TEETERING ON THE EDGE OR TOO LATE? CONSERVATION AND RESEARCH ISSUES FOR AVIFAUNA OF SAGEBRUSH HABITATS

STEVEN T. KNIC1,2, DAVID S. DOBKN3, JOHN T. ROTENBERRY3, MICHAEL A. SCHROEDER4, W. MATTHEW VANDER HAEGEN5 AND CHARLES VAN RIPER III6

1USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street, Boise, ID 83706
2High Desert Ecological Research Institute, 15 S.W. Colorado Ave., Suite 300, Bend, OR 97702
3Center for Conservation Biology and Department of Biology, University of California, Riverside, CA 92521
4Washington Department of Fish and Wildlife, P.O. Box 1077, Bridgeport, WA 98813
5Washington Department of Fish and Wildlife, 600 North Capitol Way, Olympia, WA 98501
6USGS Southwest Biological Science Center, Northern Arizona University, P.O. Box 5614, Bldg. 24, Flagstaff, AZ 86011

Abstract. Degradation, fragmentation, and loss of native sagebrush (Artemisia spp.) landscapes have imperiled these habitats and their associated avifauna. Historically, this vast piece of the Western landscape has been undervalued: even though more than 70% of all remaining sagebrush habitat in the United States is publicly owned, <3% of it is protected as federal reserves or national parks. We review the threats facing birds in sagebrush habitats to emphasize the urgency for conservation and research actions, and synthesize existing information that forms the foundation for recommended research directions. Management and conservation of birds in sagebrush habitats will require more research into four major topics: (1) identification of primary land-use practices and their influence on sagebrush habitats and birds, (2) better understanding of bird responses to habitat components and disturbance processes of sagebrush ecosystems, (3) improved hierarchical designs for surveying and monitoring programs, and (4) linking bird movements and population changes during migration and wintering periods to dynamics on the sagebrush breeding grounds. This research is essential because we already have seen that sagebrush habitats can be altered by land use, spread of invasive plants, and disrupted disturbance regimes beyond a threshold at which natural recovery is unlikely. Research on these issues should be instituted on lands managed by state or federal agencies because most lands still dominated by sagebrush are owned publicly. In addition to the challenge of understanding shrubsteppe bird-habitat dynamics, conservation of sagebrush landscapes depends on our ability to recognize and communicate their intrinsic value and on our resolve to conserve them.

Key words: Artemisia, conservation, landscape change, land use, priority research issues, sagebrush ecosystems, shrubland loss.

¿Tambaleando en el Borde o Demasiado Tarde? Asuntos de Conservación e Investigación para la Avifauna de Ambientes de Matorral de Artemisia spp.

Resumen. La degradación, fragmentación y pérdida de paisajes nativos de matorrales de Artemisia spp. han puesto en peligro a estos ambientes y su avifauna asociada. Históricamente, esta vasta porción del paisaje occidental ha sido subvalorada: aunque más del 70% de todo el hábitat de matorral de Artemisia de los Estados Unidos es de propiedad pública,

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7 E-mail: steve_knick@usgs.gov
INTRODUCTION

The increasingly rapid and widespread degradation, fragmentation, or total loss of sagebrush (Artemisia spp.) ecosystems throughout western North America presents a grave challenge to natural-resource agencies charged with their management and restoration. Sagebrush once covered roughly 63 million ha in western North America, but very little now exists undisturbed or unaltered from its condition prior to Eurasian settlement (West 1996, Miller and Eddleman 2001). Perhaps 50–60% of the native sagebrush steppe now has either exotic annual grasses in the understory or has been converted completely to non-native annual grasslands (West 2000). Sagebrush habitats are among the most imperiled ecosystems in North America (Noss and Peters 1995, Mac et al. 1998).

Human activities have caused most of the loss of sagebrush (West and Young 2000). Land managers have used prescribed fires, mechanical treatments (including shredding, roller chopping, hand slashing, bulldozing, beating, chaining, root plowing, and disk plowing), 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). Agriculture, mining, oil, gas, and coal-bed methane development, 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). Other activities, such as livestock grazing, have facilitated the spread of invasive plant species, intensified wildfires, and altered disturbance regimes through indirect but often synergistic effects on vegetation communities and soils (Mack 1981, d’Antonio and Vitt 1992). These changes have pushed many sagebrush systems beyond thresholds from which recovery to a pre-Eurasian-settlement condition is unlikely (Laycock 1991, West and Young 2000). The cumulative effects of land use and habitat degradation raise the greater threat of imminent large-scale collapses of sagebrush ecosystems.

Loss of sagebrush habitats and concern for sagebrush-dependent birds were detailed over a quarter of a century ago by the Conservation Committee of the Wilson Ornithological Society (Braun et al. 1976). Since then, numbers of sage-grouse (Centrocercus spp.) have continued to decline throughout their range (Connelly and Braun 1997, Braun 1998, Connelly, Schroeder, et al. 2000) and individual populations have become increasingly separated (Schroeder, Hays, Livingston, et al. 2000, Beck et al. 2003). The Gunnison Sage-Grouse (C. minimus) has candidate status for federal listing as a threatened or endangered species (U.S. Fish and Wildlife Service 2000). As of March 2003, four petitions for subpopulations and one rangewide petition had been filed to list Greater Sage-Grouse (C. urophasianus), Columbian Sharp-tailed Grouse (Tympanuchus phasianellus columbiaus) also have declined dramatically and now exist only in small, isolated populations (McDonald and
Reese 1998, Schroeder, Hays, Murphy, and Pierce 2000). Other taxa dependent on sagebrush also are declining: the Columbia Basin population of pygmy rabbits (Brachylagus idahoensis) was listed under the Endangered Species Act in March 2003 (U.S. Fish and Wildlife Service 2003).

Shrubland and grassland birds 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, but have seen little conservation action until recently. Now, Brewer’s Sparrow (Spizella breweri), Sage Sparrow (Amphispiza belli), and Sage Thrasher (Oreoscoptes montanus), the three primary passerine species of sagebrush habitats, receive special conservation status in one or more western states (Knick and Rotenberry 2002). In addition, these birds 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).

Conservation and restoration of sagebrush lands now are top priorities of natural-resource agencies (Bureau of Land Management 2002a). This recent emphasis may represent changing attitudes about the intrinsic value of sagebrush ecosystems, or it may be a reaction to the threat of petitions to list species under the Endangered Species Act. If the Greater Sage-Grouse or any of the other species living in sagebrush ecosystems were to be listed, there would be major ramifications for use and management of large areas of the western United States. Approximately 30% (22.4 million ha) of the total area in the lower 48 states managed by the U.S. Bureau of Land Management, 50% (300 000 ha) of the total area managed by the U.S. Department of Energy, 20% (3.6 million ha) of the total area managed by the U.S. Fish and Wildlife Service, and 11.5% (2.1 million ha) of the total area managed by state agencies is sagebrush habitats (Table 1). Less than 3% of the area dominated by

### TABLE 1. Sagebrush area and management responsibility by ecoregions (Nature Conservancy 2001) in the western United States. We included only those ecoregions in which >1% of the total land area was in sagebrush cover, as measured from current distribution (Comer et al. 2002).

<table>
<thead>
<tr>
<th>Ecoregion</th>
<th>Total area (ha)</th>
<th>Sagebrush area (ha)</th>
<th>% total area (% sagebrush area)</th>
<th>Management responsibility&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Private</th>
<th>BLM</th>
<th>Other federal agency&lt;sup&gt;c&lt;/sup&gt;</th>
<th>State</th>
<th>Public</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wyoming Basins</td>
<td>13 365 544</td>
<td>7 366 521 (55)</td>
<td>34 (30)</td>
<td>51 (56)</td>
<td>8 (8)</td>
<td>6 (7)</td>
<td></td>
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<tr>
<td>Columbia Plateau</td>
<td>29 145 809</td>
<td>14 064 004 (48)</td>
<td>45 (23)</td>
<td>41 (60)</td>
<td>9 (12)</td>
<td>4 (5)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Great Basin</td>
<td>29 304 818</td>
<td>8 844 892 (30)</td>
<td>16 (13)</td>
<td>62 (70)</td>
<td>17 (17)</td>
<td>2 (1)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Utah High Plateaus</td>
<td>4 590 548</td>
<td>816 128 (18)</td>
<td>21 (27)</td>
<td>35 (31)</td>
<td>37 (33)</td>
<td>7 (9)</td>
<td></td>
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</tr>
<tr>
<td>Utah-Wyoming Rocky Mtns.</td>
<td>10 952 783</td>
<td>1 825 576 (17)</td>
<td>22 (34)</td>
<td>7 (16)</td>
<td>66 (43)</td>
<td>3 (6)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle Rockies</td>
<td>21 420 221</td>
<td>3 389 493 (16)</td>
<td>33 (34)</td>
<td>10 (36)</td>
<td>52 (24)</td>
<td>4 (6)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Modoc Plateau</td>
<td>5 813 901</td>
<td>589 075 (10)</td>
<td>29 (24)</td>
<td>7 (28)</td>
<td>60 (43)</td>
<td>3 (5)</td>
<td></td>
<td></td>
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<tr>
<td>Southern Rocky Mtns.</td>
<td>16 165 717</td>
<td>1 389 004 (9)</td>
<td>37 (51)</td>
<td>11 (28)</td>
<td>48 (15)</td>
<td>4 (6)</td>
<td></td>
<td></td>
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<tr>
<td>Northern Great Plains Steppe</td>
<td>64 234 604</td>
<td>3 290 725 (5)</td>
<td>73 (67)</td>
<td>11 (21)</td>
<td>8 (4)</td>
<td>7 (8)</td>
<td></td>
<td></td>
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<tr>
<td>Colorado Plateau</td>
<td>19 648 973</td>
<td>841 092 (4)</td>
<td>15 (20)</td>
<td>31 (60)</td>
<td>47 (11)</td>
<td>7 (8)</td>
<td></td>
<td></td>
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<tr>
<td>Okanogan</td>
<td>8 842 564</td>
<td>288 010 (3)</td>
<td>31 (55)</td>
<td>1 (6)</td>
<td>9 (25)</td>
<td>7 (14)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Sierra Nevada</td>
<td>5 017 618</td>
<td>71 916 (1)</td>
<td>7 (35)</td>
<td>5 (7)</td>
<td>87 (54)</td>
<td>1 (3)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Remaining ecoregions&lt;sup&gt;d&lt;/sup&gt;</td>
<td>73 159 711</td>
<td>82 486 (&lt;1)</td>
<td>56 (80)</td>
<td>2 (&lt;1)</td>
<td>36 (15)</td>
<td>6 (6)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>314 712 432</td>
<td>43 099 867 (14)</td>
<td>37 (28)</td>
<td>24 (52)</td>
<td>32 (15)</td>
<td>6 (5)</td>
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</table>

<sup>a</sup> Sagebrush communities include Wyoming and Basin big sagebrush, black sagebrush, low sagebrush, low sagebrush–mountain big sagebrush, low sagebrush–Wyoming big sagebrush, mountain big sagebrush, scabland sagebrush, threetip sagebrush, Wyoming big sagebrush, and Wyoming big sagebrush–squaw apple.

<sup>b</sup> GIS maps of land ownership and management authority were developed from individual state coverages.

<sup>c</sup> Includes the following U.S. agencies: Fish and Wildlife Service, Bureau of Indian Affairs, National Park Service, Department of Energy, Department of Agriculture, and Department of Defense.

<sup>d</sup> Includes Black Hills, Canadian Rocky Mountains, Central Shortgrass Prairie, Fescue-Mixed Grass Prairie, Klamath Mountains, and West Cascades.
sagebrush lies within national parks or wilderness areas that receive permanent legal protection from conversion of land cover (Scott, Murray, et al. 2001, Wright et al. 2001). From a conservation perspective, these reserves provide neither the geographic distribution nor at least 10% of their total area estimated to be necessary for long-term species conservation (Scott, Davis, et al. 2001). Less than 30% of all sagebrush lands are owned privately. Consequently, the future of sagebrush ecosystems will be affected primarily by use of public lands and policies of the management agencies (Raphael et al. 2001).

Here, we identify priority research issues needed for conservation of birds in sagebrush ecosystems in western North America. We also review and synthesize existing information providing the foundation for these issues. We begin by documenting the numerous impacts contributing to loss and degradation of sagebrush habitats across their widespread distribution. Such documentation is critical if we are to implement science-based policies to conserve these ecosystems under increasing demand for their resources.

The primary research issues that we present were developed to (1) understand the impacts of land-use practices on sagebrush habitats and birds; (2) examine relationships between birds and habitat characteristics; (3) identify population trends, distribution, and abundance; and (4) link our understanding of breeding-ground dynamics with those encountered during migration and on wintering grounds. These issues originated at a multiagency workshop held in August 2001 in Boise, Idaho. The different missions of the agencies and individuals involved (see Acknowledgments) reflect varying applications, but with a common need for improved information on birds living in sagebrush habitats.

THE SAGEBRUSH REGION

Our review focused on shrublands dominated by sagebrush in the western United States (Fig. 1). Unless otherwise indicated, statistics were derived for 13 ecoregions (Nature Conservancy 2001) in 14 states, in which >1% of land surface was sagebrush cover. Data presented by states include California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, and Wyoming. States having limited geographic distribution of sagebrush (Nebraska, North Dakota, South Dakota) or for which reliable maps of sagebrush distribution were not available (Arizona, New Mexico) were excluded from state summaries.

Woody species of sagebrush are divided into tall and low groups (Miller and Eddleman 2001, West and Young 2000). Three subspecies within the tall sagebrush group, Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis), basin big sagebrush (A. t. ssp. tridentata), and mountain big sagebrush (A. t. ssp. vaseyana), are most widely distributed (McArthur 1994). Low sagebrush (A. arbuscula) and black sagebrush (A. nova) are the primary species in the low sagebrush groups. With the exception of research on sage-grouse, most bird-focused studies have lumped the Artemisia groups and species, even though site characteristics, ecological relationships, and response to disturbance vary widely (McArthur 1994, Miller and Eddleman 2001).

We conducted spatial analyses on a base map of sagebrush distribution (Comer et al. 2002). Land ownership and management-authority statistics were obtained by combining individual state coverages. All GIS coverages used in our analyses can be downloaded from the SAGE-MAP website (U.S. Geological Survey 2001).

We emphasized birds that use sagebrush as their primary habitat. However, we recognize that specialized habitats within sagebrush landscapes, such as riparian and wetland areas, provide critical resources for many other birds (Dobkin et al. 1995, 1998, Haig et al. 1998, Warnock et al. 1998).

CURRENT CHALLENGES TO CONSERVING SAGEBRUSH ECOSYSTEMS

EFFECTS OF LAND-USE PRACTICES

Past and current uses of public lands have impacted virtually all sagebrush ecosystems (Bock et al. 1993, West and Young 2000, Miller and Eddleman 2001). Livestock grazing, conversion to agriculture or urban areas, energy and natural resource development, habitat treatment, and even restoration activities, have had direct as well as indirect consequences. The magnitude of these effects is difficult to quantify. Direct effects, such as extent of fragmentation or total area lost, rarely have been linked to specific land uses (Dobler et al. 1996, Hann et al. 1997, Knick and Rotenberry 1997) and cumulative effects...
FIGURE 1. Large-scale patterns of tall sagebrush distribution in the western United States can give the false impression that conservation of sagebrush ecosystems is not critical because of their wide distribution. The map depicts the percent of land cover within a 25-km radius of each map cell dominated by tall sagebrush, produced by resampling the base map (Comer et al. 2002) to a 2.5-km resolution. Tall sagebrush species include basin big sagebrush, Wyoming big sagebrush, mountain big sagebrush, and silver sagebrush. Ecoregions (Nature Conservancy 2001) with >1% of their land surface dominated by sagebrush are shown (Table 1).
have not been estimated over the large geographic extent of sagebrush. These analyses have been hindered because large-scale maps have been unavailable, inconsistent across administrative boundaries, or limited by coarse spatial and thematic resolution. Similarly, an assessment of landscape changes caused by land use has been precluded by lack of maps depicting habitats at comparable resolutions to contrast different times.

Other effects, such as altered or depleted understories, have been well documented in local site-specific contexts but are difficult to quantify for large areas because of our inability to translate local events into broad-scale dynamics (Allen and Starr 1982, Wiens 1989a). Technological challenges also limit mapping these conditions in semiarid regions using remote sensing (Knick et al. 1997). As a result, the wide geographic distribution of sagebrush in maps depicting only a dominant cover type (Fig. 1) provides a deceptive mask and false sense of security. Land uses influence site-specific factors as well as landscape features to form a complex mosaic of varied conditions and histories. Thus, analyses of additional landscape metrics, such as fragmentation (Fig. 2), may be necessary to identify the potential consequences for disturbance regimes, invasions of exotic plants, and trajectories of future vegetation dynamics (Turner et al. 2001).

LIVESTOCK GRAZING

Livestock grazing and associated habitat alterations have had the most widespread impact on western ecosystems of any land use (Bock et al. 1993, Fleischner 1994). Virtually all sagebrush lands are managed principally for livestock grazing. In 2001, 15,000 permits were issued for >10.2 million animal unit months of forage consumption on lands managed by the U.S. Bureau of Land Management (Bureau of Land Management 2002b). (One animal unit month = the quantity of forage required by 1 mature cow weighing 454 kg and calf, or equivalent, for 1 month.) Livestock grazing can change habitat features that directly influence birds; for example, by reducing plant species diversity and biomass (Reynolds and Trost 1981, Bock and Webb 1984, Saab et al. 1995). Alternatively, changes in water and nutrient cycling caused by grazing can promote the spread of invasive species, which then degrade native bird habitats by altering fire and disturbance regimes (Rotenberry 1998). In addition, activities associated with livestock production, such as feedlots, can facilitate nest predators or parasitism by Brown-headed Cowbirds (Molothrus ater; Vander Hagen and Walker 1999, Goguen and Matthews 2000).

Many areas of sagebrush steppe in western North America historically did not support herds of large ungulates. Large native herbivores had disappeared by 12,000 years BP, and native vegetation communities developed in the absence of significant grazing pressure (Grayson 1994). Because of semiarid climate and the absence of grazing in their recent evolutionary history, sagebrush systems are particularly sensitive to grazing disturbance (Mack and Thompson 1982). Excessive grazing by domestic livestock during the late 1800s and early 1900s, coupled with severe drought, significantly impacted sagebrush ecosystems (Yensen 1981, Young and Sparks 2002). Long-term effects persisting today include widespread changes in plant community composition and soils that have increased the spread of exotic vegetation and altered natural disturbance regimes (Yensen 1981, Young 1994, Miller and Rose 1999).

Manipulation of sagebrush landscapes to increase forage production for livestock has dominated our perspective and shaped our use of sagebrush ecosystems (Holechek et al. 1998). Large expanses of sagebrush have been eradicated and reseeded with non-native grasses (primarily crested wheatgrass [Agropyron cristatum]) to increase production of forage for livestock grazing (Hull 1974, Evans and Young 1978, Shane et al. 1983). An estimated 2–6 million ha of sagebrush lands were treated to reduce or eliminate sagebrush cover by the 1970s (Schneegas 1967, Vale 1974). Thinning or prescribed burning to reduce cover density of sagebrush and promote forb and grass production continues to be practiced widely (Olson and Whitson 2002, Bureau of Land Management 2002a, Wambolt et al. 2002).

AGRICULTURE AND URBANIZATION

Crop production on lands previously dominated by sagebrush has completely converted vast tracts of sagebrush habitats and fragmented many remaining landscapes (Wisdom et al. 2000; Fig. 3). Similarly, urbanization, roads, and powerlines continue to fragment ecological sys-
FIGURE 2. Small-scale patterns of habitat complexity indicate that much of the tall 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 tall 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 (Comer et al. 2002) to 500-m resolution and measuring the proportion of total edge between sagebrush and other habitat patches within 2.5 km of each map cell.
tems (Trombulak and Frissell 2000, Wright et al. 2001). This loss represents a major challenge for restoration (and may be irreversible) because essential components of the system are disrupted or lacking entirely.

Lands converted to agriculture occur primarily at low elevations in areas containing deep, highly productive soils (Dobler et al. 1996, Scott, Murray, et al. 2001). In central Washington, 75% of the shrubsteppe regions containing loamy soils have been converted to agriculture or other land uses, compared to <15% of the shrubsteppe communities on shallow soils (Vander Haegen et al. 2000). An estimated 99% of the basin big sagebrush habitats in the Snake River Plain now are used for cropland (Hironaka et al. 1983).

Development of the agricultural landscape has fragmented sagebrush steppe regions at multiple scales (Fig. 2, 3). Fragments of intact sagebrush habitats in Washington now exist within a matrix of agriculture (Vander Haegen et al. 2001). The mean patch size of sagebrush in Washington decreased from 13,420 ha to 3,418 ha and the number of patches increased from 267 to 370 between 1900 and 1990 (Hann et al. 1997, McDonald and Reese 1998). Nest predation also increased in fragmented habitats dominated by agriculture (Vander Haegen et al. 2002). Cowbird parasitism increased in agricultural landscapes and in the presence of feedlots for livestock, although the rate of cowbird parasitism on shrubsteppe birds generally remains low (Vander Haegen and Walker 1999). At broader scales, conversion of the Snake River Plain to agriculture disconnected regions north of the Snake River from sagebrush in southern Idaho and northern Nevada (Fig. 1, 3).
NATURAL RESOURCE DEVELOPMENT

Approximately 2.7 million ha of western lands administered by the U.S. Bureau of Land Management currently are in production status for oil, gas, or geothermal energy (Bureau of Land Management 2002b). An estimated 9.3 million ha in five basins of federal lands (includes habitats in addition to sagebrush) in Montana, Wyoming, Colorado, Utah, and New Mexico, are available for oil and gas leasing with standard stipulations (U.S. Departments of Interior, Agriculture, and Energy 2003). Approval for 29,000 new oil and gas leases is anticipated by 2005 (Bureau of Land Management 2003).

Energy development and natural resource extraction directly alter sagebrush habitats at the site of operation (Braun et al. 2002). In Wyoming, existing oil and gas wells were located primarily in landscapes dominated by sagebrush (Fig. 4). Associated road networks, pipelines, and powerline transmission corridors also influence vegetation dynamics by fragmenting habitats or by creating soil conditions facilitating the spread of invasive species (Fig. 4; Braun 1998, Gelbard and Belnap 2003). Density of sagebrush-obligate birds within 100 m of roads constructed for natural gas development in Wyoming was 50% lower than at greater distances (Ingelfinger 2001). Increased numbers of corvids and raptors associated with powerlines (Steenhof et al. 1993, Knight and Kawashima 1993, Vander Haegen et al. 2002) also increase the potential impact of predation on sage-grouse and other sagebrush-breeding birds.

HABITAT TREATMENT

Land managers burn or otherwise treat large areas of sagebrush habitats on public lands every...
In 2000 and 2001, prescribed fires were used to treat 50,000 ha managed by the Bureau of Land Management; nonfire treatments (e.g., herbicides, biocontrols, mechanical alteration) were used on an additional 96,000 ha (Bureau of Land Management 2001, 2002b). The preferred alternative presented by the Bureau of Land Management in the Final Vegetation Environmental Impact Statement (Bureau of Land Management 1991) recommended treating 919,212 ha in the 13 western states annually. The appropriateness of these actions and their effects on habitats and the associated avifauna are widely debated (Connelly, Reese, et al. 2000, Wambolt et al. 2002).

Prescribed fire, herbicides, and numerous mechanical and biological means are used to thin or reduce biomass of woody vegetation, improve forage production for livestock, control invasive weeds or insects, or obtain a desired seral condition. Our understanding of the effects of these habitat treatments on diversity, density, or productivity of shrubland birds most often has been derived from studies of specific, fine-scale management actions (Best 1972, Schroeder and Sturges 1975, Castrale 1982, Petersen and Best 1987, Howe et al. 1996). With few exceptions (Kerley and Anderson 1995), most studies address short-term effects immediately post-treatment. Of 35 papers investigating perturbation effects, 94% did not sample pretreatment conditions, had no controls, or were of short duration (Petersen and Best 1999). Planned experiments that incorporate habitat manipulations are rare (Wiens and Rotenberry 1985, Winter and Best 1985, Wiens et al. 1986, Fischer et al. 1997, Connelly, Reese, et al. 2000) but provide greater insights into mechanisms underlying habitat change and bird response.

EXOTIC PLANTS IN SAGEBRUSH ECOSYSTEMS

Exotic plant species, such as cheatgrass (Bromus tectorum), yellow starthistle (Centaurea solstitialis), spotted knapweed (C. biebersteinii [= maculosa]), tamarisk (Tamarix ramosissima), medusahead wildrye (Taeniatherum caput-medusae), and rush skeleton-weed (Chondrilla juncea), are rapidly invading breeding and wintering ranges of birds. Invasion of alien plants causes changes in the vegetation composition and structure and alters disturbance regimes (Brooks and Pyke 2001). The area infested by exotic plants increased from 1.1 million ha in 1985 to 3.2 million ha in 1994 on lands managed by the Bureau of Land Management (Bureau of Land Management 1996). Rate of spread for noxious weeds has been estimated to be approximately 931 ha day⁻¹ on BLM lands and 1862 ha day⁻¹ on all public lands in the West (Bureau of Land Management 1996).

SAGEBRUSH REHABILITATION AND RESTORATION

The accelerating frequency of large wildfires in sagebrush ecosystems has resulted in extensive rehabilitation efforts to control erosion, return stability to the system and, in some cases, re-establish a shrubland landscape (Roundy et al. 1995). During 2000–2001, $91 million was approved to treat 755,000 ha of lands managed by the Bureau of Land Management in the emergency fire rehabilitation program, whose primary objective is to stabilize soils (Bureau of Land Management 2001, 2002b). Federal agencies encourage the use of native seeds (Richards et al. 1998), but in reality the use of non-native grasses (such as crested wheatgrass) will continue to increase because of the demand caused by large fires coupled with low availability of native seeds from commercial seed sources (Asay et al. 2001). The effects of non-native grasses on dynamics of birds in sagebrush communities have not been well studied (Reynolds and Trost 1981, McAdoo et al. 1989), particularly in the context of the landscape in which the rehabilitation project is embedded.

Land-management agencies are developing major programs for restoration of sagebrush ecosystems (Beever and Pyke 2002, Bureau of Land Management 2002a). Restoration will be difficult, expensive, and may require decades or even centuries (U.S. Department of Interior 1996, Hemstrom et al. 2002). The process of recovery is relatively unknown, although we have extensive documentation of deterioration in sagebrush ecosystems (Allen-Diaz and Bartolome 1998). Not all areas previously dominated by sagebrush can be restored because alteration of vegetation, nutrient cycles, topsoil, cryptobiotic crusts, and disturbance processes have pushed these systems past critical thresholds from which recovery is unlikely (Allen 1988, Belnap and Lange 2001, McIver and Starr 2001) or because we lack the political agenda and economic incentives (Allen and Jackson 1992).
BIRD RESPONSE TO HABITAT CHANGES

Changes in composition and configuration of sagebrush habitats from land use influence temporal dynamics such as disturbance or successional pathways. These spatial and temporal components of sagebrush ecosystems form the environmental template on which birds respond (Rotenberry and Wiens 1980a, 1980b, Rotenberry et al. 1995, Rotenberry and Knick 1999, Knick and Rotenberry 2000). Therefore, our ability to identify those habitat components and link them to mechanisms of bird population change is critical to developing land-management and conservation plans (Morrison 2001, Noon and Franklin 2002, Wiens 2002).

LIFE-HISTORY ATTRIBUTES OF BIRDS IN SAGEBRUSH HABITATS

Sagebrush ecosystems support few bird species compared to other ecosystems due to relatively low floristic structure and diversity coupled with low productivity and seasonal environments (Rotenberry 1998, Vander Haegen et al. 2001). Perhaps 18 bird species associated with sagebrush ecosystems are of conservation concern (Appendix; Paige and Ritter 1999). Our understanding of bird and habitat relationships in sagebrush systems, however, is based largely on studies of three game species (Greater Sage-Grouse, Gunnison Sage-Grouse, Sharp-tailed Grouse) and three passerines (Sage Thrasher, Brewer's Sparrow, Sage Sparrow). We know little basic life history of other bird species that use sagebrush habitats.

BIRD-HABITAT RELATIONSHIPS

The relationship of vegetation characteristics to bird distribution and abundance has been the most widely investigated aspect of birds associated with sagebrush habitats (Rotenberry and Wiens 1978, Wiens and Rotenberry 1981, Rotenberry 1985, Wiens et al. 1987, Schroeder et al. 1999, Connelly, Schroeder, et al. 2000, Vander Haegen et al. 2000). Most studies of bird and habitat relationships have been site specific. However, additional insights into composition and disturbances structuring habitats used by shrubsteppe birds might be obtained from a meta-analysis of multiple sites. For example, we used data collected in Oregon, Nevada, Idaho, and Washington (Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981, Dobler 1994, Knick and Rotenberry 1995) in a detrended correspondence analysis to determine the primary habitat and disturbance gradients along which shrubsteppe birds were distributed (Fig. 5). The first axis captured the primary distribution of bird species along a gradient from grassland to shrubland. We inferred an increasing fire frequency associated with greater amounts of grassland. The second axis contrasted a vegetationally open to dense habitat structure, which resulted from increasing likelihood of invasion by juniper and other woody vegetation correlated in part with decreasing fire frequency. By developing models of bird and habitat relationships at multiple scales of investigation, we can attempt to understand and predict the response of shrubsteppe bird communities to habitat changes.

Statistical models used to derive relationships between animals and their habitats may fit a high proportion of the variation in the sample (Verner et al. 1986, Morrison 2001, Scott et al. 2002), but often these models do not perform well in regions or times outside of the sampling space (Rotenberry 1986, Knick and Rotenberry 1998). We may need to develop a different paradigm in the way we assess habitats. Instead of deriving habitat characteristics that are highly correlated with bird abundance, we might seek to identify a minimum or constant set of habitat characteristics required by a species to be present (Knopf et al. 1990). By modeling basic or minimum requirements, we may develop a better understanding of components necessary to maintain bird populations, as well as improve capability to predict response of populations to habitat changes (Rotenberry et al. 2002).

SCALES OF BIRD-HABITAT RELATIONSHIPS

Most research on response to habitat change by birds, conducted at fine spatial and temporal scales, suggests that cumulative effects of local changes significantly influence population dynamics of birds in sagebrush habitats. Site-specific studies have provided a good understanding of components of sagebrush habitats associated with breeding birds. However, we recently have noted the relationship between landscape-level habitat variables and local abundances of birds (Knick and Rotenberry 1995, Knick and Rotenberry 1999, Vander Haegen et al. 2000). Occupancy of a home range is based on multiple variables operating at different scales: local vegetation coupled with landscape characteristics
FIGURE 5. Primary habitat gradients along which birds in shrubland habitats are distributed. A detrended correspondence analysis (DCA) was conducted on three geographically separate data sets containing similar habitat variables from Oregon, Nevada, and Washington (Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981); Washington (Dobler 1994); and Idaho (Knick and Rotenberry 1995). Bird species are Gray Flycatcher (GRFL), Loggerhead Shrike (LOSH), Horned Lark (HOLA; Eremophila alpestris), Rock Wren (ROWR; Salpinctes obsoletus), Sage Thrasher (SATH), Green-tailed Towhee (GTTO), Brewer’s Sparrow (BRSP), Vesper Sparrow (VESP), Lark Sparrow (LASP), Black-throated Sparrow (BTSP), Sage Sparrow (SAGS), Grasshopper Sparrow (GRSP; Ammodramus savannarum), and Western Meadowlark (WEME; Sturnella neglecta; see Appendix for additional scientific names).

MECHANISMS OF BIRD RESPONSE TO HABITAT CHANGE

The processes by which birds respond to changes in habitat composition and configuration remain elusive, and identifying them requires knowledge of local population dynamics and their variations across the landscape (Knick and Rotenberry 2002). Local abundance derives from a complex interaction of habitat characteristics coupled with variation in survival, productivity, and dispersal (Wiens 1989b, 1989c, 2002). In sagebrush ecosystems, we do not understand how habitat fragmentation influences productivity, density of breeding adults, size of home range, or probability of predation or Brown-headed Cowbird parasitism.

We lack the necessary demographic information to reliably model population growth and to ascertain source-sink status for birds dependent on sagebrush habitats. Much of the focus of productivity studies for shrubsteppe passerines has been on regional and annual variation (Rotenberry and Wiens 1989). Clutch size, nest success, and fledging rates vary significantly among years (Petersen and Best 1987, Rotenberry and Wiens 1989) and may be related to weather be-
fore and during the nesting season (Rotenberry and Wiens 1991). More recently, the effect of large-scale habitat fragmentation on productivity of shrubland birds has been studied by integrating satellite imagery with field studies in Washington state, with the conclusion that nest success decreases in more-fragmented landscapes (Vander Haegen et al. 2002). Ultimately, criteria defining source-sink habitat gradients need to be based on measures of productivity per area or on population growth rates (Van Horne 1983, Morrison 2001, Misenhelter and Rotenberry 2000).

RECOMMENDATIONS

We recommend research and management strategies based on the primary challenges to better understand the effects of land use on sagebrush habitats and to improve our knowledge of bird and habitat relationships. We strongly recommend integrated approaches that tier individual studies into larger programs conducted over the long term to address multiscale relationships.

EFFECTS OF LAND-USE PRACTICES

Accurate rangewide estimates of total area degraded, fragmented, converted to agriculture, or invaded by exotic weeds are needed to grasp fully the magnitude of changes and their impact on birds. For some pervasive land uses, such as livestock grazing, empirical data to test the effects on bird populations are limited (Bock and Webb 1984, Saab et al. 1995). We need experiments having strong statistical designs that include treatments and controls at spatial and temporal scales relevant to the impacts to vegetation and soils and the dynamics of recovery (Fleischner 1994, Tewksbury et al. 2002, Wambolt et al. 2002). Long-term studies incorporating a widespread system of exclosures (Bock et al. 1993) and ability to control treatment levels are necessary to determine effects of land use on habitats and birds. The treatment projects planned by management agencies and the large number of areas to be treated represent a tremendous opportunity to design a sound experimental approach. In addition, a commitment to monitoring at appropriate scales would provide feedback to evaluate treatment effects and provide a basis for adaptive management strategies (Walters 1986, Morrison 2002).

Implementation of sound management based on an understanding of the effects of land-use practices, and enforced accountability to those policies, may be the only way to ensure long-term survival of sagebrush habitats and their birds. Protection from economic use (as national parks or monuments) is not viable for all sagebrush lands but could be an option in specific areas that retain native plants or are important regions for biodiversity. Purchasing lands for protection (Shaffer et al. 2002) also is not a complete solution because the areas required to encompass natural disturbance patterns are too large. Approximately 4.3 million ha of sagebrush lands would need to be placed in nature reserves if we are to meet the conservation goal of protecting 10% of the distribution. To develop this network of reserves, we need to prioritize the landscape by identifying and providing protection or other appropriate management to those relatively large areas of sagebrush in good condition. We then need to enlarge existing protected blocks, increase connectivity in the landscape, and employ basic principles of landscape management to ensure long-term survival of sagebrush habitats and birds.

Complete restoration of habitats requires that we understand critical patterns and processes at the appropriate spatial scales (Whisenant 1993). For sage-grouse, which may use ranges encompassing >2500 km² (Schroeder et al. 1999), creating suitable habitats will require that we focus efforts to restore entire landscapes rather than pursue individual unconnected efforts (Dobkin 1995, Wisdom, Rowland, et al. 2002, Wisdom, Wales, et al. 2002). However, the ecological foundation for development of overarching management prescriptions based on sage-grouse (Dobkin 1995, Rich and Altman 2002) or other single-taxon approaches (such as birds) needs to be tested for its capability to accommodate all species associated with sagebrush ecosystems.

In the absence of active restoration, exotic grasses will continue to invade sagebrush landscapes and degrade habitat (Hemstrom et al. 2002, Wisdom, Rowland, et al. 2002). To counter this disastrous scenario, we strongly recommend a federal policy to require use of ecologically appropriate native plant species in all shrubsteppe restoration projects on public lands. Such a policy will provide the incentive for the private sector to create sufficient commercial sources of native seed. Mandatory use of native seed in public-land restoration is a relatively simple step with great potential for redirecting
the ecological trajectory of these landscapes away from ecological dysfunction and toward ecological resiliency.

BIRD RESPONSE TO HABITAT CHANGE

Questions about basic life history for birds living in sagebrush habitats should form an integrated foundation for testing broader hypotheses about relationships between birds and their habitats (Noon and Franklin 2002, Wiens 2002). Because of their increasing dominance in sagebrush systems, we need to focus research on the influence of exotic plants on habitat dynamics and bird response. Understanding mechanisms underlying bird response to habitat characteristics will require that we determine population information across a range of habitat conditions. We recommend establishing a coordinated network of study sites across a gradient of habitat conditions at which demographic information, such as reproductive success, adult and juvenile survival, adult return rates, and patterns of juvenile dispersal, can be obtained. An intensive program to mark birds at such sites could yield great insight into population dynamics (Sherry and Holmes 2000) but will require a long-term commitment to maintain. Long-term studies involving marked individuals also could assess the potential for birds’ site fidelity to delay population response to habitat changes, a possible cause of confounded bird-habitat models (Wiens et al. 1986). Ultimately, development of population models based on life-stage information collected from such a network of sites (Caswell 2001) could yield significant insights into critical life stages, survival during breeding, migration, and wintering periods, and the influence of habitat on population dynamics.

MONITORING AND SURVEY ISSUES

Robust sampling over spatial and temporal scales that we view as necessary must involve methods that permit detectability estimates and describe sources of variation. Existing large-scale bird-monitoring programs, such as the North American Breeding Bird Survey (Robbins et al. 1986, Peterjohn and Sauer 1999) and the Christmas Bird Count (Root 1988) may not adequately sample many of the species in sagebrush ecosystems (Saab and Rich 1997). These surveys also have come under increasing criticism because of their inability to estimate biases in detectability of birds, which vary with respect to species, observers, and vegetation type, and their subsequent failure to incorporate differential detectabilities into trend analyses (Johnson 1995, Anderson 2001). For some species, targeted surveys (i.e., lek counts for sage-grouse) and new methods may be required to estimate population trends.

Almost all sampling of shrubsteppe bird populations has been based on counts of singing males on survey plots. Yet, the relationship between singing males and population parameters has not been established. Seasonal variation also may be critical in adjusting estimates based on large regions sampled throughout the breeding period (Best and Petersen 1985). Estimates based on counts of singing males may actually overestimate the breeding segment of the population by including nonbreeding territorial males, confounding our conclusions about habitat associations or population trends.

Sampling effort of current monitoring programs is distributed unevenly within sagebrush habitats among individual states. Even though many Breeding Bird Survey routes in western states sample sagebrush habitats, the proportion of sagebrush area sampled varies greatly compared to the proportion within the states (Table 2). Thus, Breeding Bird Survey routes likely capture neither the large-scale habitat features nor the smaller-scale dynamics along the gradient of habitat configurations available to shrubsteppe birds. Similar to most other habitats, surveys based on road networks may limit our ability to estimate abundance over the full range of available landscapes (Anderson 2001). Small-scale bias due to presence of unpaved or little-used roads on bird counts was insignificant in sagebrush habitats (Rotenberry and Knick 1995). Therefore, development of a new survey network that samples the existing sagebrush distribution but using unpaved roads still may be the most practical means to survey large areas.

To address gradients in habitat and bird dynamics, surveys need to be based on a standard set of sampling methods for habitats and birds that incorporate local efforts into a broader program in a hierarchical design. Ultimately, counts, indexes, or density estimates need to be related to habitat components and translated into estimates of fitness or productivity per unit of area or habitat to understand source-sink dynamics and mechanisms underpinning population trends (Morrison 2001, Noon and Franklin 2002)
TABLE 2. Proportion of sagebrush habitats within individual states relative to representation of sagebrush habitats sampled on Breeding Bird Survey routes. Only routes sampled at least once from 1995 through 2001 are included to reflect current conditions.

<table>
<thead>
<tr>
<th>State</th>
<th>Total area (ha)</th>
<th>Area of sagebrush ha (% of total)</th>
<th>Breeding Bird Survey routes</th>
<th>No. of BBS routes</th>
<th>No. that include sagebrush n (%)</th>
<th>Area sampled by all BBS routes (ha)</th>
<th>Sagebrush area sampled by BBS routes ha (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>California</td>
<td>40 865 326</td>
<td>1 264 557 (3)</td>
<td></td>
<td>237</td>
<td>8 (3)</td>
<td>474 000</td>
<td>3058 (1)</td>
</tr>
<tr>
<td>Colorado</td>
<td>26 963 052</td>
<td>1 898 437 (7)</td>
<td></td>
<td>136</td>
<td>38 (28)</td>
<td>272 000</td>
<td>17 993 (7)</td>
</tr>
<tr>
<td>Idaho</td>
<td>21 586 670</td>
<td>5 652 438 (26)</td>
<td></td>
<td>63</td>
<td>43 (68)</td>
<td>126 000</td>
<td>21 076 (17)</td>
</tr>
<tr>
<td>Montana</td>
<td>38 137 543</td>
<td>2 421 715 (6)</td>
<td></td>
<td>67</td>
<td>24 (36)</td>
<td>134 000</td>
<td>5 388 (3)</td>
</tr>
<tr>
<td>Nevada</td>
<td>28 664 409</td>
<td>10 876 551 (38)</td>
<td></td>
<td>43</td>
<td>26 (61)</td>
<td>86 000</td>
<td>8 683 (10)</td>
</tr>
<tr>
<td>Oregon</td>
<td>25 142 837</td>
<td>5 662 882 (23)</td>
<td></td>
<td>127</td>
<td>29 (23)</td>
<td>254 000</td>
<td>9 348 (4)</td>
</tr>
<tr>
<td>Utah</td>
<td>21 982 503</td>
<td>3 740 229 (17)</td>
<td></td>
<td>103</td>
<td>86 (84)</td>
<td>206 000</td>
<td>35 183 (17)</td>
</tr>
<tr>
<td>Washington</td>
<td>17 428 664</td>
<td>2 012 649 (12)</td>
<td></td>
<td>99</td>
<td>45 (46)</td>
<td>198 000</td>
<td>22 709 (12)</td>
</tr>
<tr>
<td>Wyoming</td>
<td>21 982 503</td>
<td>3 740 229 (17)</td>
<td></td>
<td>117</td>
<td>27 (23)</td>
<td>234 000</td>
<td>6871 (3)</td>
</tr>
<tr>
<td>Totals</td>
<td>246 102 816</td>
<td>43 098 435 (18)</td>
<td></td>
<td>992</td>
<td>326 (33)</td>
<td>1 984 000</td>
<td>128 308 (6)</td>
</tr>
</tbody>
</table>

a As defined in Table 1.
b Estimated by buffering each Breeding Bird Survey route by 250 m along each side of the 40-km transect.

MIGRATION AND WINTERING-GROUND PROCESSES

Improving our ability to track migrating birds, identify wintering areas, and estimate mortality during the nonbreeding period may be the most significant contributions that we can make toward understanding population dynamics of shrubsteppe birds. Because population dynamics of birds may be strongly influenced by mortality during the nonbreeding period (Fretwell 1972), focusing our attention solely on sagebrush breeding areas risks overlooking the importance of migration routes and wintering grounds. Wintering areas for some species breeding in sagebrush habitats have been identified in the southwestern United States and Mexico (Fig. 6). However, we do not know the migration pathways these birds use or their yearly fidelity to wintering ranges.

We need a new system of surveys designed to identify the spatial and temporal distribution of wintering birds. From these surveys, we can determine habitats or regions important to wintering birds, determine the influence of weather on seasonal or yearly variation in areas used, and assess risks to birds from contaminants or habitat loss.

The ability to link habitat and population components of shrubsteppe birds during breeding, migration, and wintering periods may provide insights into annual fluctuations in populations and area-specific productivity (Wiens and Dyer 1975). To achieve this, technological advances in marking and tracking individuals and populations will be necessary. Banding information is limited because banded birds are rarely recovered. Most species, such as Sage and Brewer’s Sparrows, are too small (<25 g) to carry radio-transmitters that currently are available. For larger birds, such as Sage Thrasher (35–50 g), battery life of radio-transmitters and detection distances are too short to track between breeding and wintering ranges. We only now are developing transmitters sufficiently small for attachment to small birds and powerful to track their movements over large distances and for longer periods. Other techniques that do not distinguish individuals, such as stable isotopes (Marra et al. 1998), may hold potential to determine the extent to which breeding populations mix or concentrate during the wintering period as well as link wintering ranges of birds to their breeding ranges in northern sagebrush ecosystems.

CONCLUSION

Since the report of the Conservation Committee of the Wilson Ornithological Society (Braun et al. 1976), land-use practices, invasion by exotic plants, disrupted ecosystem processes, and altered disturbance regimes have continued to impact sagebrush ecosystems. The continued threats to sagebrush ecosystems are numerous, and their consequences either will require long and expensive recovery or are largely irreversible (Rotenberry 1998, Knick 1999). Aggressive
FIGURE 6. Combined breeding and wintering ranges of Brewer’s Sparrow, Sage Sparrow, Sage Thrasher, Green-tailed Towhee, and Gray Flycatcher. For conservation to succeed, researchers and managers must recognize the continental scale at which sagebrush-breeding birds live. Ranges were delineated from individual Birds of North America accounts (Appendix).
management actions might stabilize current conditions. However, most management scenarios in the interior Columbia River basin forecast declines in habitat condition and extent (Raphael et al. 2001, Wisdom, Rowland, et al. 2002).

Responsibility for maintaining sagebrush habitats and bird populations rests squarely on public land management agencies because most species’ summer ranges are owned publicly and managed by state or federal agencies. The issues also are largely contained within the United States and Mexico because many of the birds breeding in sagebrush ecosystems are short-distance migrants (Fig. 6). State and federal management agencies appreciate the importance of birds and habitats in sagebrush ecosystems. However, resources currently expended on shrubland birds fall far short of those necessary to address the issues. Development of a comprehensive approach to bird conservation in sagebrush habitats requires a broad range of partnerships, including state and federal agencies, academia, and private organizations and landowners. Our research agenda incorporates a diversity of management needs and develops an integrated approach to understanding the dynamics of bird communities in sagebrush habitats.

Our primary challenge, presented over a quarter of a century ago (Braun et al. 1976), may be to convince our society of the intrinsic value of sagebrush ecosystems and their unique biodiversity. This change in mindset will have to be followed by a firm commitment by federal and state agencies to provide the resources necessary to resolve issues presented in this paper. Only with this concerted effort and commitment can we afford to be optimistic about the future of sagebrush ecosystems and their avifauna.

ACKNOWLEDGMENTS

This paper was written in response to a request by Terrell D. Rich during his tenure as President of the Cooper Ornithological Society, to report on the current status of sagebrush ecosystems and provide a research agenda for birds living in sagebrush habitats. Many of the ideas were discussed at a workshop, “The Effects of Multiscale Landscape Changes on Populations of Birds in Arid Lands of the Intermountain West,” in August 2001 in Boise, Idaho. The workshop was organized by the USGS Forest and Rangeland Ecosystem Science Center. Sixty-five people attended the workshop representing the U.S. Geological Survey, U.S. Fish and Wildlife Service, U.S. Bureau of Land Management, U.S. National Park Service, U.S. Department of Energy, U.S. Department of Defense, and USDA Forest Service; state wildlife agencies of Idaho, Nevada, Utah, and Washington; the University of California-Riverside; Boise State University; University of Montana; Michigan State University; University of Nevada; Albertson College of Idaho; Idaho State University; the Center for Conservation Research, Audubon Society; The Nature Conservancy; the High Desert Ecological Research Institute; Partners in Flight; Point Reyes Bird Observatory; Idaho Bird Observatory; and Idaho Power Company. The workshop was funded by the USGS Forest and Rangeland Ecosystem Science Center, Biological Resources Discipline and the USGS Southwest Arid Lands Group, Geologic Discipline. Boise State University provided additional support. We thank R. E. Kirby, L. W. Oring, M. J. Wisdom, B. C. Schoeberl, B. A. Maurer, A. Hughes, F. L. Knopf, S. M. Haig, T. L. Sohl, L. S. Schueck, T. D. Rich, E. G. Campbell, M. A. Hilliard, and C. McCarthy for their presentations and participation, S. E. Hanser, M. Leu, L. S. Schueck, and C. W. Meinke assisted with the GIS analysis. We appreciate reviews of the manuscript by C. E. Braun, J. W. Connelly, M. Leu, T. D. Rich, J. Sauder, J. M. Scott, and J. A. Wiens.

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APPENDIX. Bird species associated with sagebrush habitats, their primary habitat association (Paige and Ritter 1999:12), and reference to the respective *Birds of North America* species account.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sagebrush association</th>
<th>Birds of North America species account</th>
</tr>
</thead>
</table>
| Swainson’s Hawk  
*Buteo swainsoni*               | Shrubland, grassland  | England et al. 1997                    |
| Ferruginous Hawk  
*Buteo regalis*                | Shrubland, grassland  | Bechard and Schmutz 1995               |
| Prairie Falcon  
*Falco mexicanus*            | Shrubland, grassland  | Steenhof 1998                          |
| Columbian Sharp-tailed Grouse  
*Tympanuchus phasianellus columbianus* | Shrubland, grassland  | Connelly et al. 1998                   |
| Greater Sage-Grouse  
*Centrocercus urophasianus* | Sagebrush obligate    | Schroeder et al. 1999                  |
| Gunnison Sage-Grouse  
*Centrocercus minimus*     | Sagebrush obligate    | Schroeder et al. 1999                  |
| Long-billed Curlew  
*Numenius americanus*       | Grassland             | Dugger and Dugger 2002                 |
| Burrowing Owl  
*Athene cunicularia*        | Grassland             | Haug et al. 1993                       |
| Short-eared Owl  
*Asio flammeus*            | Grassland             | Holt and Leasure 1993                  |
| Gray Flycatcher  
*Empidonax wrightii*        | Dry woodland          | Sterling 1999                          |
| Loggerhead Shrike  
*Lanius ludovicianus*       | Shrubland, grassland  | Yosef 1996                             |
| Sage Thrasher  
*Oreoscoptes montanus*      | Sagebrush obligate    | Reynolds et al. 1999                   |
| Green-tailed Towhee  
*Pipilo chlorurus*          | Shrubland             | Dobbs et al. 1998                      |
| Brewer’s Sparrow  
*Spizella breweri*          | Sagebrush obligate    | Rotenberry et al. 1999                 |
| Vesper Sparrow  
*Poecetes gramineus*       | Grassland             | Jones and Cornely 2002                 |
| Lark Sparrow  
*Chondestes grammacus*     | Shrubland             | Martin and Parrish 2000                |
| Black-throated Sparrow  
*Amphispiza bilineata*      | Shrubland             | Johnson et al. 2002                    |
| Sage Sparrow  
*Amphispiza belli*         | Sagebrush obligate    | Martin and Carlson 1998                |