type maps made before and after the prescribed burn). Over half (56%) of sagebrush and 33% of juniper within the study area burned, while the remaining cover types were

Figure 3.2. Area burned and unburned for each cover type following prescribed fire, estimated from GIS maps of study area on Steens Mountain, Oregon (percent of cover type burned).



minimally effected (Fig. 3.2). The fire also burned unevenly, creating a mosaic of burned and unburned cover types with a wide range of patchiness at the local scale and patch sizes at the landscape scale (Table 3.2).

Table 3.2. Summary statistics for local and landscape variables measured at 205 sites located on Steens Mountain, Oregon.

<i>Variable^a</i>	<i>Mean</i>	<i>S.D.</i>	<i>Minimum</i>	<i>Maximum</i>
ABURN _{100m}	36.21	37.27	0.00	100.00
ASAGE _{100m}	51.90	33.77	0.00	100.00
APOTR _{100m}	4.42	14.10	0.00	86.08
DJUNP _{100m}	17.93	42.82	0.00	268.79
HTSAGE _{100m}	60.68	18.94	0.00	94.00
HTPOTR _{100m}	1.34	3.20	0.00	14.00
CSAGE _{100m}	11.70	7.30	0.00	25.00
RICH _{100m}	2.74	0.91	1.00	5.00
ABURN _{1km}	35.53	23.10	0.00	78.50
ASAGE _{1km}	22.02	13.65	4.33	69.11
APOTR _{1km}	7.83	8.34	0.00	30.41
AJUNP _{1km}	10.90	13.74	0.12	66.39
ED _{1km}	66.64	18.10	23.48	107.83
SDI _{1km}	1.39	0.24	0.81	1.84

^a See Table 3.1 for descriptions of habitat measures.

Avian Community

We detected 56 species and 1,921 individual birds at the survey sites during the 2000 breeding season (Appendix C). The majority of bird species were detected only at sites where aspen and other riparian habitats occurred. However, more than 60% of the total bird detections were of 4 species associated with sagebrush. This was expected, since approximately 52.6% of the study area was dominated by sagebrush.

Table 3.3. Ranking of candidate models relating habitat characteristics to avian species richness and species diversity (H') based on minimum AIC_c on Steens Mountain, Oregon (only models with $\Delta AIC_c < 10$ and global and null models shown).

<i>Model</i>	<i>AIC_c</i>	<i>K^a</i>	<i>ΔAIC_c</i>	<i>w</i>
Species Richness				
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + SDI_{1km}$	-1762.13	4	0.00	0.45
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + RICH_{100m}$	-1760.67	4	1.47	0.22
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m})$	-1760.61	3	1.52	0.21
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + \ln(ASAGE_{100m})$	-1759.45	4	2.68	0.12
Global model	-1739.71	13	22.43	<0.001
Null model	-1698.92	1	63.21	<0.001
Species Diversity (H')				
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + RICH_{100m}$	172.61	4	0.00	0.52
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + SDI_{1km}$	174.78	4	2.17	0.18
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + \ln(ASAGE_{100m})$	174.81	4	2.20	0.17
$\ln(APOTR_{100m}) + \ln(DJUNP_{100m})$	175.58	3	2.97	0.12
Global model	182.10	13	9.49	0.01
Null model	270.04	1	97.97	<0.001

^a Number of estimated parameters in model.

Species Richness

We analyzed 114 models that included the 64 a priori models and 50 model variations to evaluate the effect of habitat characteristics on bird species richness. Model variations consisted of the pseudothreshold form for all habitat area measures. The best approximating a priori model $\{\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + SDI_{1km}\}$ predicted an increase in species richness with increasing habitat diversity within 1 km, and a curve-linear relationship with local juniper density and aspen area. This model was two times as likely based on Akaike weights as the next ranked model containing local habitat richness $\{\ln(APOTR_{100m}) + \ln(DJUNP_{100m}) + RICH_{100m}\}$ (Table 3.3). The non-linear relationship with aspen and juniper represents

a threshold beyond which bird species richness will no longer increase with increases in either habitat (Table 3.4; Fig. 3.3). The pseudothreshold form was retained for analysis because all top-ranked models contained non-linear measures of area aspen and juniper density [i.e. $\ln(\text{APOTR}_{100\text{m}})$]. There was some evidence based on minimum AIC_c values that local habitat richness was also associated with bird species richness. However, the top ranked models all contained $\text{APOTR}_{100\text{m}}$ and $\text{DJUNP}_{100\text{m}}$, suggesting that these variables were the most important predictors of bird species richness, while measures of habitat diversity and richness contributed relatively little to the model.

