Sage Sparrow (*Amphispiza belli*): A Technical Conservation Assessment

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COVER PHOTO CREDIT

Sage Sparrow (*Amphispiza belli*). Photograph by Greg Lasley. Used with permission.

Summary of Key Components for Conservation of Sage Sparrow

The sage sparrow (*Amphispiza belli*) is a sagebrush obligate that can be common in its sagebrush shrubsteppe habitat. This assessment focuses on the only subspecies found within Region 2 of the USDA Forest Service, *A. b. nevadensis*. Breeding Bird Survey data indicate a decline in sage sparrow populations between 1966 and 1991 throughout the western United States. Within Region 2, sage sparrow populations in the Wyoming Basin and Southern Rockies physiographic strata have exhibited long-term declines. The sage sparrow is listed as a priority species in the Colorado and Wyoming Partners in Flight bird conservation plans.

Reported sage sparrow population declines are likely linked to extensive alteration of sagebrush (*Artemisia* spp.) shrubsteppe habitat on the species' breeding grounds. Though widespread, this habitat constitutes one of the most endangered ecosystems in North America due to extensive, ecologically transformative influences of livestock grazing and, to a lesser degree, alteration of natural fire regimes and invasion by exotic plant species. Loss and fragmentation of habitat due to agricultural, urban, suburban, energy, and road development also threaten the species.

Conservation and management of sage sparrows in Region 2 should focus on creating and maintaining a sagebrush landscape that replicates conditions historically created by climate and natural processes, including fire frequencies. Because sagebrush habitats and their dominant disturbance processes likely vary across Region 2, a simple set of strategic guidelines for sage sparrow management and conservation will not work. Sage sparrows thrive in unfragmented landscapes of sagebrush. *Amphispiza belli nevadensis* are most abundant where big sagebrush (*Artemisia tridentata*) occurs in large stands with clumps of sagebrush and open ground for foraging and nesting. The creation and maintenance of these conditions will require managing at large spatial and temporal scales and assessing at these larger scales the cumulative impact of activities that fragment habitat.

Successful conservation efforts for sage sparrows and sagebrush shrubsteppe communities will require new and innovative strategies. Region 2 sagebrush habitats represent a relatively small fraction of the sage sparrow's natural range, and management of Region 2 habitats alone is unlikely to ensure long-term population viability of the species. Therefore, it will be necessary to develop partnerships among other federal and state agencies, private landowners, and conservation organizations to ensure the long-term conservation of complex, biologically rich sagebrush ecosystems.

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Introduction

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). The sage sparrow is the focus of an assessment because it is listed as a sensitive species for Region 2, and the conservation of sensitive species is to be integrated into National Forest System land management planning. The sage sparrow is also a Management Indicator Species (MIS) on multiple national forests within Region 2 (**Figure 1**). Management Indicator Species serve as barometers for species viability at the Forest level and have two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a)(1)); and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a)(6)).

This assessment addresses the biology of the sage sparrow throughout its range, focusing on Region 2 (**Figure 1**). The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, biologists, other agencies and organizations, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on existing scientific knowledge. These assessments do not seek to develop prescriptive management

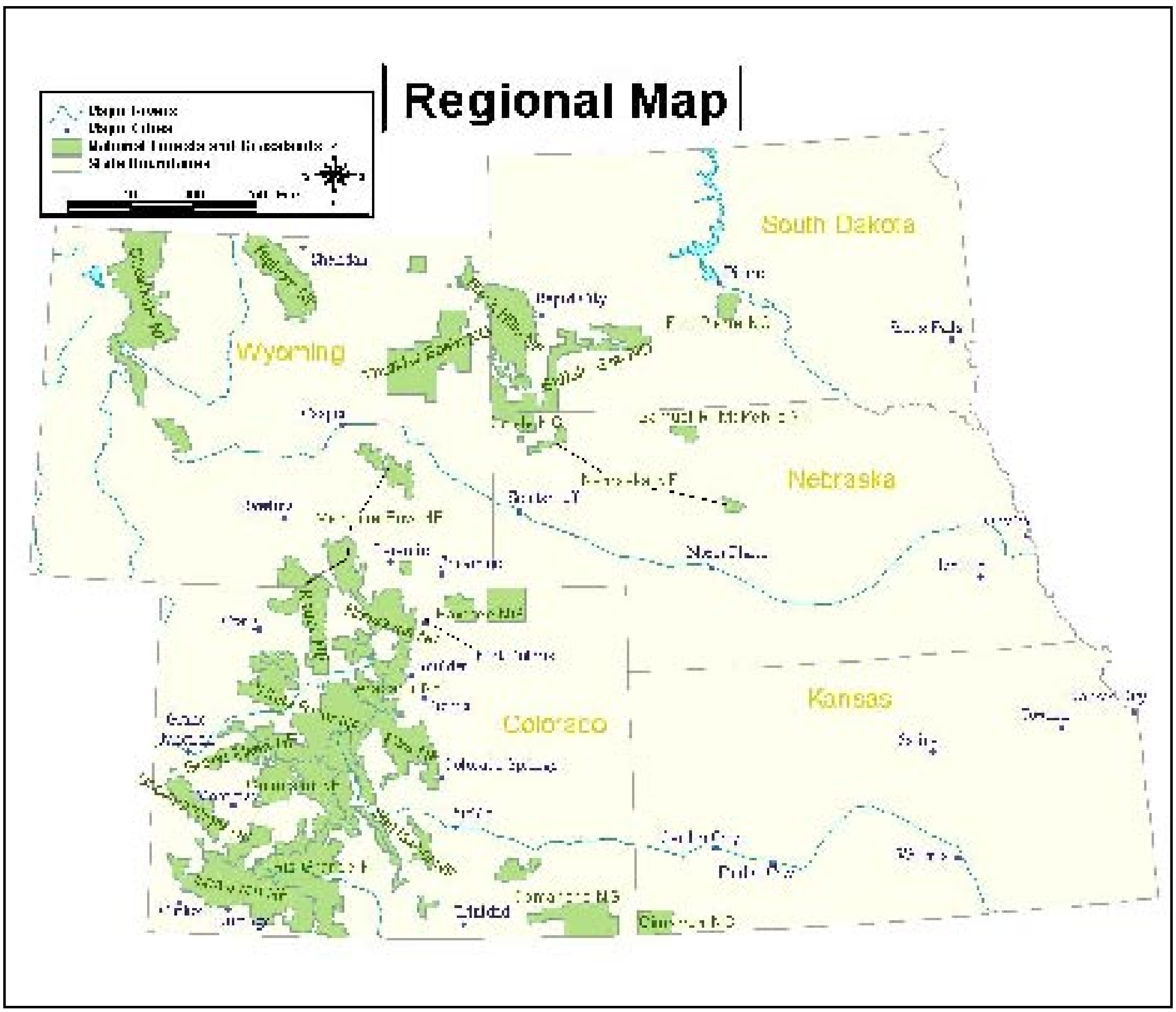

Figure 1. Regional map of USDA Forest Service Region 2. National grasslands and forests are shaded in green.

recommendations. Rather, they provide the ecological background upon which management must be based and focus on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, they discuss and evaluate management recommendations currently in use or proposed elsewhere.

Scope

This assessment examines the biology, ecology, conservation and management of the sage sparrow, with specific reference to the geographic and ecological characteristics of USFS Region 2. It focuses on the ecology of the only one of five recognized subspecies, *Amphispiza belli nevadensis*, found within Region 2. Although some of the literature on the species originates from field investigation outside the region, this document places that literature in the ecological and social context of the Rocky Mountain Region. This assessment is concerned with the reproductive behavior, population dynamics, and other characteristics of the sage sparrow in the context of the current environment. The evolutionary environment of the species is considered in conducting the syntheses, but it is placed in a current context.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on sage sparrows were used in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because it is the accepted standard in science. We chose to use some non-refereed literature when refereed information was unavailable elsewhere, but non-refereed publications and reports were regarded with greater skepticism.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, we note the strength of evidence for particular ideas, and we describe alternative explanations where appropriate.

Publication of Assessment on the World Wide Web

To facilitate the use of species conservation assessments, they are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Conservation assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology using at least two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Special management status of this species on USFS lands and states within Region 2.

- **Federal Endangered Species Act:** U.S. Fish and Wildlife Service (USFWS) lists the San Clemente Island subspecies, *Amphispiza belli clementeae*, as threatened under the U.S. Endangered Species Act (U.S. Department of Interior 2001). The other four subspecies are not listed.

- **USFWS Birds of Conservation Concern:** species is considered a bird of conservation concern in Bird Conservation Region (BCR) 9 (Great Basin), BCR 16 (Southern Rockies/Colorado Plateau), BCR 33 (Sonoran and Mojave deserts — U.S. portion only), and BCR 34 (Sierra Madre Occidental — U.S. portion only). (U.S. Department of Interior 2002a).

- **USFS Rocky Mountain Region:** species is designated a sensitive species in Region 2 (U.S. Department of Agriculture 2003) and a MIS on the Bighorn, Shoshone, and White River national forests.

- **Bureau of Land Management (BLM):** species is listed as sensitive in all counties of Wyoming (U.S. Department of Interior 2002b).

- **Migratory Bird Treaty Act:** species is protected from "take" (U.S. Department of Interior 2002c).

- **State Status:**
  - *Colorado Division of Wildlife (2003):* species is not listed on the state threatened and endangered species list.
  - *Kansas Department of Wildlife and Parks (2003):* species is not listed on the state threatened and endangered species list.
  - *Nebraska Game and Parks Department (2000):* species is not listed on the state threatened and endangered species list.
  - *South Dakota Game Fish and Parks (2000):* species is not listed on the state threatened and endangered species list.
  - *Wyoming Natural Diversity Database (1997):* species is listed on the state species of concern list.

- **Natural Heritage Program (NHP) Conservation Status:** global rank of G5 (secure).

- **State Heritage Program Conservation Status:**
  - *Colorado Natural Heritage Program (2002):* species is ranked S3B (vulnerable through its breeding range or found locally in a restricted range) and SZN (migrant whose occurrences are too irregular, transitory, and/or dispersed to be reliably identified, mapped, and protected.
  - *Wyoming Natural Diversity Database:* species is ranked S3 (rare or local throughout its range or found locally in restricted range) and of moderate concern within the state (uncertain abundance trends, moderate biological vulnerability, moderate external threats, patchy distribution), with high state contribution (Wyoming populations contribute substantially to the species' rangewide persistence) (www.natureserve.org).
  - *South Dakota Natural Heritage Program, Nebraska Natural Heritage Program, and Kansas Natural Heritage Inventory:* species is not listed as a species of concern (www.natureserve.org).

- **Partners in Flight (PIF) Bird Conservation Plans:**
  - *Colorado Land Bird Conservation Plan (Biedleman 2000):* Priority Species for Colorado Plateau and Southern Rocky Mountain Physiographic Areas in the Priority Habitat Sagebrush Shrubland.
  - *Wyoming Bird Conservation Plan (Cerovski et al. 2001):* Level I (Conservation Action) species in shrubsteppe Highest Priority Habitat.
  - *Southern Rocky Mountains, Colorado Plateau, and Wyoming Basin Physiographic Areas:* sage sparrow and shrubsteppe or sagebrush habitat are Priority Species and Priority Habitats.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The sage sparrow is protected under the Migratory Bird Treaty Act of 1918, which prohibits "take" of migratory birds unless permitted by regulations. Take is defined by the Act to mean "hunt, take, capture, offer for sale, offer to purchase, export, at any time, or in any manner, including any part, nest, or egg of any such bird." (16 U.S.C. 703).

The USFS Rocky Mountain Region includes the sage sparrow on the Regional Forester's sensitive species list. Under Region 2's sensitive species policy (http://www.fs.fed.us/im/directives/field/r2/fsm/2600/2670.doc), conservation strategies are to be developed and implemented for sensitive species and their habitats, in coordination with other USFS units, managing agencies, and landowners. Region 2 will coordinate management objectives to conserve sensitive species with state and federal agencies and other cooperators as appropriate. Approaches may include collaboratively developing individual species or multi-species conservation strategies, formalizing interagency conservation agreements, and incorporating recommendations into management direction set forth in Land and Resource Management Plans. Scientific information, including Regional species evaluations, species and ecosystem assessments, and conservation strategies, is to be integrated into USFS planning and implementation. Additionally, appropriate inventories and monitoring of sensitive species are to be conducted to improve our knowledge of the species' distribution, status, and responses to management activities, coordinating efforts within the Region and with other agencies and partners where feasible (U.S. Department of Agriculture 2003).

Under the National Forest Management Act the USFS is required to sustain habitats that support healthy populations of native and desired non-native plant and animal species on national forests and grasslands. Legally required activities include monitoring population trends of MIS in relationship to habitat change, measuring the effects of management practices, monitoring the effects of off-road vehicles, and maintaining biological diversity.

The standards and guidelines of the USFS Government Performance Results Act ensure that resources are managed in a sustainable manner. The National Environmental Policy Act requires agencies to specify environmentally preferable alternatives in land use management planning. Additional laws with which USFS land management plans must comply are the Endangered Species, Clean Water, Clean Air, Mineral Leasing, Federal Onshore Oil and Gas Leasing Reform, and Mining and Minerals Policy acts; all are potentially relevant to sage sparrow conservation.

The BLM is developing major programs for restoration of sagebrush ecosystems throughout the western United States (Paige and Ritter 1999, Beever and Pyke 2002, U.S. Department of Interior 2002d). These areas include important habitat for sage sparrows, especially extensive areas of sagebrush habitat that are maintained with shrubs occurring in tall, clumped, and vigorous stands.

Declines in numerous bird populations have led to concern for the future of migratory and resident bird species. In 1990, the National Fish and Wildlife Foundation brought together federal, state, and local government agencies, private foundations, conservation groups, industry, and the academic community to form a program to address the problem. Thus, Partners in Flight (PIF) was conceived as a voluntary, international coalition dedicated to "keeping common birds common" and "reversing the downward trends of declining species". Landbird conservation plans have been or are being developed for each state and/or physiographic area (modified from original strata devised by the Breeding Bird Survey Robbins et al. 1986). These Bird Conservation Plans form the foundation for PIF's long-term strategy for bird conservation. They identify priority species and habitats and establish objectives for conserving and monitoring bird populations and their habitats. Although priorities and biological objectives are identified at the physiographic area level, implementation of PIF objectives is meant to take place at different scales, including individual states, federal agency regions, joint ventures, and Bird Conservation Regions (BCRs). These plans have identified the sage sparrow and its habitats within USFS Region 2 as priorities for conservation.

States within USFS Region 2 that have completed PIF Bird Conservation Plans are Colorado and Wyoming. The Colorado Land Bird Conservation Plan (Biedleman 2000) lists the sage sparrow as a Priority Species for the Colorado Plateau Physiographic Area in the Priority Habitat Sagebrush Shrubland and for the Southern Rocky Mountain Physiographic Area in the Priority Habitat Sagebrush Shrubland. Likewise, the Wyoming Bird Conservation Plan (Cerovski et al. 2001) lists the sage sparrow as a Level I (Conservation Action) species for one of Wyoming's Highest Priority Habitats: Shrubsteppe. The Physiographic Areas in Region 2 include Central Rocky Mountains (No. 64), Southern Rocky Mountains (No. 62), Colorado Plateau (No. 87), Wyoming Basin (No. 86), Northern Shortgrass Prairie (No. 39), Central Shortgrass Prairie (No. 36), West River (No. 38), and Central Mixed-grass Prairie (No. 34). Of these, the Southern Rocky Mountains, the Colorado Plateau, and the Wyoming Basin plans list sage sparrow, sagebrush shrubland, and shrubsteppe habitat as a Priority Species and Priority Habitats, respectively.

The Land Bird Conservation Plan for Colorado (Biedleman 2000) contains Implementation Strategies for conserving priority species and habitats. For sage sparrows and their associated habitat of sagebrush shrubland, the plan calls for monitoring sage sparrows to document distribution, population trends, and abundance. They propose using Breeding Bird Survey (BBS) data and incorporating Monitoring Colorado Bird (MCB) data as it becomes available. MCB was implemented in sagebrush habitat in 1999; currently no results of this monitoring have been published. The plan also proposes to document the amount, condition, and ownership of sagebrush habitat in Colorado and to conserve unique representatives and/or large ecologically-functioning examples of sagebrush habitat in Colorado. These efforts have not been initiated, but the Colorado Division of Wildlife is working on a rangewide conservation plan for the Gunnison sage grouse (*Centrocercus minimus*), a species that may use habitat in a similar way to the sage sparrow and/or respond similarly to threats, management, and conservation activities (Biedleman 2000).

Both the Colorado and Wyoming bird conservation plans propose implementing a list of "Best Management Practices" for shrublands to benefit birds. These are excerpted from "Birds in a Sagebrush Sea" (Paige and Ritter 1999) and are detailed in the section on "Potential Management." These practices have not yet been implemented by federal or state agencies. There is no information on the extent to which private entities are implementing these management practices.

The sage sparrow is not listed as a species of concern on the current Kansas, South Dakota, and Nebraska species of concern lists, and therefore, these states do not have direct management or conservation goals for this species. Currently, programs under the State Game and Fish Departments or State Heritage Programs do not have conservation or restoration objectives for sagebrush ecosystems. Management and conservation plans are being developed and should be available in the near future (personal communications, Kansas Department of Wildlife and Parks, Nebraska Game and Parks Commission, and South Dakota Game, Fish, and Parks). The only current plans in these states that apply to sagebrush conservation are The Nature Conservancy's Northern Great Plains Steppe Ecoregional Plan (The Nature Conservancy 2000).

State and federal management agencies have the capability to conduct the actions needed to conserve sagebrush ecosystems as an integral part of their larger missions. These agencies have identified the importance of birds and habitats in sagebrush ecosystems. However, the resources currently available for shrubland birds fall far short of what is necessary to adequately address the issues. Development of a comprehensive approach to bird conservation in sagebrush habitats requires a broad range of partnerships, which should include state and federal agencies, academia, and private organizations.

Adequacy of laws and regulations to conserve the species

The existing regulatory mechanisms, management plans, and conservation strategies described above may be adequate to protect the species. Yet, political will and public support is needed to fully implement these policies and strategies and to effectively conserve this species and its habitats. The processes that destroy, fragment, and degrade sagebrush shrubsteppe continue to affect virtually all sagebrush habitats and have led to the current situation where the bird species perhaps most in need of conservation attention are those most typical of undisturbed shrubsteppe, including the sage sparrow (Rotenberry 1998).

In some cases, current management practices are inadequate to conserve sage sparrow populations or sagebrush shrublands. The following are just a few management practices that can have detrimental effects on the conservation of this species and its habitat.

1. Improper management of livestock can result in changes to native ecosystems, including invasion of non-native species and alteration of fire regimes. Historically, heavy livestock grazing altered much of the sagebrush range, changing plant composition and densities (Saab et al. 1995). In some cases, changes in water and nutrient cycling caused by grazing can promote the spread of invasive species, which then degrade habitat for native bird species by altering fire and disturbance regimes (Rotenberry 1998).

2. There is uniform agreement that fire frequencies in the Intermountain West have been altered greatly over the past 150 years (Dobkin and Sauder 2004). In some areas, as a result of fire suppression and the loss of fine fuels to grazing, fire-return intervals are now much longer. In other places, fire-return intervals are dramatically shorter due to the spread and dominance of fire-promoting exotic species (Dobkin and Sauder 2004). Fire kills sagebrush, and where non-native grasses dominate, the landscape can be converted to annual grassland as the fire cycle becomes shorter, removing preferred habitat (Paige and Ritter 1998). These changes have not affected Region 2 to the degree that has occurred across the Intermountain region (C. Quimby 2004 personal communication).

3. Management practices, such as manipulation of sagebrush to increase forage for livestock and road development for energy production, result in disturbance that promotes the invasion of exotic grasses, such as cheatgrass (*Bromus tectorum*). These

> annual exotics have come to dominate the grass-forb community of more than half the sagebrush region in the West, replacing native bunchgrasses (Rich 1996). Crested wheatgrass (*Agropyron cristatum*) and non-native annuals have fundamentally altered the grass-forb community in many areas of sagebrush shrubsteppe.

The ongoing threats to sagebrush ecosystems are numerous, and their consequences will require long and expensive recovery or, in some areas, are largely irreversible (Rotenberry 1998, Knick 1999, Knick et al. 2003). In the absence of active restoration, sagebrush landscapes will continue to be invaded by exotic grasses and to degrade in quality (Wisdom et al. 2000). Aggressive management actions might stabilize current conditions (Knick et al. 2003). However, declines in habitat condition and extent were projected outcomes of most management scenarios in sagebrush habitats in the Interior Columbia River Basin (Raphael et al. 2001, Wisdom et al. 2002, Knick et al. 2003).

Enforcement of existing laws and regulations

Protection from use is not a viable option for sagebrush lands. Very little of the geographic distribution of the sage sparrow's habitat has protected status in the form of national parks, USFS and BLM wilderness areas, or national wildlife refuges (Scott et al. 2001, Wright et al. 2001). For example, less than 2 percent of the sagebrush lands in the Columbia Plateau and 3 percent in the Great Basin are within National Parks or in reserves managed by the Department of Energy or Department of Defense. These reserves do not necessarily provide protection from management practices that may be detrimental to the sage sparrow and its habitat. For instance, BLM designated wilderness areas are managed for grazing and other uses (U.S. Department of Interior 2002d). Purchasing lands for protection (Shaffer et al. 2002) is not feasible because the areas likely required to maintain intact sagebrush ecosystems are too large and costly. Rather, enforcement of sound management policies based on an understanding of the effects of land use practice may be the only way to ensure long-term survival of sagebrush ecosystems and their associated avifauna (Knick et al. 2003).

Approximately two-thirds of the total area occupied by sagebrush in the western United States is managed by federal government agencies, primarily the BLM (Knick et al. 2003, Dobkin and Sauder 2004). Therefore, responsibility for maintaining sagebrush habitats and associated avifauna rests on public land management policies. Because many of the birds breeding in sagebrush ecosystems (i.e., sage sparrow, Brewer's sparrow [*Spizella breweri*]) are short-distance migrants, the issues are largely contained within the United States. The primary challenge is to respect the intrinsic value of sagebrush ecosystems and its unique biodiversity, a challenge presented over a quarter of a century ago by Braun et al. (1976) (Knick et al. 2003).

Biology and Ecology

Systematics and general species description

There are five recognized subspecies, or allospecies, of sage sparrow (*Amphispiza belli*): *A. b. belli*, *A. b. anescens*, *A. b. cinerea*, *A. b. clementeae*, and *A. b. nevadensis*. Only *A. b. nevadensis*is occurs within USFS Region 2, and this assessment focuses on this subspecies. The five subspecies are geographically separate and vary in morphometrics, plumage coloration, and habitat selection (Martin and Carlson 1998). These features roughly correlate with observed genetic and biochemical variation (Johnson and Marten 1992, Martin and Carlson 1998). Allozyme analysis indicates that *belli*, *canescens*, and *nevadensis* are each distinctive integrated units. The *belli* and *canescens* races are each other's closest relatives, and populations of *canescens* and *nevadensis* show no intergradation where subspecies meet at the northern end of the White Mountains, California (Johnson and Cicero 1991, Martin and Carlson 1998).

Sage sparrows are sexually monomorphic (i.e., both genders look alike) and medium-sized sparrows. *Amphispiza belli nevadensis* is pale and large with distinct streaking on the back. Its outermost retrices are widely edged with white, and it has longer wings than other races (Martin and Carlson 1998).

The sage sparrow's song consists of a series of short musical buzzes on different frequencies, with abrupt beginnings and endings (Rich 1981, Martin and Carlson 1998). While only the male sings, both sexes produce a short musical "tink" note, often repeated, as a location call. The warning call is similar but sharper and shorter. Also, females (but occasionally males) give a hoarse "quid quid" call during intra- and interspecific conflicts (Martin and Carlson 1998).

Distribution and abundance

Current and historic global distribution

Breeding ranges of the five subspecies do not overlap (Martin and Carlson 1998). *Amphispiza belli belli* is an uncommon to common but localized resident (i.e., non-migratory) in the Coast Ranges of California and along the western slope of the central Sierra Nevada. *Amphispiza belli canescens* breeds in interior south-central California. It is a short-distance migrant; it migrates upslope after breeding and has limited southward dispersal in the winter. *Amphispiza belli cinerea* is resident in west-central Baja California to about latitude 29° N, where it contacts *A. b. belli*. *Amphispiza belli clementeae* is resident on San Clemente Island, off the coast of southern California.

The subspecies that breeds within USFS Region 2, *Amphispiza belli nevadensis*, breeds over much of the Great Basin east of the Cascades and Sierra Nevada and west of the Rocky Mountains, including east-central Washington, southern Idaho, south-central Montana, Utah, Wyoming, and western and south-central Colorado south to northeastern California, east-central California, central and northern Nevada, northeastern Arizona, and northwestern New Mexico (Andrews and Righter 1992, Oakleaf et al. 1992, Lambeth 1998, Martin and Carlson 1998; **Figure 2**). It winters from central California and central Nevada, southwestern Utah, all but northeastern Arizona, west-central and southeastern New Mexico, south to northern Baja California, northern Sonora, and southwestern Chihuahua in Mexico, and west Texas (Martin and Carlson 1998). The sage sparrow's distribution in winter, based on Christmas Bird Counts, is shown in **Figure 3**.

There are few data on large-scale historical changes in sage sparrow distribution. Local populations in southern California have been extirpated as a result of urbanization and agricultural conversion (Martin and Carlson 1998). Because of the sage sparrow's close association with sagebrush shrubsteppe habitats (Wiens 1985, Martin and Carlson 1998) and because of the increased loss, fragmentation, and degradation of these habitats since historic times, the distribution of sage sparrow has most likely been altered from pristine conditions (Braun et al. 1976, Martin and Carlson 1998, Knick et al. 2003). However, no large-scale changes in distribution have been documented (Dobkin and Sauder 2004).

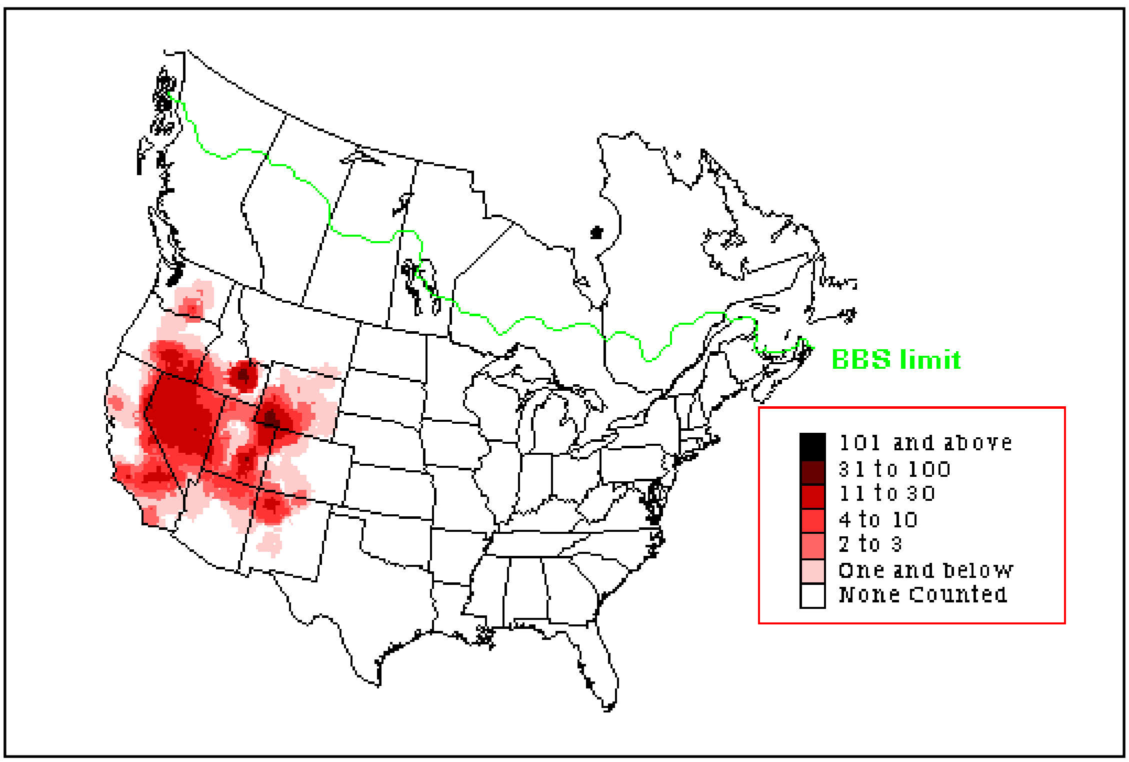

Figure 2. Relative breeding season abundance (average number of birds per route) of sage sparrow in the United States, based on Breeding Bird Survey data from 1982 to 1996 (Sauer et al. 2003).

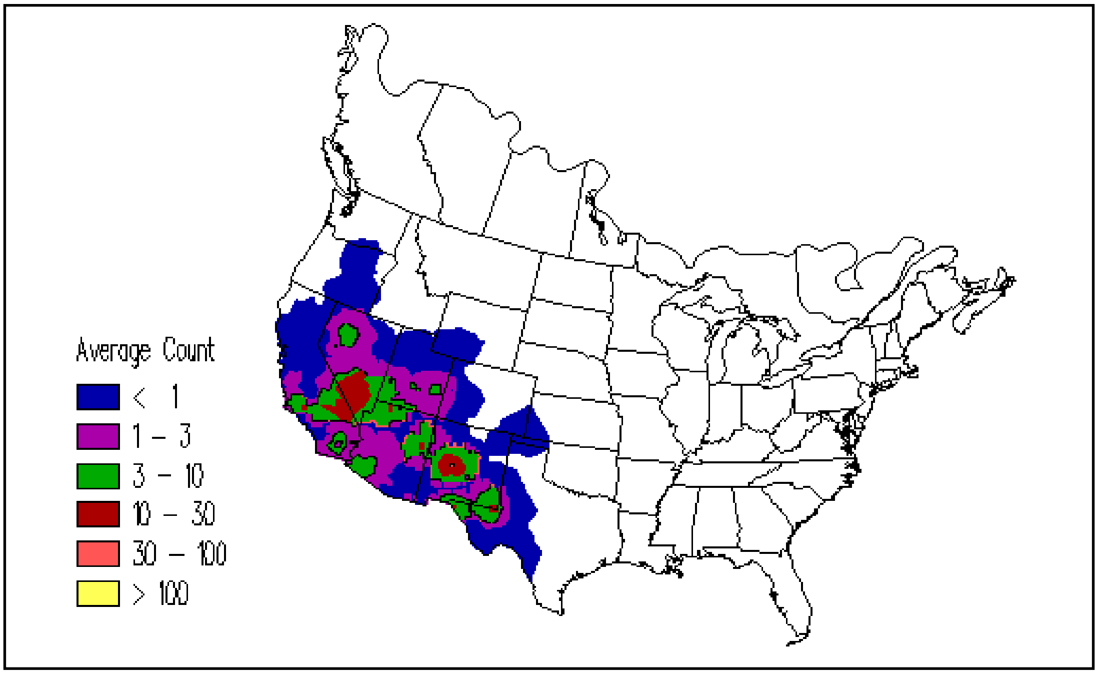

Figure 3. Winter season distribution and relative abundance of the sage sparrow in the United States, based on Christmas Bird Count data (Sauer et al. 1996b).

Regional current and historic distribution and abundance

Within Region 2, the sage sparrow breeds in portions of western, central, and northeastern Wyoming (Oakleaf et al. 1992, Martin and Carlson 1998), and in western and south-central (San Luis Valley) Colorado (Andrews and Righter 1992, Lambeth 1998).

Breeding season surveys indicate that sage sparrows reach their highest densities within *nevadenisis*' distribution, in Idaho, west-central Nevada, northeastern Utah, and southwestern Wyoming (**Figure 2**; Martin and Carlson 1998). Breeding densities of *nevadensis*, calculated using a modified Emlen's line transect method (Emlin 1977) for 14 to 16 plots in the Great Basin, were estimated at 57 to 145 individuals per km^2 (Rotenberry and Wiens 1980, Martin and Carlson 1998). In an east-central Nevada study from 1981 to 1982, densities of this subspecies in sites of lightly grazed sagebrush, cheatgrass, and Sandberg bluegrass (*Poa secunda*) were 0.90, 0.85, and 0.95 individuals per ha, respectively (Medin 1992, Martin and Carlson 1998). In southeastern Idaho, there were 95 to 126 individuals per km^2 (n = 2 plots); plots were sampled two to three years (Petersen and Best 1987b). Local numbers appear to be negatively influenced by increasing landscape-level fragmentation of shrublands (Knick and Rotenberry 1995), and breeding numbers of sage sparrows have recently declined throughout much of the West (Martin and Carlson 1998). Therefore, although historic abundances and distribution are not known, they may have differed from current measures.

Discontinuities in distribution and degree of isolation of populations

Breeding populations of the sage sparrow occur in several disjunct populations (**Figure 2**; Robbins et al. 1986, Sauer et al. 1996b, Martin and Carlson 1998). High abundances are relatively widespread and contiguous in Nevada. Other areas of high abundance occur in east-central Idaho and southwestern Wyoming, where populations tend to be slightly disjunct from the main intermountain distribution, with intervening areas of low abundance or absence (**Figure 2**). Lowest abundances occur at the boundary of the species' distribution. It is not known to what extent populations of *nevadensis* are currently isolated.

Population trend

North American Breeding Bird Survey (reference period 1966 to 2002)

Breeding Bird Surveys (BBS) were designed to provide a continent-wide perspective of population change. These surveys produce an index of relative abundance rather than a complete count of breeding bird populations. The data analysis assumes that fluctuations in these indices of abundance represent the population as a whole (Sauer et al. 2001). However, these data should be viewed with some caution. Local trends are sometimes difficult to interpret and can be quite different from larger-scale BBS trends (Peterjohn 1989).

Surveys are conducted throughout North America during the peak of the breeding season, primarily in May and June, earlier in desert regions and some southern states where the breeding season begins earlier. Each route is 24.5 miles long with a total of 50 point count stations at 0.5-mile intervals along the route.

BBS data for sage sparrows at the national and western regional scales have shown slight, non-significant increases between 1966 and 2002. When the time period is portioned, these two regions show significant declines for the time period of 1966 to 1979 and non-significant increases from 1980 to 2002 (**Table 1**). The central regional scale shows a slight, non-significant increase between 1966 and 2002. There is insufficient data to calculate trends for the 1966 to 1979 time period, but there was a non-significant increase between 1980 and 2002 (**Table 1**, **Figure 4**; Sauer et al. 2003). The Wyoming Basin physiographic stratum shows an overall non-significant decrease from 1966 to 2002; the data shows a non-signfiicant increase for the first time period, followed by a non-significant decrease. The Great Basin stratum shows a slight non-significant increase from 1966 to 2002 and between 1980 and 2002, while data for the 1966 to 1979 period shows a non-significant decline. The only significant regional trend from BBS data within USFS Region 2 is that of the Southern Rockies physiographic stratum, where data from 1966 to 2002 show a significant declining trend in relative abundance of minus 36 percent per year. No physiographic stratum shows significant increasing trends. Outside Region 2 there are no significant trends. These results differ somewhat from those reported by Martin and Carlson (1998) who reported that throughout the West, BBS data indicated a decline between 1966 and 1991 of 1.0 to 2.3 percent, with Arizona, Idaho, and Washington showing the largest declines (1982 to 1991) (Robbins et al. 1986, Sauer et al. 1996b). Yet, as Martin and Carlson (1998) indicate, for the western states there are too few routes to sufficiently assess trend data. Thus, there are substantial limitations on BBS data to accurately track sage sparrow population trends.

Colorado trends

Within Colorado, trend estimates show non-significant increases from 1966 to 2000 (**Table 1**; Sauer et al. 2003). The average count of sage sparrows per route (n =12) in Colorado from 1966 to 2002 was 1.26. Sage sparrows were present on an average of 14.82 percent (SE = 2.65) of the BBS routes in Physiographic Area 87 in Colorado between 1989 and 1997, at an average abundance of 2.97 (SE = 0.74) individuals per route (Biedleman 2000). The mean number of routes each year was 11.4 (SE = 1.55).

Wyoming trends

Sage sparrows are found across most of Wyoming where sagebrush is present (Cerovski et al. 2001), with highest abundances in southwestern Wyoming,. Yet

Table 1. Breeding Bird Survey trend data for sage sparrow, 1966-2002 (From Sauer et al.).

	1966-2002			1966-1979			1980-2002		
Location	Trend	*P* value	N	Trend	*P* value	N	Trend	*P* value	N
United States	1.06	0.377	222	-6.11	0.016	69	1.47	0.222	193
Western Region	1.05	0.380	217	-6.12	0.016	68	1.46	0.227	189
Central Region	0.06	0.997	5	a	a	a	5.83	0.785	4
Wyoming Basin	-0.31	0.903	29	8.09	0.104	9	-1.84	0.561	28
Great Basin	0.04	0.988	19	-4.73	0.747	7	1.79	0.293	15
Southern Rockies	-35.99	0.002	4	a	a	a	-36.10	0.003	4
Colorado	2.13	0.723	12	a	a	a	4.52	0.549	12
Wyoming	-0.35	0.890	36	7.8	0.113	10	-1.85	0.549	34
Kansas	a	a	a	a	a	a	a	a	a
Nebraska	a	a	a	a	a	a	a	a	a
South Dakota	a	a	a	a	a	a	a	a	a

a = No data.

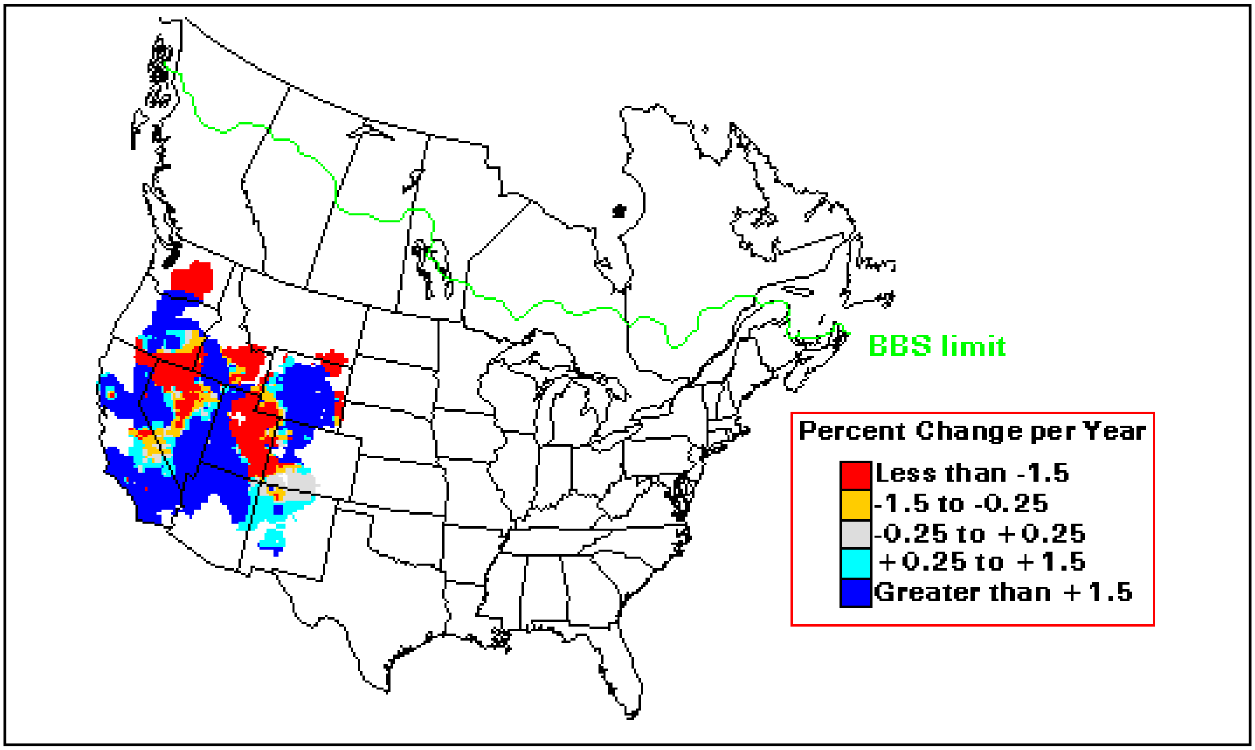

Figure 4. Sage sparrow trends (average percent population change per year) in the United States based on Breeding Bird Survey data from 1966 to 1996 (Sauer et al. 2003).

trend estimates show insignificant decreases between 1966 and 2002 (averaging minus 0.35 percent per year) and from 1980 to 2002 (averaging minus 1.85 percent per year). Declines were more pronounced between 1980 and 2000 than between 1966 and 1979, where there was no decline (**Table 1**). The average number of sparrows per route between 1966 and 2002 was 7.98 (number of routes = 36).

Kansas, Nebraska and South Dakota trends

BBS data for Kansas, Nebraska and South Dakota are insufficient to provide trend estimates.

Winter counts

Christmas Bird Count (CBC) data for the United States from 1959 to 1988 (Sauer et al. 1996a) indicate significant declines survey-wide (-2.1 percent average annual decrease, $p < 0.05$, $n = 160$) and in Texas (-2.2 percent average annual decrease, $p < 0.05$, $n = 16$) and non-significant declines in New Mexico (-0.8 percent average annual decrease, $p > 0.10$, $n = 17$) and Arizona (-4.9 percent, average annual decrease, $p > 0.10$, $n = 35$). California had a negligible non-significant increase (0.1 percent average annual increase, $p > 0.10$, $n = 67$). Mapped CBC data show highest United States abundance in southern Nevada and west-central New Mexico. There is no information on abundances in Mexico (**Figure 3**).

Activity pattern and movements

Circadian, seasonal, circannual

No formal daily (circadian) time budgets for sage sparrow have been reported. Wiens et al. (1986, 1987) made periodic behavioral observations of sage sparrow breeding pairs during the breeding season (1976 to 1983) and found that in 51 percent of the observation periods males were singing, in 35 percent individuals were foraging, in 12 percent they were inactive, in 4 percent they were in locomotion, and 3 percent of the observation periods involved aggression. When vegetation structure was altered by the removal of various amounts of shrubs, the proportion of time spent in these activities changed. The time spent singing decreased significantly to 35 percent, foraging increased to 40 percent, inactivity increased to 19 percent, and locomotion increased to 6 percent (Martin and Carlson 1998). Because the analyses used different sets of observation strings for each type of activity, the proportions sum to greater than 100 percent (Wiens et al. 1986, 1987). Singing typically takes place from the top, or just below the top, of shrubs, which are usually the highest locations within the territory (Rich 1980b, Martin and Carlson 1998), and this activity appears to be uniform throughout the day in *nevadensis* (Wiens 1982, Martin and Carlson 1998).

Only two of the five recognized subspecies of sage sparrow are generally migratory: *canescens* and *nevadensis*. The latter breeds farther north than the other subspecies and migrates the longest distances (Martin and Carlson 1998). Spring arrival time on the eastern Sierra escarpment is mid-March. In Colorado they begin to arrive in February and reach full numbers in mid-April (Andrews and Righter 1992, Lambeth 1998). The latest observed arrival of *nevadensis* was in early April near the Mexican border, and in late April in Organ Mountains, New Mexico (Martin and Carlson 1998). The actual migration pathways that sage sparrows use are unknown (Knick et al. 2003).

Generally, males arrive on the breeding grounds and begin establishing territories from mid-March to mid-April. The timing of territory establishment and pair formation may depend on average temperatures in late April, as these were later following colder temperatures (Best and Petersen 1985). The nesting season of the sage sparrow extends from mid-April to early August, with most nesting activity concentrated between April and late July.

After fledging, postjuvenile molt (Prebasic I) is incomplete and occurs from June through August, in breeding areas. Adult post-breeding molt (Definitive Prebasic) is complete and generally occurs in the breeding areas beginning in June and finishing by mid-September.

The *nevadensis* subspecies is on its wintering grounds in Arizona, along the Colorado River Valley, from September to late March or early April (Meents et al. 1982, Martin and Carlson 1998). In New Mexico, they are first observed in late September through October (Martin and Carlson 1998). Wintering birds have been recorded in northern Mexico by October (Howell and Webb 1995, Martin and Carlson 1998). In winter, sage sparrows move in small flocks or singly, sometimes in mixed-species flocks with other sparrows (Martin and Carlson 1998). Their daily activity patterns on the wintering grounds are not recorded.

The extent of dispersal and redistribution by individuals following migration and return to breeding areas is largely unknown. In southeastern Idaho 55 percent (n = 46) of color-banded males returned to the breeding site they used in the previous year, while 25 percent (n = 82) of the females returned (Petersen and Best 1987b, Martin and Carlson 1998).

Regional differences in migration and other broad scale movement patterns

In fall, *nevadensis* migrants peak in mid-September in Oregon, with stragglers to mid-November. They depart western Colorado by mid-October, with stragglers to early November (Andrews and Righter 1992). Some *nevadensis* individuals may be resident, but displacement by more northern individuals could account for year-round occurrence on sites (Weathers 1983, Martin and Carlson 1998). There is some evidence of winter site fidelity. In the lower Colorado River Valley, wintering individuals returned to previous capture sites in subsequent years, even though the vegetation was changing over time (Martin and Carlson 1998).

Habitat

Macrohabitat

The sage sparrow is considered a sagebrush obligate associated with shrublands dominated by big sagebrush with a perennial bunchgrass understory (Braun et al. 1976, Paige and Ritter 1999). While it is evident that the distribution of sage sparrows is largely affected by the distribution of sagebrush, few studies have related distribution and abundance of shrubland birds to the composition and configuration of landscapes (Knick and Rotenberry 1995, Vander Haegen et al. 2000, Knick and Rotenberry 2002). At a broad, regional scale, sage sparrow abundance has been correlated with cover of various shrub species (Wiens and Rotenberry 1980, 1981). Local densities are negatively influenced by landscape-level habitat changes that increase fragmentation of shrublands, and those numbers appear to be more sensitive to variation in landscape-level attributes than local-scale habitat attributes (Knick and Rotenberry 2000).

Landscape level attributes that are positively associated with sage sparrow density include high sagebrush cover, large patch size, spatially similar patches, low disturbance, and little fragmentation (Knick and Rotenberry 1995). Knick and Rotenberry (2002) found that the occurrence of sage sparrows increased with increasing area of sagebrush patches and decreasing fragmentation. In eastern Washington, the percent cover of sagebrush shrubsteppe within 5 km was significantly related to the occurrence of sage sparrows. They occurred more frequently on sites embedded in a matrix dominated by shrubsteppe, indicating a negative relationship with fragmentation (Vander Haegen et al. 2000).

The minimum patch size and degree of patch isolation required for breeding have not been measured; Knick and Rotenberry (2002) found that equal probabilities of sage sparrow occupancy were possible with different combinations of ground cover of sagebrush and patch size. Research in eastern Washington suggests that sage sparrows are area-limited and nest only in large blocks of shrubsteppe, even though their territories are <2 ha in size (Vander Haegen et al. 2000). In this study, sage sparrows were not found in patches smaller than about 130 ha (W. M. Vander Haegen personal communication, cited *in* Paige and Ritter 1999). Studies examining the influence of landscape level habitat characteristics within Region 2 have not been conducted; however, it is likely that here too the amount of sagebrush cover, patch size, spatial distribution of patches, and the extent of disturbance and fragmentation influence sage sparrow occupancy and abundance.

Microhabitat

Within its sagebrush shrubsteppe breeding habitat, local (e.g., within-patch) components that have been positively correlated with sage sparrow densities are the amount of big sagebrush, shrub cover, bare ground, and above-average shrub height. Conversely, density of sage sparrows has been negatively correlated with greasewood (*Sarcobatus vermiculatus*) and grass cover (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Larson and Bock 1984, Paige and Ritter 1999). The negative correlation with grass cover indicates that they prefer areas dominated by shrubs compared to those dominated by grass (Paige and Ritter 1999). The breeding habitat of *nevadensis* consists of stands of big sagebrush or big sagebrush interspersed with bitterbrush (*Purshia tridentata*), saltbush (*Atriplex canescens*), shadscale (*A. confertifolia*), rabbitbrush (*Chyrsothamus* spp.), or greasewood. Sage sparrows are rarely found in sagebrush-juniper (*Juniperus* spp.) communities, except in ecotones adjacent to shrubsteppe habitat (Martin and Carlson 1998).

In Region 2, sage sparrows occur across Wyoming in prairie and foothills habitat where sagebrush dominates (Cervoski et al. 2001). In Colorado, breeding sage sparrows select only sizeable, low-elevation stands of big sagebrush or mixed sagebrush and greasewood for nesting. High-country sagebrush (*Artemisia* spp.) and plains sandsage (*A. filifolia*), both plentiful in Colorado, do not provide suitable nesting habitat (Lambeth 1998).

Nest sites are in shrubs, bunchgrasses, and occasionally on the ground under a shrub (Martin and Carlson 1998). The shrub species used depends on the sparrow subspecies and geographic location. *Amphispiza belli nevadensis* uses big sagebrush in Idaho; in Oregon, Nevada, and Bonneville Basin, Utah it uses big sagebrush, bitterbrush, rabbitbrush, greasewood, tumbleweed (*Salsola iberica*), or bunchgrasses (Wiens and Rotenberry 1981, Wiens 1985, Martin and Carlson 1998). In an Idaho study site where sage sparrows nested exclusively in big sagebrush, they placed their nests in areas where the mean canopy cover of sagebrush was less and where shrubs were more clumped and taller than on the study area in general (Petersen and Best 1985).

Mean nest shrub height in Washington, Oregon, and Nevada was 68.7 ± 21.7 cm (n = 92); in an Upper Snake River, Idaho site mean nest shrub height was 66.0 ± 12.0 cm (n = 135); in southeast Idaho it was 66.0 ± 19.0 cm (n = 16); near Blackfoot Idaho mean nest shrub height was 67.1 ± 8.4 cm (n = 14) (Martin and Carlson 1998). In Idaho, Petersen and Best (1985) found that sage sparrows used big sagebrush shrubs for nesting that were 50 to 100 cm tall in greater proportions than their availability (i.e., those sized shrubs are preferred). They did not nest in shrubs greater than 100 cm tall, possibly because their spreading, open branch structure offered less cover (Petersen and Best 1985).

Sage sparrows prefer to place nests in shrubs that are entirely alive or mostly alive. In Idaho, 96 percent (n = 135) of all nests were in shrubs that were 75 percent or more living. Some partly dead shrubs were used, but nests were not placed in the dead portion of the shrub. Although sage sparrows select live shrubs with foliage, there is no preference among live shrubs for denser than average foliage (Petersen and Best 1985).

Seasonal differences in habitat associations

During spring and fall migration sage sparrows have been observed in creosote (*Larrea tridentate*), low desert scrub, and coastal sagebrush scrub (Weathers 1983, Martin and Carlson 1998). In the northern portions of its range, it favors big sagebrush year around. In wintering areas further south, they appear to use a wider range of habitats and are fairly common to uncommon in desert washes, big sagebrush, creosote, sparse cactus scrub, arid grasslands, and arboreal yucca

(*Yucca* spp.) mixed with greasewood (Martin and Carlson 1998). Along the lower Colorado River, honey mesquite (*Prosopsis glandulosa*) with high densities of inkweed (*Suaeda torreqana*) had higher densities of sage sparrows than honey mesquite without inkweed (Meents et al. 1982, Martin and Carlson 1998).

Geographic distribution of habitat and change in extent over time

The majority of *nevadensis* habitat consists of the Intermountain sagebrush shrubsteppe. This area historically consisted of large expanses of sagebrush, salt desert shrubs (primarily *Atriplex* spp.), and an understory of bunchgrasses interspersed with grassland patches. The historic fire regime produced a mosaic of grasslands and different-age patches of shrubland embedded within a larger shrub-dominated landscape (Knick and Rotenberry 2002). The sagebrush biome previously covered 63 million hectares (156 million acres) of western North America. Although the current geographic distribution of the sagebrush biome remains the same, very little remains undisturbed or unaltered from its condition prior to Euro-American settlement (West 1996, