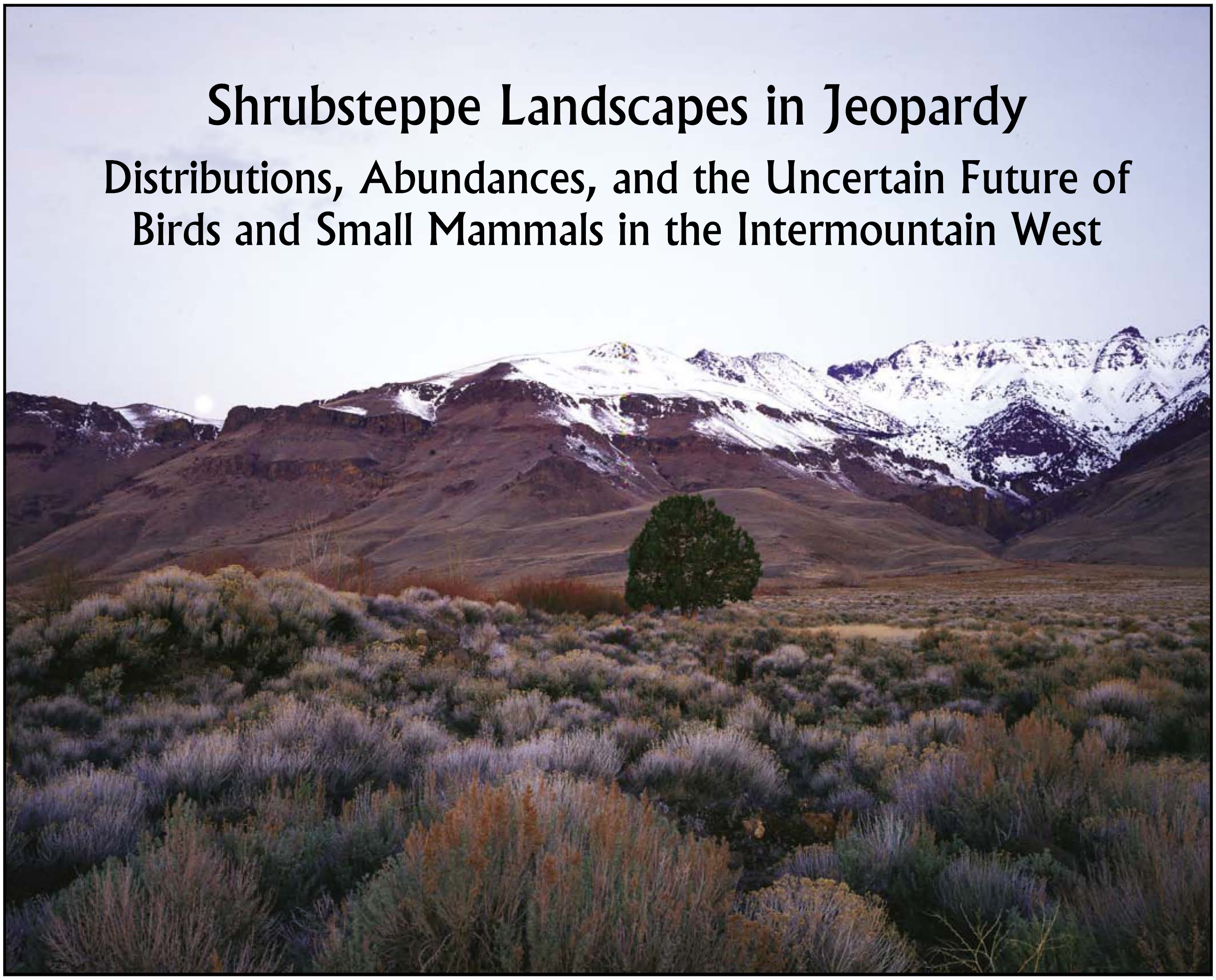

Shrubsteppe Landscapes in Jeopardy

Distributions, Abundances, and the Uncertain Future of Birds and Small Mammals in the Intermountain West

David S. Dobkin and Joel D. Sauder

High Desert
Ecological
Research Institute

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COVER: Moonrise over shrubsteppe on Steens Mountain in southeast Oregon's Great Basin. Photograph by Greg Burke.

The High Desert Ecological Research Institute, under the direction of Dr. David S. Dobkin, was established in 1993 to serve as a regional center for ecological research and policy analysis with a primary focus on natural resource issues related to the Intermountain West and the Pacific Northwest. The Institute conducts cooperative, multidisciplinary, long-term research on a wide range of problems in natural resource management and conservation in western North America. The High Desert Ecological Research Institute is an independent, nonprofit, research and educational organization.

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EXECUTIVE SUMMARY

Landscapes dominated by sagebrush (*Artemisia* spp.) extend across large portions of 11 states in the Intermountain West, but very little of the sagebrush biome remains undisturbed or unaltered from its condition prior to Euro-American settlement. Sagebrush shrubsteppe is now one of North America's most imperiled and neglected ecosystems due to the profound, ecologically transformative influences of numerous human-caused impacts that have fragmented and degraded sagebrush habitats across their widespread distribution.

We considered the entire suite of bird and small-mammal species that occur in shrubsteppe landscapes, and distilled a list of 61 species that are completely or extensively dependent on shrubsteppe ecosystems in the Intermountain West. We conducted a broad-scale analysis of distributions, abundances, and sensitivity to habitat disturbance in order to assess the current state of knowledge and the conservation needs of these species in the 11 western states. We further focused our analyses on the three ecoregions (Columbia Basin, Great Basin, and Wyoming Basin) with the greatest percentages of sagebrush land cover.

In our assessment of shrubsteppe-dependent birds, we analyzed regional and subregional population trends using Breeding Bird Survey (BBS) data for 25 upland species and 12 riparian species, and mapped the geographic patterns of avian population change in these ecoregions. We examined population trends of birds for the Western BBS Region as a whole, and for each of the four physiographic provinces that comprise the Columbia Plateau, Great Basin, and Wyoming Basin ecoregions for the periods 1968–1983, 1984–2001, and 1968–2001.

Remarkably little is known about the actual distributions or population trend patterns of small mammals because there is no standardized survey comparable to the BBS. We compiled an extensive database from the published literature for 18 upland and 6 riparian small-mammal species. We incorporated the database into a geographic information system (GIS) to map presence and absence of each species in relation to presumed historical distributions, and determined the actual proportion of studies that documented presence of each species in suitable habitats across the Intermountain West.

We mapped geographic patterns of species richness for birds and mammals across the Intermountain West based on BBS presence/absence data and historical distributions.

Avian Population Trends and Responses to Habitat Alteration

We found significant declining population trends for 16 of the 25 upland bird species (64%) in one or more of the regions considered over at least one of the three periods examined. Only three of the 25 species (12%) exhibited significant long-term increases across the Western BBS Region, but none of these showed significant increasing population trends in any of the constituent physiographic provinces. Five of the 12 riparian species (42%) declined significantly over both the long term and short term across the Western BBS Region. Only one riparian species showed any significant increase in any region or time period at all. No significant trends were found for 14 of the 37 species (38%), but for 13 of these the lack of trends appeared to be a consequence of undersampling by the BBS rather than evidence of stability.

Birds that depend on native vegetation for their nests clearly are jeopardized by the loss or degradation of native vegetation. We examined each species' dependence on ground and shrub vegetation for nesting and foraging and found that nearly all of the 25 upland species (88%) are obligate ground/shrub nesters or foragers. Eighteen of the 25 species (72%) are obligately dependent on native ground and shrub vegetation both for nesting and foraging. Nine of the 12 riparian species (75%) are obligate ground or shrub nesters in riparian habitats of the three focal ecoregions.

The Columbia Plateau, Great Basin, and Wyoming Basin are among the least consistently sampled of all physiographic provinces covered by the BBS. The BBS routes that do exist in this region underrepresent sagebrush habitats, and some of the species we considered are poorly detected by BBS methodology. Given these limitations, it is both remarkable and alarming to find that nearly two-thirds of the upland bird species and nearly half of the riparian species we considered have declining population trends, especially given our strongly conservative filtering of BBS data. The most striking pattern seen in the significant trends at the ecoregion level was the overwhelmingly negative picture across the long-term period for the Columbia Basin.

Mammal Distributions and Abundances

Eleven of the 24 mammals we considered are endemic to the Intermountain West shrubsteppe: five ground squirrels, pygmy rabbit, four heteromyid rodents (Great Basin pocket mouse, dark kangaroo mouse, pale kangaroo mouse, chisel-toothed kangaroo rat), and the Townsend's pocket gopher.

Of the 19 species for which adequate trapping data were available, only one species (Great Basin pocket mouse) was found in more than 62% of potentially suitable localities. Based on a combination of field studies and known ecological requirements, 21 of 24 (88%) small-mammal species respond negatively to the effects of livestock grazing. Eleven of 18 (61%) upland mammals responded negatively to the presence of exotic plant species, but most riparian species exhibited essentially neutral responses to the presence of exotic vegetation if it supplied dense cover.

Our analysis of field studies that used appropriate trapping methods in suitable habitats is the first comprehensive attempt to quantify actual presence and absence of species across the region. We were surprised by the high frequency with which species were found to be missing in studies that had focused exclusively on suitable locations. The high percentages of studies that failed to find species where expected should raise concern regarding the actual current extent of populations relative to standard range maps of these species.

Geographic Patterns of Species Richness and Community Stability

Species richness for upland birds was concentrated in the three primary shrubsteppe ecoregions, indicating an extraordinary degree of dependence by this suite of species on shrubsteppe landscapes of the Columbia Plateau, Great Basin, and Wyoming Basin. Areas of highest species richness included the breadth of the Columbia Plateau extending from southeastern Oregon to easternmost Idaho, the eastern two-thirds of the Great Basin, and the southwestern portion of the

Wyoming Basin. Virtually no areas within these three ecoregions exhibited high species richness for riparian birds.

Species composition of upland shrubsteppe bird communities compared between the 1968–1983 and 1984-2001 periods varied little across most of the three primary shrubsteppe ecoregions. In sharp contrast to upland birds, community composition of riparian birds varied substantially between the two periods. Given the relative rarity and ecological importance of riparian habitats within shrubsteppe landscapes, the high degree of instability in community structure of riparian birds should raise great concern as a reflection of the poor ecological condition of riparian habitats across much of the Columbia Plateau, Great Basin, and Wyoming Basin ecoregions.

Species richness for small mammals was far more concentrated within the three primary shrubsteppe ecoregions compared to the results for birds. For the 18 upland mammals, highest species richness occurred in southeastern Oregon and northwestern Nevada in the Columbia Plateau, and across all but the southeasternmost portion of the Great Basin. Species richness for mammals was markedly lower in the Wyoming Basin, partly as a consequence of the restricted geographic ranges for many of the endemic species. The high degree of endemism among small mammals of the shrubsteppe is likely even greater than species-level ranges indicate. We believe that genetic analyses of upland and riparian small mammals would provide further examples of such "cryptic" species as the narrowly distributed, endemic ground squirrels.

In addition to the much lower species richness found for upland mammals in the Wyoming Basin, north-central Oregon and eastern Washington were relatively depauperate in both shrubsteppe bird and mammal species. We interpret this pattern as a reflection of the high proportion of these landscapes that has been converted to agricultural production.

Our maps of species richness for birds and for small mammals can be integrated with the recent detailed vegetation-mapping results of Knick et al. (2003) to guide future conservation efforts from the standpoint of overall biodiversity of species most closely tied to shrubsteppe landscapes.

Conclusions

Range maps created by connecting the dots among sites where a species has been captured do not paint a realistic picture, especially in the highly altered and fragmented shrubsteppe landscapes of today. For small terrestrial mammals in particular, our results support the view that many of these species now exist only as small, disconnected populations isolated from each other by unsuitable habitats across which they cannot disperse. Many of the bird and mammal species we examined have broad geographic ranges, but our spatially explicit analyses of actual trapping and BBS data, along with previous work on shrubsteppe bird population dynamics emphatically demonstrate this point: It is completely untenable to assume species' presence based simply on presence of appropriate habitat in shrubsteppe landscapes of the Intermountain West.

Some of the species included in our analyses were already known to be declining or rare. Nevertheless, given the number of species analyzed and the breadth of ecological roles encompassed, we expected to find that conservation concern would prove unwarranted for a significant number of the species we examined. Based on the information presented in this report, we find no basis for optimism about the prospects in the Intermountain West of any of the 61 species we examined. The results of our analyses present an overall picture of an ecosystem teetering on the edge of collapse (Knick et al. 2003). It is clear that the bird and small mammal species dependent upon Intermountain West shrubsteppe landscapes are providing the signals that they are at risk.

INTRODUCTION

Landscapes dominated by sagebrush (*Artemisia* spp.) extend across large portions of 11 states in the Intermountain West and comprise one of the most extensive habitat types in the entire United States. These cold-desert ecosystems, the so-called western rangelands, appear relatively simple in their ecological structure and function. Less than 150 years ago, however, sagebrush ecosystems were considerably more complex and biologically rich. Today, sagebrush shrubsteppe constitutes one of North America's most imperiled and neglected ecosystems (Noss and Peters 1995, Mac et al. 1998) due to the profound, ecologically transformative influences of livestock grazing, followed by alteration of natural fire regimes and consequent invasion by exotic plant species (Bock et al. 1993, Fleischner 1994, Saab et al. 1995, Rotenberry 1998, Young and Sparks 2002).

The sagebrush biome previously covered 63 million hectares (156 million acres) of western North America, but very little remains undisturbed or unaltered from its condition prior to Euro-American settlement (West 1996). The inherent resilience of these ecosystems has been lost and the ability to resist invasion and respond to disturbance has been compromised. More than 60% of remaining sagebrush steppe now has either exotic annual grasses in the understory or has been converted completely to non-native annual grasslands (West 2000). Enormous areas have been transformed into monocultures of introduced, noxious plant species useful to neither native animals nor livestock (Mack 1981, West 1996, Brooks and Pyke 2001). More than 90% of the region's flowing waters and their associated riparian habitats, the critical lifeblood of these arid and semiarid landscapes, have been compromised by domestic livestock and agricultural development (Chaney et al. 1990, Ohmart 1994). Many streams that once flowed year-round now flow only intermittently; many others have disappeared in their entirety.

The extensive geographic distribution of sagebrush depicted in vegetation maps (Fig. 1) conveys a sense of optimism for the conservation health of this plant community and its animal inhabitants. That presumption, however, is misplaced. Numerous human-caused impacts have contributed to the extraordinary fragmentation (Fig. 2) and degradation of sagebrush habitats across their widespread distribution, resulting in severe ecological and economic challenges (Knick et al. 2003). Land managers have used prescribed fires, mechanical treatments, biological agents, and herbicides to remove sagebrush from large areas for reseeding with non-native grasses, principally to provide forage for livestock (Pechanec et al. 1965, Vale 1974, Bureau of Land Management 1991). Ag-

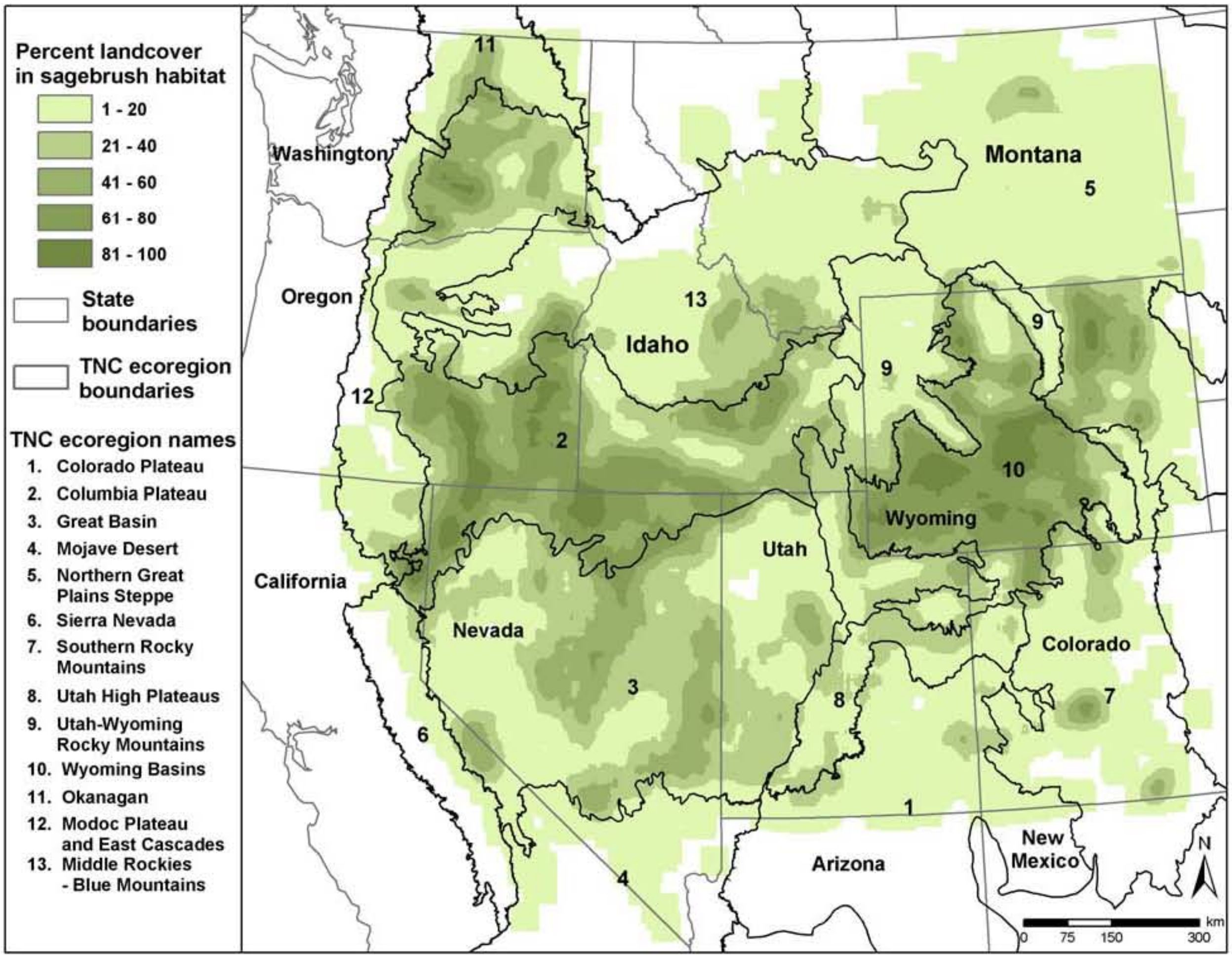

Figure 1. Distribution of sagebrush (from Knick et al. 2003). Map depicts percent of land cover within 25-km radii of each map cell dominated by tall sagebrush, produced by resampling the base map to a 2.5 km resolution. Reprinted by permission of the Cooper Ornithological Society.

riculture, mining, energy development (oil, gas, and coal-bed methane), powerline and natural-gas corridors, urbanization, and expansion of road networks have fragmented landscapes or completely eliminated sagebrush from extensive areas (Noss et al. 1995, Hann et al. 1997). These changes have pushed many sagebrush systems beyond ecological thresholds for potential recovery (Laycock 1991, West and Young 2000). The cumulative effects of land use and habitat degradation are moving sagebrush ecosystems toward ecological collapse and dysfunction.

Widespread concern for sagebrush-dependent wildlife due to loss of sagebrush habitats is a relatively recent phenomenon, and has focused primarily on sage-grouse (*Centrocercus* spp.), the flagship gamebird of these landscapes (Dobkin 1995, Connelly and Braun 1997, Braun 1998, Connelly et al. 2000). The federal government presently is in the midst of an assessment of Greater Sage-Grouse (*C. urophasianus*) in response to a petition filed to list the species as Endangered across its entire range (see Connelly et al. 2004). A listing of the Greater Sage-Grouse or any of the other widespread species dependent on sagebrush ecosystems would have major ramifications

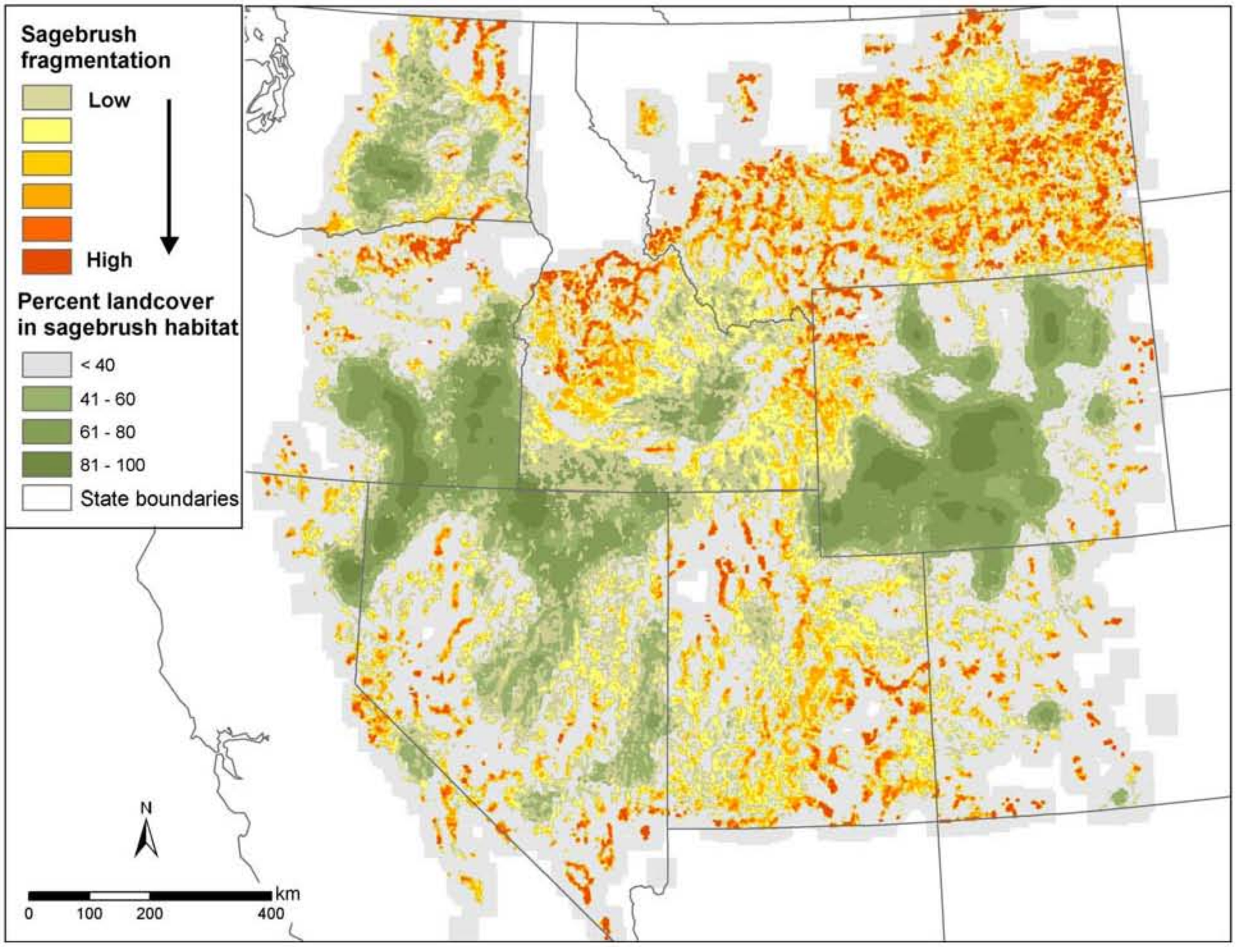

Figure 2. Sagebrush distribution is highly fragmented and much less extensive than large-scale maps suggest. The map depicts the ratio of the percent of land cover containing sagebrush (Fig. 1) to the amount of perimeter with other habitats. Dark-green areas indicate extensive distribution of sagebrush as the dominant feature in the landscape (area is much larger than perimeter), grading into gray areas (small area, small perimeter), and crossing a threshold at which fragmentation of sagebrush patches (low area, high perimeter) becomes the dominant landscape feature. Small-scale measures of perimeter were estimated by resampling the base map to a 500-m resolution and measuring the proportion of total edge between sagebrush and other habitat patches within 2.5 km of each map cell. Reprinted from Knick et al. (2003) by permission of the Cooper Ornithological Society.

for use and management of large areas of the western United States. Approximately two-thirds of the total area occupied by sagebrush in the western United States (Fig. 1) is managed by federal government agencies, primarily the U.S. Bureau of Land Management (Knick et al. 2003).

When an entire ecosystem is in trouble, it is not just the flagship species that face risks. Just as the Spotted Owl (*Strix occidentalis*) became a surrogate for numerous species of animals and plants that depend upon old-growth coniferous forests, there are many other wildlife and plant species besides sage-grouse that are largely or entirely dependent upon sagebrush shrub-steppe.

Among birds, shrubland and grassland species are declining faster than any other group of species in North America (Dobkin 1994, Saab and Rich 1997, Paige and Ritter 1999). These species represent an important component of the biodiversity of the western United States. Species that are most dependent on sagebrush ecosystems, such as Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphispiza belli*), and Sage Thrasher (*Oreoscoptes montanus*), may be important predictors of impending collapse in sagebrush ecosystems because of their sensitivity to multiscale habitat changes (Rotenberry and Knick 1999, Knick and Rotenberry 2000, 2002).

Aside from the pygmy rabbit (*Brachylagus idahoensis*), whose Columbia Basin populations were listed recently as Endangered (U.S. Fish and Wildlife Service 2003), little attention has been paid to the conservation status or needs of small mammal species or of other taxa (e.g., insects, amphibians, reptiles) tied to shrubsteppe ecosystems in the Intermountain West (Wisdom et al. 2002). Concern for a few scattered populations of some species (e.g., Preble's shrew [*Sorex preblei*], little pocket mouse [*Perognathus longimembris*], kit fox [*Vulpes macrotis*]) has occurred at the level of individual states, but the larger picture of regionwide conservation status or ecological condition has not been assessed. Indeed, in spite of being endemic to shrubsteppe landscapes of the region, some small mammal species have received no attention from any state or federal agencies (e.g., Townsend's pocket gopher [*Thomomys townsendii*], sagebrush vole [*Lemmiscus curtatus*]).

Based on our consideration of the entire suite of bird and small mammal species that occur in shrubsteppe landscapes of the region, we distilled a list of 61 species that are characterized by complete or extensive dependence on shrubsteppe ecosystems in the Intermountain West. We undertook a broad-scale analysis to determine what is presently known about distributions, abundances, and sensitivity to habitat disturbance in order to assess the current state of knowledge and the conservation status of these species. We compiled and analyzed information for each of these species from the 11 western states that provide significant sagebrush habitat, and summarized this information in individual species accounts that form much of this report. The individual accounts detail what is known about current and historical distributions, habitat requirements and associations, population sizes and trends, susceptibility to habitat changes and impacts, and current state or federal status or listing. Guided by the results of Knick et al. (2003), we further focused our analyses on the three ecoregions (Columbia Basin, Great Basin, and Wyoming Basin) with the greatest percentages of sagebrush land cover (hereafter referred to as the three primary shrubsteppe ecoregions). We analyzed regional and subregional population trends for birds, mapped patterns of species richness for birds and mammals, and provided the first maps to depict geographic patterns of avian population change in these ecoregions.

METHODS

SPECIES SELECTION: BIRDS

We selected species for inclusion in our analyses based on a hierarchy of criteria. For upland bird species, the primary criterion was predominant or complete association with shrubsteppe landscapes in the 11 western states. Our second criterion was the extent to which a species' total geographic range was confined to the geographic area of interest, or the extent to which important population segments of a species occurred within shrubsteppe landscapes of the 11 western states. Some species that are now much reduced in the region, such as Sharp-tailed Grouse, were included based on their more extensive distributions and greater abundances during historical times. The preceding criteria were assessed based on the relative abundance maps produced by the North American Breeding Bird Survey (BBS; Sauer et al. 2003), and the comprehensive individual species accounts of the *Birds of North America* project (American Ornithologists' Union 1992–2003).

Most riparian bird species of these landscapes are widely distributed beyond the geographic region of interest, but within shrubsteppe landscapes they occur primarily or exclusively in riparian habitats. Thus, riparian species were selected based on a combination of the preceding criteria and the species' predominant dependence on riparian habitats within the region, as determined by previous regional conservation assessments (e.g., Saab and Rich 1997, Paige and Ritter 1999) and by scientific studies of riparian birds in the region (e.g., Dobkin and Wilcox 1986, Tewksbury et al. 2002, Earnst et al. 2004).

Based on the foregoing criteria, 25 species of upland birds and 12 species of riparian birds are included in our analyses (Table 1).

TABLE 1. Upland and riparian bird species closely associated with shrubsteppe landscapes in the Intermountain West.

Common name	Scientific name
Upland species	
Greater Sage-Grouse	*Centrocercus urophasianus*
Sharp-tailed Grouse	*Tympanuchus phasianellus*
Ferruginous Hawk	*Buteo regalis*
Prairie Falcon	*Falco mexicanus*
Long-billed Curlew	*Numenius americanus*
Burrowing Owl	*Athene cunicularia*
Gray Flycatcher	*Empidonax wrightii*
Loggerhead Shrike	*Lanius ludovicianus*
Gray Vireo	*Vireo vicinior*
Horned Lark	*Eremophila alpestris*
Sage Thrasher	*Oreoscoptes montanus*
Virginia's Warbler	*Vermivora virginiae*
Green-tailed Towhee	*Pipilo chlorurus*
Chipping Sparrow	*Spizella passerina*
Brewer's Sparrow	*Spizella breweri*
Vesper Sparrow	*Pooecetes gramineus*
Lark Sparrow	*Chondestes grammacus*
Black-throated Sparrow	*Amphispiza bilineata*
Sage Sparrow	*Amphispiza belli*
Savannah Sparrow	*Passerculus sandwichensis*
Grasshopper Sparrow	*Ammodramus savannarum*
White-crowned Sparrow	*Zonotrichia leucophrys*
Western Meadowlark	*Sturnella neglecta*
Brewer's Blackbird	*Euphagus cyanocephalus*
Scott's Oriole	*Icterus parisorum*
Riparian species	
Yellow-billed Cuckoo	*Coccyzus americanus*
Belted Kingfisher	*Ceryle alcyon*
Willow Flycatcher	*Empidonax traillii*
Veery	*Catharus fuscescens*
Swainson's Thrush	*Catharus ustulatus*
Orange-crowned Warbler	*Vermivora celata*
Nashville Warbler	*Vermivora ruficapilla*
Yellow Warbler	*Dendroica petechia*
MacGillivray's Warbler	*Oporornis tolmiei*
Wilson's Warbler	*Wilsonia pusilla*
Song Sparrow	*Melospiza melodia*
Bullock's Oriole	*Icterus bullockii*

SPECIES SELECTION: MAMMALS

Large mammals such as ungulates and carnivores generally have been well studied and typically are central to much of wildlife management, especially in the western United States. We focused our efforts on the far less well-known spectrum of small mammals, defined as species with body mass of less than ~1 kg.

In addition to small size, we used two additional criteria for inclusion of species in the analyses. First, within the 11 western states the species must be associated predominantly or completely with shrubsteppe landscapes. Second, a majority of the species' total geographic range must fall within the geographic area of interest. Geographic distributions for each species were determined from the mammal distribution maps of Hall (1981) and from the *Mammalian Species* accounts (which generally were reproduced from Hall with little alteration) published by the American Society of Mammalogists (1974–2002). Hall (1981) created his maps for each species simply by circumscribing the most peripheral distribution records. Between sparse

TABLE 2. Upland and riparian mammal species closely associated with shrubsteppe landscapes in the Intermountain West.

Common name	Scientific name
Upland species	
Merriam's shrew	*Sorex merriami*
Preble's shrew	*Sorex preblei*
Spotted bat	*Euderma maculatum*
Pallid bat	*Antrozous pallidus*
Pygmy rabbit	*Brachylagus idahoensis*
Idaho ground squirrel	*Spermophilus brunneus*
Merriam's ground squirrel	*Spermophilus mollis*
Piute ground squirrel	*Spermophilus canus*
Townsend's ground squirrel	*Spermophilus townsendii*
Washington ground squirrel	*Spermophilus washingtoni*
Little pocket mouse	*Perognathus longimembris*
Great Basin pocket mouse	*Perognathus parvus*
Dark kangaroo mouse	*Microdipodops megacephalus*
Pale kangaroo mouse	*Microdipodops pallidus*
Chisel-toothed kangaroo rat	*Dipodomys microps*
Desert woodrat	*Neotoma lepida*
Sagebrush vole	*Lemmiscus curtatus*
Kit fox	*Vulpes macrotis*
Riparian species	
Water shrew	*Sorex palustris*
Townsend's pocket gopher	*Thomomys townsendii*
Western harvest mouse	*Reithrodontomys megalotis*
Long-tailed vole	*Microtus longicaudus*
Montane vole	*Microtus montanus*
Western jumping mouse	*Zapus princeps*

distribution records, Hall made informed guesses to fill out distributions. Detailed geographic distributions are nonexistent for virtually all small mammals of the western United States. Habitat affinities were assessed from individual species accounts of the *Mammalian Species* series, regional handbooks devoted to mammals (e.g., Verts and Carraway 1998), and recent studies from the primary scientific literature.

Based on the foregoing criteria, 18 species of upland mammals and 6 species of riparian mammals are included in our analysis (Table 2).

Population Trends and Spatial Analyses: Birds

For birds, we report significant ($P \leq 0\ .05$) regional BBS trends developed using a linear route regression methodology (hereafter called standard BBS analysis; Sauer et al. 2003). We recognize that low sample sizes confound the ability to accurately discern population trends. This problem is especially common in the Intermountain West, which is the region most undersampled by the BBS in the conterminous 48 states (Lawler and O'Connor 2004). We adopted a conservative approach to population trend assessments by using a minimum sample size criterion of $n > 10$ BBS routes for presence of a species within a physiographic province for each time period analyzed. Statistically significant (but biologically questionable) trends with marginal sample sizes are identified as such. For species with $n \leq 10$ BBS routes in a physiographic province, we did not attempt to estimate population trends, as such trends are so unreliable statistically as to be meaningless.

BBS trend analyses can only be calculated by physiographic provinces, which roughly follow the same geographic boundaries as Nature Conservancy ecoregions (Fig. 3). The only exception in our area is division of the Great Basin ecoregion into two physiographic provinces (Great Basin Desert, Basin and Range). Because of the general pattern of very small sample sizes in these two physiographic provinces, we frequently present combined results from both provinces and simply refer to them collectively as "Great Basin."

For the avian literature review, we relied heavily on the *Birds of North America* species accounts to provide the requisite information. Where further information was needed, recent primary literature was reviewed for additional information about habitat affinities and for specific factors known to influence populations. To depict the distribution of bird species across the region, we modified the relative abundance

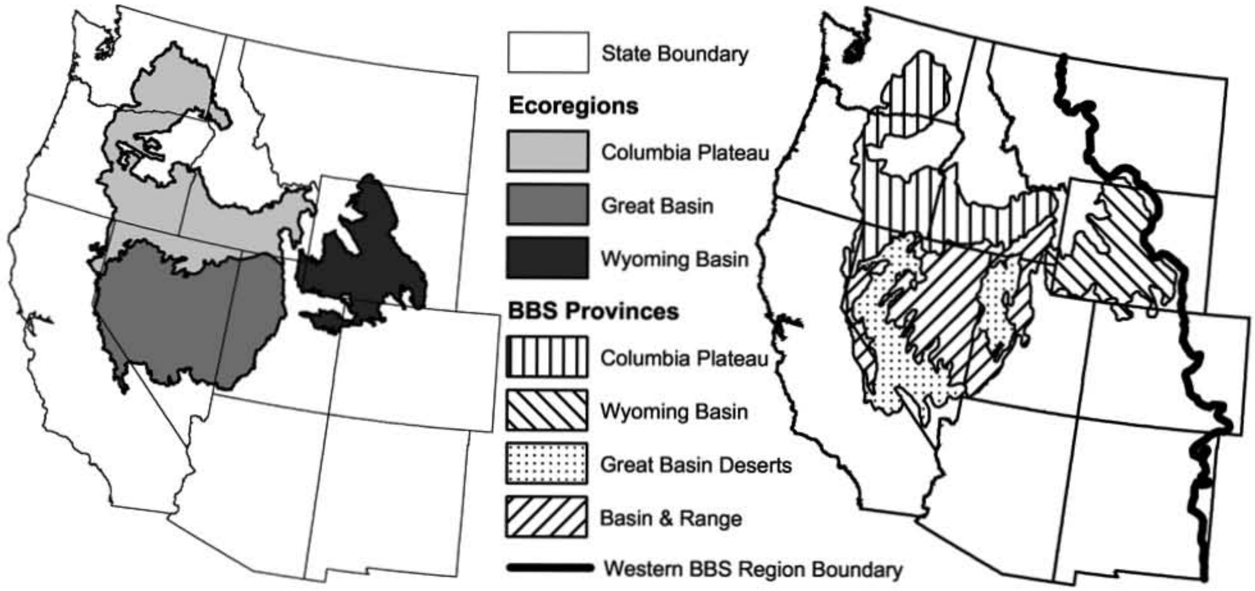

Figure 3. Overlap between the three primary shrubsteppe ecoregions (left) and four Breeding Bird Survey (BBS) physiographic provinces (right). Together, the BBS provinces Great Basin Deserts (stippled) and Basin and Range (right hatch) correspond closely to the Great Basin ecoregion. The Western BBS Region encompasses the entire area west of the indicated boundary (bold line).

maps produced from BBS data by Sauer et al. (2003).

For each species, we acquired BBS data for the years 1968–2001 from the 11 western states. Bird abundance and weather data were synthesized by plot and year to create a single database for each species that described where a species was and was not detected. Data collected under adverse weather conditions were excluded from our analyses. We created new maps from these databases using inverse distance weighting in conjunction with a smoothing function (ESRI 2003). Because many survey routes have been abandoned over the years and inconsistent data are well known to skew analyses, we filtered the data conservatively to include only routes that had been surveyed at least four times in each of the time periods we evaluated (1968–1983, 1984–2001). These criteria were met by 349 routes. Mean abundances over each period were used in the natural neighbor function of ArcGIS (ESRI 2003) to interpolate potential abundances at locations between routes. The product grids were reclassified into discrete categories and converted into shapefiles. These shapefiles depicted the distribution of locations with potentially higher bird abundances for each species and showed changes in abundances between the two analysis periods. Additionally, the differences in mean abundances between the two periods were processed, using similar methodology, so that spatial patterns of declines and increases in abundances could be examined.

Population and Spatial Analyses: Mammals

In contrast to the BBS for birds, no long-term, standardized surveys exist to monitor small-mammal populations. As a result, no index to relative abundances exists across the geographic distribution of species. Thus, the only available data was what could be mined from literature sources. We focused on retrieving data concerning habitat associations, preferred habitat characteristics, population density estimates, and factors that influence population numbers. We reviewed the scientific literature for the selected mammal species by using three database search engines widely available in university libraries and elsewhere: BIOSIS Previews (1990–Summer 2003), Biological Abstracts (1991–Summer 2003), and Wildlife & Ecology Studies Worldwide (1935–2003). We specifically selected and reviewed studies that were conducted in the Intermountain West, and reviewed the literature cited in each paper for additional studies that were older or otherwise absent from the search engines. This continued as an iterative process until no new papers could be located that addressed applicable topics or contained useful data.

We used the authors' study area descriptions for all field studies going back to 1938 to incorporate all localities into a geographic information system (GIS) that mapped sampling methodology, habitats sampled, and species occurrence onto study locations. Some papers reported data from multiple study sites, and we incorporated each site separately into the GIS if the study area descriptions provided sufficient information. Using the compiled database, we mapped presence and absence of each species based on the trapping results in relation to presumed historical distributions, and determined the actual proportion of studies that documented presence of each species in suitable habitats across the Intermountain West.

Geographic Patterns of Species Richness and Community Stability

To evaluate broad-scale patterns of species richness, we created maps of total species richness by using presence-absence data derived from BBS data for birds, and by overlaying the maps derived from Hall (1981) for mammals. To evaluate the temporal stability of community structure for birds, we compared Jaccard's index values (Magurran 1988) for riparian and for upland bird species compared between the 1968–1983 and 1984–2001 periods. For each BBS route, the Jaccard index is a simple binary measure of species presence and absence that ranges from 0 if the two time periods have no species in common to 1 if both sets of species are identical.

We recognize that the presumed distributions for birds (Sauer et al. 2003) and mammals (Hall 1981) are not without errors, particularly as a result of ecologically unsuitable habitats embedded in matrices of suitable habitat (or the converse). These distributions, however, are the best science-based maps available and they adequately achieve their intended purpose, which is to depict the general distribution of the species and to demonstrate the species' association with Intermountain West landscapes.

RESULTS

Avian Population Trends

Population trends calculated by standard BBS analysis for each species are shown in Table 1 of each individual species account (see accounts for animal scientific names and Appendix A for plant scientific names). We examined trends for the Western BBS Region as a whole (Fig. 3), and for each of the four physiographic provinces that comprise the focal region (Columbia Plateau, Great Basin Desert, Basin and Range, and the Wyoming Basin), for the 1968–1983, 1984–2001, and 1968–2001 periods.

Upland species. Significant declining population trends were found for 16 of the 25 upland bird species in one or more of the regions considered over at least one of the three periods examined (Table 3). Long-term declines (1968–2001) were found for 10 species across the Western Region as a whole, and for eight species within one or more of the four physiographic provinces. Among the latter eight species, all but one (Sage Thrasher) also exhibited long-term declines across the Western Region. Significant short-term declines (1968–1983 or 1984–2001) occurred for 13 species across the

TABLE 3. Population trends for birds based on Breeding Bird Survey (BBS) data for the Western Region and for the Columbia Plateau, Great Basin Desert, Basin and Range, and Wyoming Basin physiographic provinces. Only statistically significant long-term (1968–2001) and short-term (1968–1983 or 1984–2001) trends are shown. For each analysis, a species must have been present on more than 10 BBS routes within a province or region.

	Western BBS Region				Individual provinces			
	Long-term decline	Long-term increase	Short-term decline	Short-term increase	Long-term decline	Long-term increase	Short-term decline	Short-term increase
Upland species								
Greater Sage-Grouse								
Sharp-tailed Grouse	×		×					
Ferruginous Hawk		×						
Prairie Falcon			×					
Long-billed Curlew						×		
Burrowing Owl		×						
Gray Flycatcher		×						
Loggerhead Shrike	×		×		×		×	
Gray Vireo								
Horned Lark	×		×		×		×	
Sage Thrasher					×		×	
Virginia’s Warbler								
Green-tailed Towhee			×				×	
Chipping Sparrow	×		×		×			
Brewer’s Sparrow	×				×			×
Vesper Sparrow							×	×
Lark Sparrow			×					
Black-throated Sparrow	×		×		×		×	
Sage Sparrow			×	×				×
Savannah Sparrow				×				×
Grasshopper Sparrow	×		×		×		×	
White-crowned Sparrow	×		×					
Western Meadowlark	×		×				×	×
Brewer’s Blackbird	×		×		×			
Scott’s Oriole								
Total (of 25 upland species)	10	3	13	2	8	1	8	5
Riparian species								
Yellow-billed Cuckoo								
Belted Kingfisher								
Willow Flycatcher	×		×				×	
Veery								
Swainson’s Thrush								
Orange-crowned Warbler	×		×					
Nashville Warbler								
Yellow Warbler								
MacGillivray’s Warbler								
Wilson Warbler	×		×					
Song Sparrow	×		×			×		
Bullock’s Oriole	×		×					
Total (of 12 riparian species)	5	0	5	0	0	1	1	0
Total (of 37 species)	15	3	18	2	8	2	9	5

Western Region, and for eight species in one or more physiographic provinces. Among the latter eight species, all but two (Sage Thrasher and Vesper Sparrow), also exhibited short-term declines across the Western Region.

Only three of the 25 species exhibited significant long-term increases across the Western Region (Table 3), but none of the three exhibited significant increasing trends in any of the four physiographic provinces across any time period. Two species (Sage Sparrow and Savannah Sparrow) showed significant short-term increases across the Western Region, and both exhibited short-term increases at the physiographic province level as well. Sage Sparrows did not exhibit any significant long-term population trends, but declined significantly across the Western Region during 1968–1983, followed by significant increasing trends in 1984–2001 in the Western Region as a whole and in the Great Basin. Similarly, Savannah Sparrows showed no significant long-term trends in any region, but increased significantly across the 1968–1983 period in the Western Region and in 1984–2001 in the Wyoming Basin. Three additional species (Brewer's Sparrow, Vesper Sparrow, and Western Meadowlark) exhibited short-term increases in some physiographic provinces, but Brewer's Sparrow also showed long-term declining trends across the Western Region and Columbia Plateau, and the other two species both had significant long-term (Western Meadowlark) and short-term (Vesper Sparrow and Western Meadowlark) declining trends in other physiographic provinces.

Riparian species. Five of the 12 riparian species exhibited significant long-term and short-term declines across the Western Region (Table 3). Only the Willow Flycatcher showed significant declines in at least one physiographic province as well. No riparian species showed any significant increases for any region or time period considered, with the sole exception of a long-term increasing trend by the Song Sparrow in the Basin and Range province.

For the majority of species considered, BBS sample sizes were inadequate to detect statistically reliable trends at the physiographic province level. The few significant trends found for species at these smaller scales (Table 4) generally mirrored significant trends for the BBS Western Region as a whole (Table 3). Of the 11 species with significant declining trends at the ecoregion level, eight had significant declines in a single ecoregion, two had significant declines in two of the three ecoregions (Sage Thrasher and Grasshopper Sparrow), and only the Loggerhead Shrike had significant declines in all three ecoregions. Six of the seven species with significant declines in the Columbia Basin and all three species with significant declines in the Great Basin were declining across the entire 1968–2001 period (Table 4). The five species with significant declines in the Wyoming Basin showed a more mixed temporal picture of decline (two long term and three in 1968–1983). The most striking pattern seen in the significant trends at the ecoregion level was the overwhelmingly negative picture across the long-term period for the Columbia Basin (Table 4).

Based on our analyses of the selected BBS routes and their spatial distribution of per route abundances, we categorically ranked species by relative abundances across the region as a whole (Table 5). In spite of substantial differences in relative abundance among species, relative rarity did not completely preclude finding a statistically significant population trend in the Western BBS Region for some of these species (e.g., Sharp-tailed Grouse, Ferruginous Hawk, Prairie Falcon). The four upland bird species for which no significant population trends were detected (Greater Sage-Grouse, Gray Vireo, Virginia's Warbler, Scott's Oriole), however, comprised 50% of all species in the lowest relative abundance category (Table 5). For riparian birds, the most abundant species were comparable in relative abundances to upland species in the

TABLE 4 Avian population trends derived from Breeding Bird Survey data for the three primary shrubsteppe ecoregions of the Intermountain West (Columbia Plateau, Great Basin[a], Wyoming Basin). Survey data were analyzed over a long-term period (1968–2001) and two short-term periods (1968–1983 and 1984–2001). Only statistically significant increases (+) or decreases (–) are shown; the relevant periods are indicated.

	Columbia Plateau		Great Basin		Wyoming Basin	
	Trend	Period	Trend	Period	Trend	Period
Upland species						
Long-billed Curlew	+	1968–2001				
Loggerhead Shrike	–	1968–2001	–	1968–2001	–	1968–1983
Horned Lark	–	1968–2001				
	–	1984–2001				
Sage Thrasher	–	1968–2001	–	1968–2001		
			–	1968–1983		
Green-tailed Towhee					–	1968–1983
Chipping Sparrow					–	1968–2001
Brewer's Sparrow	–	1968–2001			+	1984–2001
Vesper Sparrow			+	1968–1983	–	1968–2003
					+	1984–2001
Black-throated Sparrow	–	1968–2001				
	–	1984–2001				
Sage Sparrow			+	1984–2001		
Savannah Sparrow					+	1984–2001
Grasshopper Sparrow	–	1968–2001			–	1968–2001
	–	1984–2001				
Western Meadowlark	+	1968–1983				
	–	1984–2001				
Brewer's Blackbird			–	1968–2001		
			–	1984–2001		
Riparian species						
Willow Flycatcher	–	1984–2001				
Song Sparrow			+	1968–2001		

[a]Great Basin ecoregion includes data from two BBS physiographic provinces: Great Basin Desert, Basin and Range.

intermediate range of abundances. For all birds, most of the least abundant species appeared too infrequently or too inconsistently in the BBS data set at the level of individual shrubsteppe ecoregions to detect any statistically significant population trends.

Avian Spatial Analyses

Mapping based on temporal changes in BBS data generally corroborated our BBS population trend analyses. Our spatial analyses illustrated the geographic pattern of change in relative abundances for each species (Figure 2 in each of the species accounts that follow), and the spatial pattern of changes in absolute abundances over time (Figure 3 in the species accounts). For each species, we can now see the actual geographic pattern of declines and increases within each ecoregion.

For example, our spatial analyses suggested that Loggerhead Shrike population declines were widespread in the Western BBS Region, and especially severe in the three primary shrubsteppe ecoregions. Comparison of shrike distributions between the 1968–1983 and 1984–2001 periods indicated population losses from

TABLE 5. Relative abundances of bird species based on analyses of 349 Breeding Bird Survey (BBS) routes surveyed at least four times in each of two periods, 1968–1983 and 1984–2001, in the Western BBS Region. Symbols indicate significant declining (–) or increasing (+) trends found for at least one of three time periods in at least one region or physiographic province. Five species had both positive and negative trends.

TABLE 5A. Upland Species

Relative abundance

Less abundant ⟶ More abundant

Sharp-tailed Grouse (–)	Loggerhead Shrike (–)	Sage Thrasher (–)	Horned Lark (–)	Brewer's Blackbird (–)
Prairie Falcon (–)	Green-tailed Towhee (–)	Chipping Sparrow (–)		
	Grasshopper Sparrow (–)	Lark Sparrow (–)	Brewer's Sparrow (–, +)	Western Meadowlark (–, +)
Greater Sage-Grouse		Black-throated Sparrow (–)		
Gray Vireo	Long-billed Curlew (+)	White-crowned Sparrow (–)		
Virginia's Warbler	Gray Flycatcher (+)			
Scott's Oriole		Vesper Sparrow (–, +)		
		Sage Sparrow (–, +)		
Ferruginous Hawk (+)				
Burrowing Owl (+)		Savannah Sparrow (+)		

TABLE 5B. Riparian Species

Relative abundance

Less abundant ⟶ More abundant

Yellow-billed Cuckoo	Orange-crowned Warbler (–)	Willow Flycatcher (–)	Song Sparrow (–, +)
	Wilson's Warbler (–)	Bullock's Oriole (–)	
			Yellow Warbler
	Belted Kingfisher		
	Veery		
	Swainson's Thrush		
	Nashville Warbler		
	MacGillivray's Warbler		

large portions of the Columbia Plateau, from the western two-thirds of the Great Basin, and from the western portion of the Wyoming Basin (Fig. 8.2 and 8.3, p. 48).

As an example of an apparently increasing species, Ferruginous Hawk population increases appeared confined to several relatively small and disjunct areas of the West. Most of the areas showing increasing population trends were in various parts of Montana and in southeastern Colorado/northeastern New Mexico, areas that lie completely outside of the primary shrubsteppe ecoregions (Fig. 3.3, p. 37).

Only five of the 37 species (Sharp-tailed Grouse, Yellow-billed Cuckoo, Gray Vireo, Virginia's Warbler, and Scott's Oriole) were detected so infrequently on BBS routes within the three primary shrubsteppe ecoregions that no meaningful spatial analyses could be conducted.

The changes in relative abundances depicted on the maps in the individual species accounts accurately show the direction of relative numerical change and the regions in which the changes occurred. The actual percentage change in area (from 1968–1983 to 1984–2001) over which each species was predicted to have higher or lower abundances, however, was strongly influenced by the spatial pattern of BBS routes included in the analyses. The problem of undersampling (too few BBS routes relative to the very large geographic area considered) across all three shrubsteppe ecoregions clearly affected the accuracy of our numerical estimates of these areas. A substantially larger number of consistently sampled BBS routes is needed in all three ecoregions to refine these estimates.

Avian Susceptibility to Habitat Alteration

Birds that depend on native vegetation for the supporting structure and protective cover of their nests clearly are jeopardized by the complete loss of native vegetation (e.g., from agricultural conversion). The effects of livestock grazing, invasion by exotic plant species, and alteration of natural fire regimes can be much less obvious and sometimes synergistic.

As an index to their dependence on intact native plant communities, we examined each species' degree of dependence on ground and shrub vegetation for nesting and foraging. Not surprisingly given their close association with shrubsteppe plant communities, virtually all upland species are obligate ground/shrub nesters or foragers (Table 6). Eighteen of the 25 species are obligately dependent on native ground and shrub vegetation both for nesting and foraging. Only Ferruginous Hawk and Prairie Falcon are not directly dependent on ground and shrub vegetation for nesting or foraging, although clearly much of their prey is wholly dependent on ground and shrub vegetation for food or cover.

Nine of the 12 riparian species are obligate ground or shrub nesters in riparian habitats of the three focal ecoregions (Table 6). Only six species obligately forage on ground and shrub vegetation, although three additional species (Orange-crowned, Nashville, and Yellow Warblers) forage extensively in the shrub layer in addition to foraging in trees.

Mammal Distributions and Abundances

Eleven of the 24 mammals we considered are endemic to the Intermountain West shrubsteppe: five ground squirrels, pygmy rabbit, four heteromyid rodents (Great Basin pocket mouse, dark kangaroo mouse, pale kangaroo mouse, chisel-toothed kangaroo rat), and the Townsend's pocket gopher. All but the gopher are upland species.

Quantitative details of trapping results (catch per unit effort, estimated densities, etc.) are provided in the Population Data section of each species account for all studies conducted in the three primary shrubsteppe ecoregions. Presence and absence of each species based on

TABLE 6. Susceptibility of upland and riparian shrubsteppe birds to livestock grazing, exotic plant invasion, and unnaturally frequent fires, as indicated by nesting and foraging dependence on native ground and shrub vegetation.

Species	Obligate ground or shrub nester	Obligate ground or shrub forager
Upland species		
Greater Sage-Grouse	×	×
Sharp-tailed Grouse	×	×
Ferruginous Hawk		
Prairie Falcon		
Long-billed Curlew	×[a]	×
Burrowing Owl		×
Gray Flycatcher	×	
Loggerhead Shrike	×	×
Gray Vireo	×	
Horned Lark	×	×
Sage Thrasher	×	×
Virginia's Warbler	×	×
Green-tailed Towhee	×	×
Chipping Sparrow		×
Brewer's Sparrow	×	×
Vesper Sparrow	×	×
Lark Sparrow	×	×
Black-throated Sparrow	×	×
Sage Sparrow	×	×
Savannah Sparrow	×	×
Grasshopper Sparrow	×	×
White-crowned Sparrow	×	×
Western Meadowlark	×	×
Brewer's Blackbird	×	×
Scott's Oriole		
Upland species total	20 of 25	20 of 25
Riparian species		
Yellow-billed Cuckoo		
Belted Kingfisher		
Willow Flycatcher	×	×
Veery	×	×
Swainson's Thrush	×	×
Orange-crowned Warbler	×	
Nashville Warbler	×	
Yellow Warbler	×	
MacGillivray's Warbler	×	×
Wilson's Warbler	×	×
Song Sparrow	×	×
Bullock's Oriole		
Riparian species total	9 of 12	6 of 12
Overall total	29 of 37	26 of 37

[a] The only obligate ground-nesting species known to fare well in exotic annual grasslands.

the trapping results are shown in the Figure 1 maps of each species account in relation to presumed historical distributions. Only five species were found in locations significantly beyond the boundaries of their presumed distributions: Preble's shrew, spotted bat, pallid bat, pygmy rabbit, and pale kangaroo mouse.

We summarized the results of all field studies that used suitable traps in appropriate habitats to determine the actual proportion of studies that documented presence of each species across the Intermountain West (Table 7). The potential for finding each species at each of these localities should be close to 100%. Numbers lower than 100% would indicate that the species had not been found consistently in appropriate habitat, despite appropriate trapping methods. As a conservative approach, we adopted a threshold of 70% as a criterion for reasonable predictability of a species' presence, given appropriate habitat within its presumed geographic range and adequate sampling effort with appropriate equipment. Of the 19 species for which suitable trapping data were available, only one species was found in more than 70% of sampled localities (Great Basin pocket mouse [80%]). No other species was found in more than 62% of potentially suitable localities (Table 7). Aside from the three species with extremely limited geographic ranges (Idaho, Townsend's, and Washington ground squirrels) and the two species devoid of suitable trapping data (Townsend's pocket gopher and kit fox), the least common species (i.e., present in ≤33% of potentially suitable sites) appeared to be Merriam's shrew, Preble's shrew, water shrew, spotted bat, pygmy rabbit, and long-tailed vole. Given the relatively large geographic ranges presumed for all but the three restricted ground squirrels, we found remarkably few field studies in the Intermountain West over the past 65 years that could be evaluated for presence of water shrew, pallid bat, and western jumping mouse (Table 7).

Mammalian Susceptibility to Habitat Alteration

Responses to loss or degradation of native plant communities due to livestock grazing or other disturbances, and responses to presence of exotic vegetation (principally cheatgrass) are provided in each species account. Comparative studies of small-mammal response to livestock grazing were found for 11 of the 24 species examined. These field studies compared small-mammal communities of moderately to heavily grazed upland or riparian habitats with those of lightly grazed or rested habitats (i.e., areas that had been withdrawn from livestock grazing, generally for one to several years). We classified each species' response as positive or negative only when the difference in mean trapping results between grazing treatments was ≥20%; we classified differences of <20% as neutral. Of the 62 comparisons, 46 were negative, nine were neutral, and seven were positive (Appendix B). Of the seven positive responses, however, five were from upland species that showed increased abundances in grazed riparian or mesic areas compared with ungrazed riparian or mesic areas, indicating that the effects of livestock grazing in moist habitats had converted them into habitats suitable for upland species.

A summary of small-mammal responses to livestock grazing based on field studies using adequate trapping methodology demonstrated overwhelmingly negative responses to the effects of livestock grazing for 12 species (Table 8). Based on the ecological requirements and known responses of ecologically similar species, an additional nine species have extremely high likelihood for negative responses to livestock grazing effects (Table 8). The likely effects of livestock grazing were not clearly negative only for the two bat species and the kit fox.

Negative responses to presence of exotic plant species have been demonstrated clearly for eight upland species, and can be inferred with high likelihood for three additional upland

TABLE 7. Presence or absence of upland and riparian small mammal species across the Intermountain West, based on field studies using suitable traps in appropriate habitats. Numbers of sites trapped are shown. Trapping success at these sites (final column), given that the species is actually present, should be close to 100%. Therefore, scores markedly lower than 100% (e.g., below 70%) suggest that the species is encountered substantially less often than expected.

	No. of sites		% of sites with species present
	Species present	Species absent	
Upland species			
Merriam's shrew	8	39	17
Preble's shrew	12	36	25
Spotted bat	17	70	20
Pallid bat	8	5	62
Pygmy rabbit[a]	19	192	9
Idaho ground squirrel[a]	54	126	30
Merriam's ground squirrel[a]	3[b]		
Piute ground squirrel[a]	22[b]		
Townsend's ground squirrel[a]	6[b]		
Washington ground squirrel[a]	46	133	26
Little pocket mouse	28	18	61
Great Basin pocket mouse[a]	51	13	80
Dark kangaroo mouse[a]	19	16	54
Pale kangaroo mouse[a]	12	11	52
Chisel-toothed kangaroo rat[a]	25	20	56
Desert woodrat	18	20	47
Sagebrush vole	31	21	60
Kit fox[c]			
Riparian species			
Water shrew	3	6	33
Townsend's pocket gopher[a,c]			
Western harvest mouse	34	38	47
Long-tailed vole	13	40	24
Montane vole	30	23	57
Western jumping mouse	8	5	62

[a]Endemic to the region.

[b]Studies conducted only at known active colonies.

[c]No site-specific trapping studies reported.

TABLE 8. Response to livestock grazing and response to dominance by cheatgrass (and other exotic plant species) by upland and riparian small mammal species across the Intermountain West, based on field studies using appropriate trapping methodology. Negative or positive responses, respectively, indicate decreased or increased abundances or productivity. Zeroes indicate no appreciable change in abundance or productivity. Parenthetical responses signify high likelihood of response based on ecological requirements and known response of ecologically similar species.

	Response to grazing	Response to exotic vegetation
Upland species		
Merriam's shrew	(–)	–
Preble's shrew	(–)	(–)
Spotted bat	unknown	unknown
Pallid bat	unknown	unknown
Pygmy rabbit[a]	(–)	–
Idaho ground squirrel[a]	(–)	–
Merriam's ground squirrel[a]	(–)	(–)
Piute ground squirrel[a]	–	–
Townsend's ground squirrel[a]	(–)	–
Washington ground squirrel[a]	–	(–)
Little pocket mouse	–	–
Great Basin pocket mouse[a]	–	0
Dark kangaroo mouse[a]	(–)	unknown
Pale kangaroo mouse[a]	(–)	unknown
Chisel-toothed kangaroo rat[a]	–	–
Desert woodrat	–	unknown
Sagebrush vole	–	–
Kit fox	unknown	unknown
Riparian species		
Water shrew	–	0
Townsend's pocket gopher[a]	(–)	(–)
Western harvest mouse	–	–/0
Long-tailed vole	–	–
Montane vole	–	–/0
Western jumping mouse	–	–/0

[a]Endemic to the region.

species (Table 8). Six upland species cannot be characterized with confidence concerning their responses to non-native vegetation. Riparian species, in contrast to most upland species, showed mixed responses to the presence of exotic vegetation. In general, if sufficient density of vegetation was present to provide the requisite amount of cover, most of the riparian small mammals exhibited essentially neutral responses (Table 8). Where exotic dominance translated into reduced cover, responses were distinctly negative. Among riparian species, only Townsend's pocket gopher is presumed to always respond negatively to dominance by exotic species, because of its complete dependence on native broad-leaved flowering plants for food.

Geographic Patterns of Species Richness and Community Stability

Birds. Based on the presence-absence data we derived from BBS survey results, we mapped species richness patterns that included 21 of the 25 upland species and 11 of the 12 riparian species. BBS data were insufficient to include Sharp-tailed Grouse, Gray Vireo, Virginia's Warbler, Scott's Oriole, and Yellow-billed Cuckoo.

The broad-scale patterns of species richness for upland and riparian birds across the 11 western states were virtual mirror images of each other (Fig. 4A). Species richness for the suite of upland bird species we examined was concentrated in the three primary shrubsteppe ecoregions, indicating an extraordinary degree of dependence by this suite of bird species on shrubsteppe landscapes of the Columbia Plateau, Great Basin, and Wyoming Basin. All 21 upland species mapped were found to co-occur, indicated by the darkest red shading in Figure 4A. Areas of highest species richness included the breadth of the Columbia Plateau ecoregion extending from southeastern Oregon to easternmost Idaho, the eastern two-thirds of the Great Basin ecoregion, and the southwestern portion of the Wyoming Basin ecoregion.

In contrast, riparian species richness was greatest in the mountains and coastal lowlands outside of the three primary shrubsteppe ecoregions. Although all 11 mapped riparian

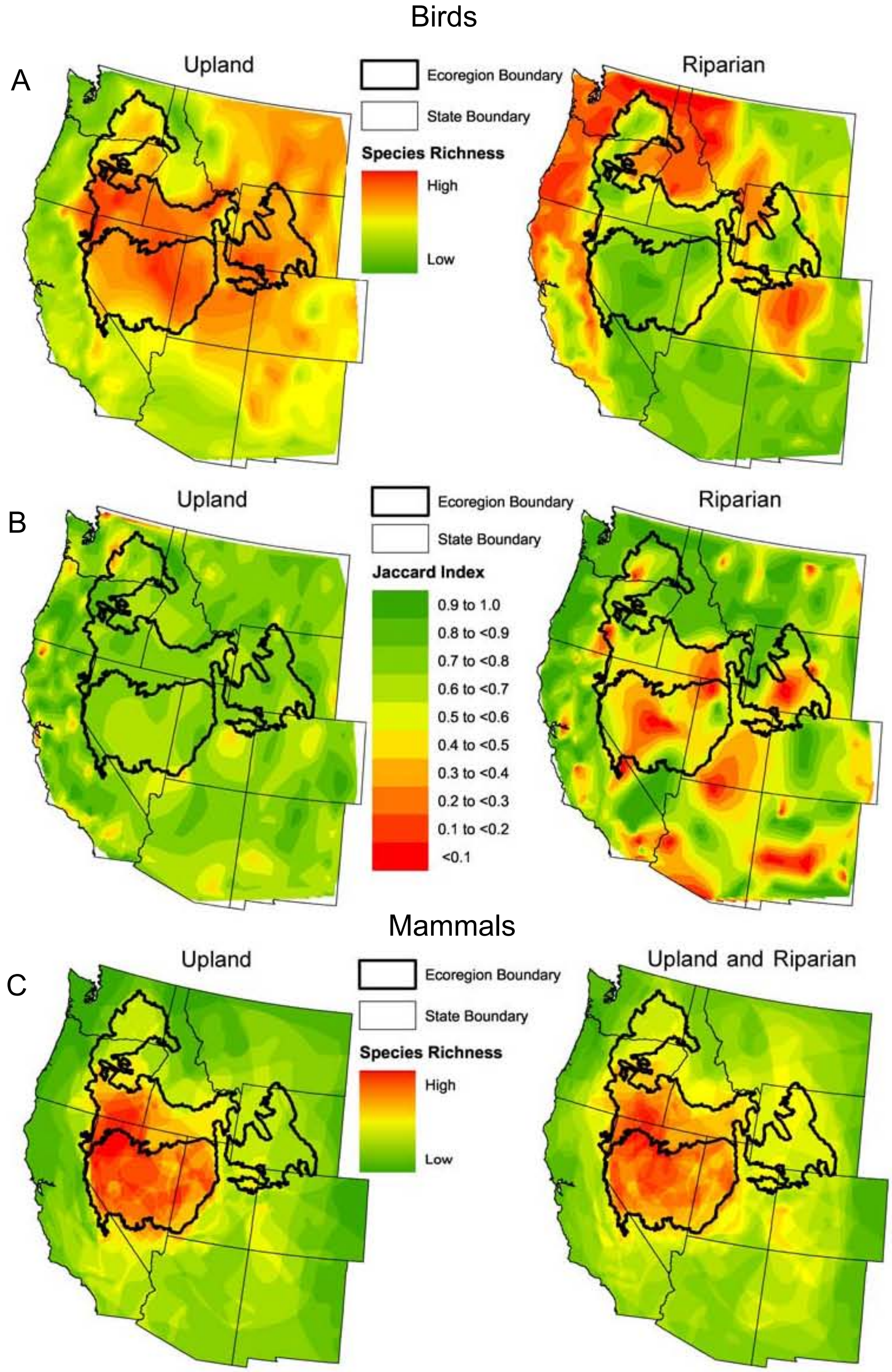

Figure 4. *Geographic patterns in bird and small-mammal communities of the western shrubsteppe.* (*A*) *Species richness for 21 upland and 11 riparian shrubsteppe bird species, based on presence-absence data from the Breeding Bird Survey. Maximum species richness on these maps is 21 species for upland birds and 11 species for riparian birds.* (*B*) *Community stability measured by Jaccard's index for upland and riparian shrubsteppe bird species. Index values compare species composition between the 1968–1983 and 1984–2001 periods based on data from the Breeding Bird Survey. Jaccard's index ranges from 1.0* (*maximum similarity*) *to 0* (*minimum similarity*). (*C*) *Species richness for small mammals based on historical range maps for 18 upland species only, and for 24 upland and riparian species combined. Maximum species richness on these maps is 13 species for upland mammals alone, and 18 species for upland and riparian mammals combined. Small sample size prevented meaningful separate analysis of riparian mammals.*

species were found to co-occur, virtually no areas within the three shrubsteppe ecoregions exhibited high species richness for the suite of riparian species.

Jaccard's index for upland bird species compared between the 1968–1983 and 1984–2001 periods suggested that community structure in appropriate habitat remained largely unchanged (Fig. 4B). Within the three primary shrubsteppe ecoregions, areas with slightly lower levels of community stability included much of the central Great Basin ecoregion, eastern Washington in the Columbia Plateau ecoregion, and the southeastern portion of the Wyoming Basin.

For riparian birds, areas of highest species richness also were areas of highest community stability, as indicated by the distribution of the highest Jaccard index values (Fig. 4B). Aside from a few relatively small areas, across most of the three primary shrubsteppe ecoregions we found relatively low to very low Jaccard Index values, indicating substantial variation in avian community structure compared between the 1968–1983 and 1984–2001 periods. The high degree of instability in riparian community structure indicates considerable fluctuation in species composition among years.

Mammals. We mapped total species richness for the 24 upland and riparian mammal species combined, and for the 18 upland species alone (Fig. 4C). Sample size was too small to provide any meaningful pattern of species richness for the six riparian species considered alone.

Patterns of high species richness were far more concentrated within the three primary shrubsteppe ecoregions compared to the results for birds, and were largely similar for both the combined and upland-only maps. For all 24 species considered together, a maximum of 18 species were found to co-occur (indicated by the darkest red shading in Fig. 4C). Areas of highest species richness occurred from southeastern Oregon to easternmost Idaho in the Columbia Plateau ecoregion, and in much of the Great Basin ecoregion. Species richness was markedly lower in the Wyoming Basin ecoregion.

Species richness for the suite of 18 upland mammal species we considered was significantly more concentrated than for all 24 species considered together. A maximum co-occurrence of 13 species was found, with areas of highest species richness occurring in southeastern Oregon and northwestern Nevada in the Columbia Plateau ecoregion, and across all but the southeasternmost portion of the Great Basin ecoregion. Distinctly fewer species of upland small mammals were supported in the Wyoming Basin and in the Columbia Plateau regions of north-central Oregon, eastern Washington, and eastern Idaho (Fig. 4C). Mammalian species richness in the Wyoming Basin was distinctly lower in the upland species map compared with the map that included riparian species.

DISCUSSION

Population Trends: Birds

The Great Basin and the Wyoming Basin are among the least consistently sampled of all physiographic provinces covered by the BBS, and sampling consistency in the Columbia Plateau is only marginally better (Lawler and O'Connor 2004). The BBS routes that do exist in this region underrepresent sagebrush habitats (Table 2 in Knick et al. 2003), and some species such as upland gamebirds are poorly detected by the BBS's method of roadside counts (Saab and Rich 1997). Given these limitations, it is both remarkable and alarming to find that nearly two-thirds (16 of 25) of the upland bird species we considered have declining population trends, especially given our strongly conservative filtering of BBS data.

BBS methodology is well known to undersample habitats that are relatively uncommon, such as the woody riparian habitats of the arid and semiarid West. Thus it is similarly surprising and worrisome that 42% (5 of 12) of the riparian species we evaluated showed significant declining population trends. To these five must be added the now rare Yellow-billed Cuckoo, (Laymon and Halterman 1987), resulting in six of the 12 considered species demonstrably in decline in the region.

Three upland species besides Greater Sage-Grouse, and seven riparian species in addition to Yellow-billed Cuckoo, exhibited no significant population trends. The absence of statistically significant trends for these species, however, cannot be taken as an indication of population stability. The Greater Sage-Grouse, which is only conspicuous when males congregate on widely scattered display grounds, is difficult to detect on BBS routes but nevertheless is clearly in decline (Connelly et al. 2004, Schroeder et al. 2004). The three other upland species without trends (Gray Vireo, Virginia's Warbler, Scott's Oriole) and six of the seven riparian species without trends (Belted Kingfisher, Veery, Swainson's Thrush, Nashville Warbler, MacGillivray's Warbler) appeared infrequently in the BBS database and virtually not at all on the BBS routes analyzed for the three primary shrubsteppe ecoregions. The lack of trends found for these species is likely a consequence of undersampling by the present BBS route coverage. Of the 14 species for which no significant trends were found, only Yellow Warbler was sampled sufficiently to conclude that populations likely were stable.

In contrast to the high percentage of significant population declines among the 37 bird species we considered, only three species exhibited increasing population trends without also showing conflicting declining trends in some areas or for some time periods.

The results of our population trend analyses present an overall picture of an ecosystem in trouble, especially across the three primary shrubsteppe ecoregions. For the great majority of bird species considered, the general pattern of decline or rarity is sounding a clear warning.

Population Trends: Mammals

Remarkably little is known about the actual distribution or conservation status of most small-mammal species that are tied to shrubsteppe landscapes of the Intermountain West. The reason is simple: there is no standardized survey comparable to the BBS to provide data for small-mammal populations. As a result, there is no general understanding of population trend patterns for small mammals across the United States.

Our analysis of field studies that used appropriate trapping methods in suitable habitats is the first comprehensive attempt to quantify actual presence and absence of species across the region. We were surprised by the high frequency with which species were found to be missing in studies that focused on suitable locations. Of 22 species, only Great Basin pocket mouse was found consistently enough to indicate a reasonable likelihood of being relatively common in suitable habitat. The distribution of study sites was surprisingly broad for most species, with the notable exceptions of water shrew, pallid bat, and western jumping mouse, which were substantially undersampled relative to the extent of their geographic range in the Intermountain West. For a few additional species, such as sagebrush vole and long-tailed vole, study sites were scattered across much of their historical range, but with some significant geographic gaps. For nearly all of the species covered, however, understanding of actual distributions clearly can be improved by additional field studies to systematically sample small-mammal communities across the three primary shrubsteppe ecoregions. As indicated by our maps in the species accounts, the small-mammal communities of the Wyoming Basin in particular have received little attention.

Additional locality information for small mammals could be compiled from specimens contained in museum collections, which would supplement our understanding of recent distributions relative to presumed historical ranges.

Lacking in such collections, however, is the even more important information of where trapping *failed* to find the species in appropriate habitat within the presumed historical range. Absent such information, our analyses remain the best quantitative sampling of presence and absence for the species evaluated.

The high percentages of studies that failed to find species where expected should raise concern regarding the actual current extent of populations relative to standard range maps. The appropriate context in which to view these results is to understand the high degree of habitat fragmentation and altered disturbance regimes across shrubsteppe landscapes (Knick et al. 2003), the overwhelmingly negative response to livestock grazing shown by nearly all of the species considered, and the very limited dispersal abilities of terrestrial small mammals. Our results support the view that many of these species now exist only as small, disconnected populations isolated from each other by unsuitable habitats across which they cannot disperse (Yensen and Sherman 2003).

The recent catastrophic decline and assured extinction of the largest known population of northern Idaho ground squirrels (Sherman and Runge 2002) well illustrates the challenges posed by the highly disrupted landscapes that now characterize much of the Intermountain West. The combined effects of loss of fire, livestock grazing, and introduction of exotic plant species eliminated suitable habitat and the native plant species on which the squirrel depended. Alarmingly, this scenario is neither unique to this one population, nor to this one species; it is the reality faced by many small-mammal species in today's shrubsteppe landscapes.

Restricted Distributions and Endemic Birds

In general, birds associated with shrubsteppe landscapes have larger geographic ranges than most of the small terrestrial mammals we evaluated. The far greater dispersal capabilities of birds and the associated high potential for gene flow among populations are reflected by the lack of endemic species among shrubsteppe birds. Nevertheless, the absence of endemic species with small geographic ranges does not preclude an extraordinary degree of dependence on shrubsteppe habitats by some avian species.

We can identify a continuum of ecological dependence on shrubsteppe habitats for upland birds based on the species' extent of habitat specificity and overall concordance of their total geographic range with the distribution of shrubsteppe landscapes. The most closely associated species, which are in essence entirely dependent on shrubsteppe, are Greater Sage-Grouse, Sage Thrasher, Brewer's Sparrow, and Sage Sparrow. A second group that is nearly as dependent includes Gray Flycatcher, Gray Vireo, Green-tailed Towhee, Black-throated Sparrow, and perhaps Scott's Oriole. The other 14 upland species comprise a third group with ranges that extend beyond the region, but which are nevertheless closely or exclusively associated with shrubsteppe habitats in the Intermountain West portion of their distribution. Some of the species in this third group have distributions that extend well east of the Rocky Mountains (e.g., Loggerhead Shrike, Horned Lark, Vesper Sparrow, Lark Sparrow, Grasshopper Sparrow), with the core of their distribution on the Great Plains. Populations that occur west of the Rockies on shrubsteppe landscapes of public lands, however, are of great importance for these species, as all are experiencing significant population declines in the eastern United States (Sauer et al. 2003), especially east of the Great Plains where grasslands continue to disappear as farmlands transition into woodland and suburban sprawl.

In comparison to upland birds, none of the riparian birds are as narrowly dependent at the species level on riparian habitats of the Intermountain West, and all have geographic ranges that extend well beyond the region. For all of these species, however, populations within the area of interest constitute important population segments that are highly to entirely dependent on riparian habitats across the vast Intermountain West. Some of these riparian species are narrowly distributed at the subspecific level (e.g., Willow Flycatcher), but the precise geographic distributions and habitat specificity for subspecies is poorly known or completely unknown in the Intermountain West for the great majority of species considered in our analyses.

Restricted Distributions and Endemic Mammals

Ten of the 18 upland mammals we evaluated are endemic to the Intermountain West shrubsteppe. An additional six species (Merriam's shrew, Preble's shrew, little pocket mouse, desert woodrat, sagebrush vole, kit fox) have geographic ranges that extend beyond the Intermountain West, but the populations in our region are nevertheless dependent on shrubsteppe habitats. Thus, aside from the two bat species evaluated, all of the upland mammals depend completely upon native shrubsteppe habitats.

In parallel with riparian birds, riparian mammals (with the exception of the endemic Townsend's pocket gopher) have distributions that extend well beyond the Intermountain West. Although within the Intermountain West all five of the riparian small mammals are highly dependent on riparian habitats, three species (western harvest mouse, long-tailed vole, montane vole) will occupy nonriparian areas in those rare instances where suitably dense grass cover is available (see species accounts).

The high degree of endemism among small mammals of the shrubsteppe is likely even greater than species-level ranges indicate. Many of these species consist of two or more described subspecies within the Intermountain West (e.g., dark kangaroo mouse, chisel-toothed kangaroo rat) or have described subspecies that occur just beyond the Intermountain West in California or the Southwest (e.g., little pocket mouse, desert woodrat, kit fox). Much of the described subspecific variation in western small mammals is based on morphological variation; relatively few species have been analyzed for the extent of genetic variation. Where thorough genetic analyses have been conducted, sufficient genetic separation has been found to warrant elevation to full species among some populations previously viewed as subspecies. The best example is the group of five *Spermophilus* ground squirrel species (Hoffman et al. 1993), all of which have relatively small to highly restricted geographic ranges. Three of the five ground squirrels (Idaho ground squirrel, Piute ground squirrel, and Merriam's ground squirrel) each consist of two genetically distinct subspecies. We believe that genetic analyses of upland small mammals would provide further examples of such "cryptic" species. Great Basin pocket mouse, for example, exhibits sufficient karyotypic variability and divergent mitochondrial DNA to indicate the existence of at least two genetically distinct, but still formally unrecognized, species in the Intermountain West (Verts and Carraway 1998).

The general lack of endemism among riparian mammals partly reflects greater extent and greater connectedness of the region's riparian habitats in the past. Beginning with the close of the Pleistocene some 12,000 years ago, riparian habitats across the arid and semiarid West became increasingly isolated as climates warmed (Grayson 1993). Many populations of water shrew, long-tailed vole, montane vole, and western jumping mouse likely have been isolated from conspecific populations for centuries or millennia. Several isolated subspecies of the montane vole occur along the southernmost portion of the species' range, but no systematic studies have examined the extent of genetic isolation shown by this or other species in riparian fragments across the Intermountain West. Vole populations restricted to the naturally fragmented riparian habitats among isolated mountain ranges of the Great Basin (Dobkin, unpubl. data) are likely candidates for genetic studies. We would not be surprised if comparisons among riparian mammal populations in such settings found genetic divergence sufficient to warrant separate species status.

Biodiversity Hotspots and Coolspots: Geographic Patterns of Species Richness

Patterns of avian species richness indicated similar species composition across substantial portions of the three primary shrubsteppe ecoregions for the 21 upland species that we mapped (Fig. 4A). The relatively uniform distribution of upland shrubsteppe species coincided quite well with mapped areas of highest sagebrush landcover (Fig. 1). Areas of highest species richness also coincided reasonably well with areas of lowest shrubsteppe fragmentation across the region (Fig. 2), although the relatively sparse coverage of BBS routes across southern Idaho failed to reflect the extensive shrubsteppe fragmentation of some areas.

Three of the four upland species omitted from the species richness maps (Gray Vireo, Virginia's Warbler, Scott's Oriole) all appear to have centers of abundance southeast of the Great Basin, and can be considered as more closely associated with the Colorado Plateau ecoregion. Virginia's Warbler may be in the process of expanding or shifting its range northward, especially into the Great Basin ecoregion (Dobkin and Fleishman, unpubl. data). If such a shift is a response to global warming, we might expect to see similar shifts by Gray Vireo and Scott's Oriole, as well. At present, there is a dearth of adequate BBS sampling effort in the southern portion of the Great Basin to detect such an expansion for any of these three species.

In stark contrast to upland birds, community composition of riparian birds varied substantially between the 1968–1983 and 1984–2001 periods. Given the relative rarity and ecological importance of riparian habitats within shrubsteppe landscapes, the high degree of instability in riparian community structure should raise great concern as a reflection of the poor ecological condition of riparian habitats across much of the Columbia Plateau, Great Basin, and Wyoming Basin ecoregions—in essence, the areas mapped as bright red to yellow in Figure 4B. In focusing that concern, the adverse effects of livestock grazing (Saab et al. 1995, Dobkin et al. 1998, Tewksbury et al. 2002, Krueper et al. 2003, Earnst et al 2004) and dewatering of riparian zones (Rood et al. 2003) can no longer be ignored for the damage exacted on riparian avifaunas and habitats.

The pattern of high species richness for upland species is much more geographically concentrated for the suite of small mammals compared to upland birds. This is perhaps not surprising given the much more limited powers of dispersal for small terrestrial mammals, and their generally narrower habitat affinities. Greater habitat specificity may also be reflected by the relatively high degree of endemism seen in the mammals. This specificity was further reflected by the absence of complete co-occurrence of species on the species richness maps for small mammals, in contrast to both the upland and the riparian bird maps. For upland mammals, compared with birds, we found much less similarity in species composition between the southern Columbia Plateau/Great Basin ecoregions and the Wyoming Basin ecoregion. Eleven of the 18 upland small mammals do not occur in the Wyoming Basin: five species of *Spermophilus* ground squirrels, four heteromyids (little pocket mouse, dark kangaroo mouse, pale kangaroo mouse, chisel-toothed kangaroo rat), desert woodrat, and kit fox.

In addition to the much lower species richness found for upland mammals in the Wyoming Basin, north-central Oregon and eastern Washington were relatively depauperate in both shrubsteppe bird and mammal species. We interpret this pattern as a reflection of the high proportion of these landscapes that has been converted to agricultural (primarily wheat) production.

The areas of highest species richness found for birds and for small mammals can be integrated with the mapping results of Knick et al. (2003) to guide future conservation efforts from the standpoint of overall biodiversity of species most closely tied to shrubsteppe landscapes.

Concluding Remarks

The species included in our analyses were selected based primarily on their dependence upon shrubsteppe landscapes in the Intermountain West, and not on demonstrated conservation jeopardy. Although there is growing concern for many of the bird species that are closely tied to native shrubsteppe and grasslands of the Intermountain West (Knick et al. 2003), there is little general understanding of the conservation needs for most of these species across the region as a whole. With few exceptions, even less attention has been paid to the conservation needs of small mammals across the region.

The multiple sources of human-caused impacts to shrubsteppe landscapes are well known (Knick et al. 2003). Less well appreciated is the importance of fire as the dominant ecological process that controlled the shifting temporal and spatial mosaic of grasslands and shrublands in these landscapes, and thus provided suitable habitats for the full suite of species from grassland dependent to shrubland dependent. Although there is some disagreement on the frequency and spatial scale of fires prior to Euro-American settlement, there is uniform agreement that fire frequencies in the Intermountain West have been altered greatly over the past 150 years. In some areas, characteristic fire-return intervals are now much longer as a result of fire suppression and the loss of fine fuels to livestock grazing; in other places, fire-return intervals are dramatically shorter due to the spread and dominance of fire-promoting exotic species, such as cheatgrass.

Across the Intermountain West, altered fire frequencies in combination with the ubiquity of livestock grazing continue to drive the loss of native plant community structure and composition on which shrubsteppe birds and small mammals depend. Exotic annual grasses flourish in the absence of competition with the eliminated native grasses and broad-leaved flowering plants, and increase fires to unnatural frequencies of only a few years. Each successive fire promotes expansion of the invaders, resulting in self-perpetuating monocultures of exotic plant species characterized by very short fire-return intervals (d'Antonio and Vitousek 1992). The difference between a sagebrush-dominated landscape with a diverse understory of native bunchgrasses and broad-leaved flowering plants versus a landscape composed of cheatgrass grasslands is as biologically unmistakable as the difference between a mature forest and agricultural cropland. The exotic-plant-dominated landscapes that replace native vegetation on which wildlife depend are uninhabitable for nearly all of the bird and small-mammal species considered in this report.

We know that shrubsteppe habitat has diminished greatly over the past 200 years. The recent detailed analysis for Greater Sage-Grouse found that at least 44% of potential habitat has disappeared (Schroeder et al. 2004), and no attempt was made to evaluate the suitability of remaining habitat in terms of fragmentation and degradation. The current pace of oil, gas, and coal development, particularly in the Wyoming Basin, promises an accelerated trajectory of landscape-scale fragmentation and soil disturbance that will promote invasion by cheatgrass and other exotic plant species, with clear negative consequences for shrubsteppe birds, mammals, and the region's hydrology. Unquestionably, range maps created by connecting the dots among sites where a species has been captured do not paint a realistic picture, especially in the highly altered and fragmented shrubsteppe landscapes of today (Knick et al. 2003). For small terrestrial mammals in particular, many species now exist not in broad ranges, but as scattered, disconnected populations isolated from each other by unsuitable habitats that preclude successful dispersal. Our analyses of trapping data for terrestrial small mammals, geographic patterns of species richness for riparian birds, and previous work on upland shrubsteppe birds (Knick and Rotenberry 2002) emphatically demonstrate that it is completely untenable to assume species' presence based simply on presence of appropriate habitat in shrubsteppe landscapes of the Intermountain West.

When we first began this assessment, some of the species included in our analyses already were known to be declining or rare (Greater Sage-Grouse, Sharp-tailed Grouse, Yellow-billed Cuckoo, pygmy rabbit, Idaho ground squirrel, Washington ground squirrel, kit fox). We expected to find, however, that conservation concern would prove unwarranted for a significant number of the species we examined. Based on the information presented in this report, we find no basis for optimism about the future prospects in the Intermountain West of any of the 61 species we examined. At best, we can conclude that the data are mixed or unclear, and not necessarily promising, for a few species (Long-billed Curlew, Gray Vireo, Virginia's Warbler, Yellow Warbler, Scott's Oriole, Great Basin pocket mouse). It is clear that the ecological integrity of Intermountain West shrubsteppe landscapes largely has been compromised, and that the bird and small mammal species dependent upon these habitats are providing the signals that they are at risk.

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