Figure 3.3. Relationship between bird species richness and area aspen and juniper density on Steens Mountain, Oregon. The two surfaces show maximum and minimum recorded values of habitat diversity.

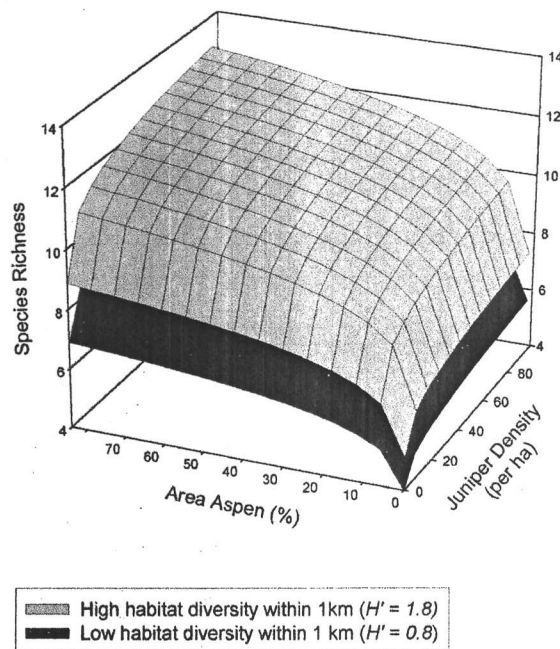


Table 3.4. Estimates of parameters in AIC_c-selected best approximating model explaining species richness and species diversity for birds on Steens Mountain, Oregon.

<i>Variable</i>	<i>Parameter Estimate</i>	<i>S.E.</i>	<i>95% C.I.</i>
Species Richness			
SDI _{1km} *	0.252	0.133	-0.008, 0.513
ln(APOTR _{100m})	0.107	0.018	0.071, 0.143
ln(DJUNP _{100m})	0.072	0.016	0.042, 0.103
Species Diversity (H')			
RICH _{100m}	0.064	0.032	0.002, 0.126
ln(APOTR _{100m})	0.129	0.019	0.091, 0.167
ln(DJUNP _{100m})	0.092	0.015	0.064, 0.121

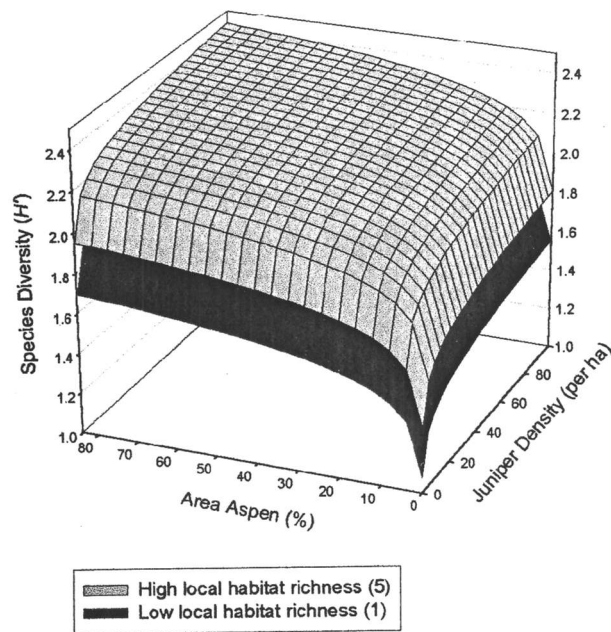
*95% C.I. includes zero.

Species Diversity

We examined 114 models relating calculated bird diversity (H') to habitat characteristics, including a pseudothreshold form of all models containing habitat area variables. The best approximating model selected by AIC_c containing area aspen, juniper density, and habitat richness, $\{\ln(\text{APOTR}_{100\text{m}}) + \ln(\text{DJUNP}_{100\text{m}}) + \text{RICH}_{100\text{m}}\}$ was almost three times as likely as the next ranked model $\{\ln(\text{APOTR}_{100\text{m}}) + \ln(\text{DJUNP}_{100\text{m}}) + \text{SDI}_{1\text{km}}\}$ with landscape scale habitat diversity based on Akaike weights (Table 3.3). The effects of area aspen and juniper density appeared to be best represented in the pseudothreshold form [i.e. $\ln(\text{APOTR}_{100\text{m}})$] because they appeared in this form most often in the top models ranked by AIC_c, than estimates in linear form. The model indicated that species diversity was positively associated

with aspen area and juniper density in a nonlinear fashion, and increased with increasing local habitat richness (Table 3.4; Fig. 3.4).

Figure 3.4. Relationship between bird species diversity (H') and area aspen and juniper density on Steens Mountain, Oregon. The two surfaces show maximum and minimum recorded values of habitat richness.



DISCUSSION

Our findings indicate that using prescribed fire to mimic natural fire regimes in sagebrush steppe landscapes can restore habitat conditions favorable to avian diversity without jeopardizing present populations. Periodic fire increases habitat heterogeneity, which is positively associated with avian diversity in this system, without severely impacting critical habitats (i.e. aspen). Furthermore, our

findings suggest that appropriate spatial scale and resolution of management prescriptions may be crucial to sustaining bird diversity in this ecosystem.

Critical Habitats

We found that the presence of trees, and especially aspen forest, were critical to the maintenance of bird diversity in this sagebrush-dominated landscape. Others have also reported aspen forests are important reservoirs of avian species richness in arid regions of the western United States (Maser et al. 1984; Knopf et al. 1988). Higher bird diversity may be related to increased structural complexity introduced by trees in an otherwise shrub-dominated landscape.

However, our models of bird diversity indicate that, while the amount of aspen habitat influenced bird assemblages, the number and calculated diversity (H') of species quickly reached a threshold or maximum potential in relatively small aspen stands. Similarly, bird species richness and calculated diversity (H') was predicted to increase with increasing juniper, but quickly leveled off at low tree density. Our findings suggest that increasing forest area, or in the case of juniper, woodland density, will have little effect on bird diversity. Woody habitats that were never part of a continuous forest may not be comparable to studies of species-area relationships in eastern forests (Blake 1986; Strong & Bock 1990). Stronger relationships have been detected between habitat area and forest-interior than forest-edge bird species richness (Freemark & Merriam 1986; Grant & Berkey 1999). Since aspen in this area occurs as narrow bands (typically <100 m in width)

along drainages and north slopes, all aspen stands in this study could be considered edge-habitat, and may only support species adapted to the naturally fragmented landscape.

Sagebrush, the habitat type most effected by fire, was not an important predictor of bird diversity in this study. While overall diversity may not be related to sagebrush, it is likely that the abundance of sagebrush-associated birds is influenced by the amount of sagebrush habitat, and sagebrush obligates may represent the most threatened species in this system (Paige & Ritter 1999). However, Noson (2002), found that the effects of fire suppression (e.g. juniper encroachment) had at least as great an impact on sagebrush bird populations as loss of sagebrush due to fire.

Importance of Habitat Heterogeneity

Uneven burning in this ecosystem increases habitat heterogeneity at multiple scales. Both species richness and calculated diversity (H') were positively associated with increasing habitat heterogeneity, as measured by habitat diversity within 1 km and local habitat richness, respectively. Our findings concur with studies conducted in other systems (Freemark & Merriam 1986; Penhollow & Stauffer 2000), and are consistent with the hypothesis that the greater number of available niches in more heterogeneous areas supports higher diversity.

Importance of Spatial Scale and Resolution

With the exception of the relationship between bird species richness and habitat diversity within 1 km (SDI_{1km}), landscape measures at the scale we considered were poor predictors of songbird diversity. Our results suggest that local measures of habitat had more influence on bird assemblages. However, another possible explanation of our findings is that the satellite data we used were too coarse to adequately depict landscape composition. Other studies attempting to use remotely sensed data to predict bird distributions have also found that species richness was better described by ground-based data than remotely-sensed data (Jorgensen & Nohr 1996; Mack et al. 1997; Saveraid et al. 2001). Mack et al. (1997) suggested that the usefulness of satellite data is limited by the inability to detect habitat patches smaller than the resolution of the image. Habitat types may be particularly difficult to map using satellite imagery in areas with high habitat heterogeneity (Jorgensen & Nohr 1996). In our study, combining landscape scale satellite data with local habitat data collected in the field did not greatly improve predictions of bird occurrence, as has been suggested by previous studies (Saveraid et al. 2001).

Conservation Implications

Aspen forests are in a state of decline across the West (Bartos & Campbell 1998; Wall et al. 2001). Because aspen supported the highest diversity in this system, maintaining this habitat type should be a high management priority. Fires

were historically less frequent in aspen stands than surrounding sagebrush habitat, occurring only under rare conditions, typically every 60-100 years (Wall et al. 2001). Burning appears to have indirectly benefited aspen by removing competing conifer (Bartos et al. 1983; Wall et al. 2001), and directly maintained stands by stimulating regeneration (Bartos & Mueggler 1981; Brown & Simmerman 1986).

The synergism between overgrazing and altered fire regimes has hastened habitat degradation in sagebrush ecosystems. Removal of fine fuels by livestock is considered one of the primary factors causing fire suppression in areas of fire-prone sagebrush (Miller et al. 1994). In addition, grazing accelerates the negative effects of fire suppression by encouraging the establishment of conifer seedlings and limiting aspen recruitment (Bartos & Mueggler 1981; DeByle 1985; Miller et al. 1994). It is important to recognize that past management practices have resulted in major changes in many ecosystems, and that simply discontinuing activities that degraded habitat will not always restore natural fire regimes nor protect biodiversity (Archer & Smeins 1991; Perry & Amaranthus 1997). In the sagebrush steppe, fuel accumulations were naturally discontinuous due to the patchiness of past fire events and variation in landscape features such as topography and soils (Christiensen 1992). However, after a century of fire suppression, the distribution of fuels across the landscape has changed, and reducing grazing alone is unlikely to immediately bring back historic fire patterns. In addition, as aspen stands age in the absence of fire, they become increasingly difficult to burn at intensities sufficient to induce regeneration (Brown &

Simmerman 1986; Bartos & Campbell 1998). Active management that mimics natural disturbance regimes, such as prescribed fire, may be necessary to restore ecosystem integrity (Christiensen 1988). Because natural conditions required for burning of aspen are relatively rare, restoration of aspen may also require manipulation of fuels by managers (e.g. cutting and burning dry juniper) (Wall et al. 2001).

Life histories of native species are fine-tuned to the natural disturbance regime (Keeley & Bond 2001). Therefore, it is imperative that the frequency, intensity, and extent of historical fires be considered in developing fire management plans (Everett & Lehmkuhl 1999). Fire history data for Steens mountain suggest that fires in aspen were intense, but typically limited, effecting only individual aspen groves (Wall et al. 2001). In contrast to forest-dominated regions, small aspen stands historically occurred in sagebrush-dominated landscapes and may provide sufficient habitat for most native species. Simply the presence of woody structure is critical in these moisture limited shrub environments. Therefore, mimicking the limited extent of historical fires should maintain long-term viability of aspen without jeopardizing present avian populations. Coarse-filter approaches to conservation are scale sensitive (Aplet & Keeton 1999). Our findings suggest that broad scale fire management, that does not consider the availability of small habitats patches at the site-level, may be inadequate in this system. This suggests that burns should be administered under conditions that create fine grain habitat heterogeneity.

The predictive models we developed quantify habitat characteristics that maximize bird diversity in this system. Caution should be used in interpreting our data, since overall species diversity may not reflect individual species habitat requirements. Management aimed at conservation of biological diversity should be viewed as complementing, not substituting for, species-level management (Baydack et al. 1999). Therefore, the habitat requirements of species of management concern should be considered separately (Noson 2002). We also note that bird species occurrence does not necessarily indicate reproductive success or habitat quality (Van Horne 1983). Demographic information for the dozens of bird species that we detected is not currently available and would be useful to obtain.

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Chapter 4

Summary Conclusions

Developing management strategies for conservation of fire-prone ecosystems, such as the sagebrush steppe, presents a major challenge to land managers (DellaSala et al. 1996). Our findings suggest that a coarse filter approach (Kaufmann et al. 1994), involving restoration of historic fire regimes can be used to maximize avian diversity, while also maintaining habitat conditions essential to bird species of high management concern in this landscape.

Following fire on Steens Mountain, we detected no negative relationships between bird diversity and area burned. Habitat features predicted to be important to bird diversity, were aspen forest, juniper density, and habitat heterogeneity. With the exception of juniper, these habitat features are maintained by periodic fire. Across the landscape, the highest species richness was detected in areas with aspen forest, and the prescribed burn minimally affected these habitats. Furthermore, our models indicate that even small aspen stands and the presence of only a few juniper trees will support avian diversity in this system.

The models we developed for individual bird species indicate that decreases in the availability of sagebrush habitat, as occurs with fire, did have an immediate negative impact on the Brewer's sparrow, sage thrasher, and green-tailed towhee. These findings concur with similar studies conducted in sagebrush steppe in other regions (Knick and Rotenberry 1995). However, changes in habitat associated with

the absence of fire also exerted a strong influence on these bird species. In particular, the abundance or occurrence of the sagebrush-associated species we modeled were negatively influenced by juniper encroachment, and even low densities of juniper had a strong impact on sage thrashers.

The presence of aspen habitat appears to be critical to bird diversity in this shrub-dominated landscape. Therefore, restoring aspen forest should be a conservation priority. Since most species of high management concern in this region are sagebrush obligates, this habitat should also be an importation consideration. Our results indicate that mimicking the patchiness of historic fires will maintain long-term viability of aspen and sagebrush habitats without jeopardizing present avian populations.

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Appendices

Appendix A. List of 77 a priori candidate models relating songbird species to habitat characteristics on Steens Mountain, Oregon 2000. Models are organized according to the predictions that guided model development.

FIRE DISTURBANCE

Models focus on the direct influence of burning on bird species included in the study. We predicted that if fire had a direct impact on bird species it would be at the local scale. We targeted these models at vesper sparrows, because they have been associated with burned areas in other studies. We predicted that vesper sparrows would be more likely to use burned areas with high grass cover.

1. ABURN_{100m}
2. ABURN_{100m} + CGRASS_{100m}

SAGEBRUSH HABITAT AMOUNT AND QUALITY

Models describe potential relationships with the amount and quality of sagebrush habitat. We predicted that all the species in our study were potentially influenced by these measures. Models without a measure of area sagebrush (ASAGE) and/or containing grass cover (CGRASS) were targeted at vesper sparrows. Models containing the amount of sagebrush in the landscape (ASAGE) were targeted at Brewer sparrows and sage thrashers.

Local scale

3. ASAGE_{100m}
4. CSAGE_{100m}
5. HTSAGE_{100m}
6. PATCH_{100m}

7. ASAGE_{100m} + CSAGE_{100m}
8. ASAGE_{100m} + HTSAGE_{100m}
9. ASAGE_{100m} + CGRASS_{100m}

10. PATCH_{100m} + ASAGE_{100m}
11. PATCH_{100m} + CSAGE_{100m}
12. PATCH_{100m} + HTSAGE_{100m}
13. PATCH_{100m} + CGRASS_{100m}
14. PATCH_{100m} + ASAGE_{100m} + CSAGE_{100m}
15. PATCH_{100m} + ASAGE_{100m} + HTSAGE_{100m}
16. PATCH_{100m} + ASAGE_{100m} + CGRASS_{100m}

Landscape scale area sagebrush

17. ASAGE_{1km}
18. ASAGE_{1km} + CSAGE_{100m}
19. ASAGE_{1km} + HTSAGE_{100m}
20. ASAGE_{1km} + PATCH_{100m}

JUNIPER ENCROACHMENT

Models focus on the influence of juniper encroachment, and explore improvements made by adding measures of fire disturbance, habitat area, and habitat quality. We predicted that all the species were potentially influenced by local increases in juniper. Models containing the amount of juniper in the landscape (AJUNP) were targeted at green-tailed towhees.

Appendix A (Continued).

Local scale juniper density

21. DJUNP_{100m} + ASAGE_{100m}
22. DJUNP_{100m} + CSAGE_{100m}
23. DJUNP_{100m} + HTSAGE_{100m}
24. DJUNP_{100m} + PATCH_{100m}

25. DJUNP_{100m} + ABURN_{100m}
26. DJUNP_{100m} + ABURN_{100m} + CGRASS_{100m}

27. DJUNP_{100m} + ASAGE_{100m} + CSAGE_{100m}
28. DJUNP_{100m} + ASAGE_{100m} + HTSAGE_{100m}
29. DJUNP_{100m} + ASAGE_{100m} + CGRASS_{100m}
30. DJUNP_{100m} + ASAGE_{100m} + DOM_{100m}

31. DJUNP_{100m} + PATCH_{100m} + ASAGE_{100m}
32. DJUNP_{100m} + PATCH_{100m} + CSAGE_{100m}
33. DJUNP_{100m} + PATCH_{100m} + HTSAGE_{100m}
34. DJUNP_{100m} + PATCH_{100m} + CGRASS_{100m}
35. DJUNP_{100m} + PATCH_{100m} + ASAGE_{100m} + CSAGE_{100m}
36. DJUNP_{100m} + PATCH_{100m} + ASAGE_{100m} + HTSAGE_{100m}
37. DJUNP_{100m} + PATCH_{100m} + ASAGE_{100m} + CGRASS_{100m}

38. DJUNP_{100m} + ASAGE_{1km}
39. DJUNP_{100m} + ASAGE_{1km} + CSAGE_{100m}
40. DJUNP_{100m} + ASAGE_{1km} + HTSAGE_{100m}
41. DJUNP_{100m} + ASAGE_{1km} + PATCH_{100m}

Landscape scale juniper area

42. AJUNP_{1km} + ASAGE_{100m}
43. AJUNP_{1km} + CSAGE_{100m}
44. AJUNP_{1km} + HTSAGE_{100m}
45. AJUNP_{1km} + ASAGE_{100m} + CSAGE_{100m}
46. AJUNP_{1km} + ASAGE_{100m} + HTSAGE_{100m}
47. AJUNP_{1km} + ASAGE_{100m} + DOM_{100m}

48. AJUNP_{1km} + ASAGE_{1km}
49. AJUNP_{1km} + ASAGE_{1km} + CSAGE_{100m}
50. AJUNP_{1km} + ASAGE_{1km} + HTSAGE_{100m}
51. AJUNP_{1km} + ASAGE_{1km} + DOM_{100m}

HABITAT FRAGMENTATION**Sagebrush Edge Density**

Models focus on the influence of sagebrush edge density, and explore improvements of models made by including measures of juniper encroachment, habitat area and quality. We predicted that all of the species we examined were potentially influenced by the fragmentation of sagebrush habitat.

52. ED_{1km}

Appendix A (Continued).

53. $ED_{1km} + ASAGE_{100m}$
 54. $ED_{1km} + ASAGE_{1km}$
 55. $ED_{1km} + CSAGE_{100m}$
 56. $ED_{1km} + HTSAGE_{100m}$
 57. $ED_{1km} + CGRASS_{100m}$
58. $ED_{1km} + DJUNP_{100m}$
 59. $ED_{1km} + DJUNP_{100m} + ASAGE_{100m}$
 60. $ED_{1km} + DJUNP_{100m} + ASAGE_{1km}$
 61. $ED_{1km} + DJUNP_{100m} + CSAGE_{100m}$
 62. $ED_{1km} + DJUNP_{100m} + HTSAGE_{100m}$
63. $ED_{1km} + DJUNP_{100m} + CGRASS_{100m}$
64. $ED_{1km} + AJUNP_{1km} + ASAGE_{100m}$
 65. $ED_{1km} + AJUNP_{1km} + ASAGE_{1km}$
 66. $ED_{1km} + AJUNP_{1km} + HTSAGE_{100m}$
 67. $ED_{1km} + AJUNP_{1km} + CSAGE_{100m}$

Largest Sagebrush Patch

Models explore the influence of the largest patch of intact sagebrush in the landscape, and include habitat area measures and juniper encroachment. Models were targeted at the sagebrush obligates, because we predicted these species be most sensitive to loss of intact sagebrush.

68. LPI_{1km}
 69. $LPI_{1km} + ASAGE_{100m}$
 70. $LPI_{1km} + CSAGE_{100m}$
 71. $LPI_{1km} + HTSAGE_{100m}$
72. $LPI_{1km} + DJUNP_{100m}$
 73. $LPI_{1km} + DJUNP + ASAGE_{100m}$
 74. $LPI_{1km} + DJUNP + CSAGE_{100m}$
 75. $LPI_{1km} + DJUNP + HTSAGE_{100m}$

GLOBAL MODEL

76. $ASAGE_{100m} + (ASAGE_{100m})^2 + CSAGE_{100m} + HTSAGE_{100m} + CGRASS_{100m} + DJUNP_{100m} + (DJUNP_{100m})^2 + PATCH_{100m} + ASAGE_{1km} + (ASAGE_{1km})^2 + AJUNP_{1km} + (AJUNP_{1km})^2 + LPI_{1km} + ED_{1km}$

NULL MODEL

77. No parameters

Notes: Local and landscape scale variables are indicated by the subscripts 100m and 1km, respectively. Variable name ABURN represents the area burned (%), CGRASS is grass cover (%), ASAGE is area sagebrush (%), CSAGE (%) is shrub cover within sagebrush cover type (%), HTSAGE is average height of sagebrush (cm), PATCH is an index of patchness (no.), DOM is the relative dominance of snowberry (1-5), DJUNP is the density of juniper/mountain-mahogany trees (ha^{-1}), AJUNP is the area juniper/mountain-mahogany (%), LPI is the area contained in the largest sagebrush patch (%), ED is the edge density of sagebrush (m/ha).

Appendix B. List of 67 a priori candidate models relating bird diversity to habitat characteristics on Steens Mountain, Oregon 2000. Models are organized according to the predictions that guided model development.

FIRE DISTURBANCE

Models focus on the direct influence of burning on avian diversity.

1. ABURN_{100m}
2. ABURN_{1km}

CRITICAL HABITAT AREA AND QUALITY

Models describe predicted relationships with the amount and quality of key habitat types at two spatial scales. We predicted that aspen was critical for maintaining avian diversity, and that sagebrush and juniper woodland were also important. We explored improvements made to model fit by including measures of fire disturbance..

Local habitat area and habitat quality

3. ASAGE_{100m}
4. DJUNP_{100m}
5. APOTR_{100m}

6. APOTR_{100m} + DJUNP_{100m}
7. APOTR_{100m} + ASAGE_{100m}
8. APOTR_{100m} + ABURN_{100m}
9. APOTR_{100m} + ASAGE_{100m} + DJUNP_{100m}

10. ASAGE_{100m} + HTSAGE_{100m}
11. ASAGE_{100m} + CSAGE_{100m}

12. HTPOTR_{100m} + APOTR_{100m}
13. HTPOTR_{100m} + DJUNP_{100m}
14. HTPOTR_{100m} + DJUNP_{100m} + ASAGE_{100m}

Landscape habitat area

15. AJUNP_{1km}
16. APOTR_{1km}
17. ASAGE_{1km}

18. APOTR_{1km} + AJUNP_{1km}
19. APOTR_{1km} + ASAGE_{1km}
20. APOTR_{1km} + ABURN_{1km}
21. APOTR_{1km} + ASAGE_{1km} + AJUNP_{1km}

HABITAT HETEROGENEITY

Models focus on the influence of habitat heterogeneity on avian diversity. We predicted that increasing habitat richness or diversity was positively associated with avian diversity. We also included sagebrush edge density to explore the potential negative influence of habitat heterogeneity on sagebrush bird abundance and consequently species evenness. We included measures of fire disturbance, critical habitat, and habitat quality to improve model fit.

Habitat Richness

With local scale measures of habitat area and quality

Appendix B (Continued).

- 22. RICH_{100m}
- 23. RICH_{100m} + APOTR_{100m}
- 24. RICH_{100m} + ASAGE_{100m}
- 25. RICH_{100m} + ABURN_{100m}
- 26. RICH_{100m} + DJUNP_{100m}

- 27. RICH_{100m} + ASAGE_{100m} + HTSAGE_{100m}
- 28. RICH_{100m} + ASAGE_{100m} + CSAGE_{100m}

- 29. RICH_{100m} + APOTR_{100m} + DJUNP_{100m}
- 30. RICH_{100m} + APOTR_{100m} + ASAGE_{100m}

- 31. RICH_{100m} + HTPOTR_{100m} + APOTR_{100m}
- 32. RICH_{100m} + HTPOTR_{100m} + DJUNP_{100m}

With landscape scale measures of habitat area

- 33. RICH_{100m} + APOTR_{1km}
- 34. RICH_{100m} + ASAGE_{1km}
- 35. RICH_{100m} + ABURN_{1km}
- 36. RICH_{100m} + AJUNP_{1km}

- 37. RICH_{100m} + APOTR_{1km} + ASAGE_{1km}
- 38. RICH_{100m} + APOTR_{1km} + AJUNP_{1km}

Sagebrush Edge

- 39. ED_{1km}

With local scale measures of habitat

- 40. ED_{1km} + APOTR_{100m}
- 41. ED_{1km} + ASAGE_{100km}
- 42. ED_{1km} + APOTR_{100m} + DJUNP_{100m}
- 43. ED_{1km} + APOTR_{100m} + ASAGE_{100km}

- 44. ED_{1km} + ASAGE_{100m} + HTSAGE_{100m}
- 45. ED_{1km} + ASAGE_{100m} + CSAGE_{100m}

With landscape scale measures of habitat

- 46. ED_{1km} + APOTR_{1km}
- 47. ED_{1km} + ASAGE_{1km}
- 48. ED_{1km} + APOTR_{1km} + AJUNP_{1km}
- 49. ED_{1km} + APOTR_{1km} + ASAGE_{1km}

Habitat Diversity (H')

- 50. SDI_{1km}

With local measures of habitat area and quality

- 51. SDI_{1km} + APOTR_{100m}
- 52. SDI_{1km} + ASAGE_{100m}
- 53. SDI_{1km} + ABURN_{100m}
- 54. SDI_{1km} + DJUNP_{100m}

Appendix B (Continued).

55. $SDI_{1km} + ASAGE_{100m} + HTSAGE_{100m}$
 56. $SDI_{1km} + ASAGE_{100m} + CSAGE_{100m}$
57. $SDI_{1km} + APOTR_{100m} + DJUNP_{100m}$
 58. $SDI_{1km} + APOTR_{100m} + ASAGE_{100m}$
59. $SDI_{1km} + HTPOTR_{100m} + APOTR_{100m}$
 60. $SDI_{1km} + HTPOTR_{100m} + DJUNP_{100m}$

With landscape scale measures of habitat area

61. $SDI_{1km} + AJUNP_{1km}$
 62. $SDI_{1km} + APOTR_{1km}$
 63. $SDI_{1km} + ASAGE_{1km}$
 64. $SDI_{1km} + ABURN_{1km}$
 65. $SDI_{1km} + APOTR + ASAGE_{1km}$
 66. $SDI_{1km} + APOTR + AJUNP_{1km}$

GLOBAL MODEL

67. $ASAGE + APOTR_{100m} + DJUNP_{100m} + ASAGE_{1km} + APOTR_{1km} + AJUNP_{1km} + RICH_{100m} + SDI_{1km} + ED_{1km} + HTPOTR_{100m} + CSAGE_{100m} + HTSAGE_{100m}$

NULL MODEL

68. No parameters

Notes: Local and landscape scale variables are indicated by the subscripts 100m and 1km, respectively. Variable name ABURN represents the area burned (%), APOTR is the area aspen (%), AJUNP is the area juniper/mountain-mahogany (%), ASAGE is area sagebrush (%), CSAGE (%) is shrub cover within sagebrush cover type (%), HTSAGE is the average height of sagebrush (cm), HTPOTR is the average height of primary aspen canopy (m), DJUNP is the density of juniper/mountain-mahogany trees (ha^{-1}), ED is the edge density of sagebrush (m/ha), RICH is the number of major cover types, SDI is Shannon's Index of cover type diversity.

Appendix C. Bird species detected in major cover types on Steens Mountain, Oregon in 2000.

Common Name <i>Scientific Name</i>	Total Detections	Juniper	Sagebrush	Aspen	Riparian
Northern harrier <i>Circus cyaneus</i>	1	x			
American kestrel <i>Falco sparverius</i>	4	x			
Killdeer <i>Charadrius vociferus</i>	1				x
Mourning dove <i>Zenaida macroura</i>	10	x			
Short-eared owl <i>Asio flammeus</i>	1		x		
Common nighthawk <i>Chordeiles minor</i>	3	x	x		
Rufous hummingbird <i>Selasphorus rufus</i>	1	x			
Belted kingfisher <i>Ceryle alcyon</i>	1				x
red-naped sapsucker <i>Sphyrapicus nuchalis</i>	2			x	
Hairy woodpecker <i>Picoides villosus</i>	2			x	
Northern flicker <i>Colaptes auratus</i>	38	x		x	
Western wood-peewee <i>Contopus sordidulus</i>	2			x	
Willow flycatcher <i>Empidonax traillii</i>	2			x	
Dusky flycatcher/grey flycatcher <i>E. oberholseri/ E. wrightii</i>	86	x		x	
Warbling vireo <i>Vireo gilvus</i>	25			x	
Steller's jay <i>Cyanocitta stelleri</i>	2			x	
Horned lark <i>Eremophila alpestris</i>	13		x		
Tree swallow <i>Tachycineta bicolor</i>	13			x	
Northern rough-wing swallow <i>Stelgidopteryx serripennis</i>	2			x	x
Mountain chickadee <i>Poecile gambeli</i>	1			x	
Rock wren <i>Salpinctes obsoletus</i>	11	x	x		
House wren <i>Troglodytes aedon</i>	24			x	
Ruby-crowned kinglet <i>Regulus calendula</i>	6	x		x	

Appendix C (Continued)

Common Name Scientific Name	Total Detections	Juniper	Sagebrush	Aspen	Riparian
Mountain bluebird <i>Sialia currucoides</i>	22	x		x	
Hermit thrush <i>Catharus guttatus</i>	4			x	
American robin <i>Turdus migratorius</i>	111	x		x	
Sage thrasher <i>Oreoscoptes montanus</i>	63		x		
Orange-crowned warbler <i>Vermivora celata</i>	5			x	
Yellow-rumped warbler <i>Dendroica coronata</i>	15	x		x	x
Black-throated gray warbler <i>Dendroica nigrescens</i>	1	x			
Yellow warbler <i>Dendroica petechia</i>	42			x	x
MacGillivray's Warbler <i>Oporornis tolmiei</i>	2				x
Green-tailed towhee <i>Pipilo chlorurus</i>	74	x	x		
Chipping sparrow <i>Spizella passerina</i>	45		x		
Brewer's sparrow <i>Spizella breweri</i>	575		x		
Vesper sparrow <i>Pooecetes gramineus</i>	291		x		
Fox sparrow <i>Passerella iliaca</i>	3			x	x
Song sparrow <i>Melospiza melodia</i>	16	x		x	x
Dark-eyed junco <i>Junco hyemalis</i>	19	x		x	
Lazuli bunting <i>Passerina amoena</i>	1				x
Red-winged blackbird <i>Agelaius phoeniceus</i>	5				x
Western meadowlark <i>Sturnella neglecta</i>	12	x	x		x
Brewer's blackbird <i>Euphagus cyanocephalus</i>	48	x	x		x
Brown-headed cowbird <i>Molothrus ater</i>	2			x	x
White-crowned sparrow <i>Zonotrichia leucophrys</i>	239		x	x	x
Cassin's finch <i>Carpodacus cassinii</i>	48	x		x	
House finch <i>Carpodacus mexicanus</i>	20	x		x	

Appendix C (Continued)

Common Name <i>Scientific Name</i>	Total Detections	Juniper	Sagebrush	Aspen	Riparian
Pine siskin <i>Carduelis pinus</i>	7	x			
Total	1921				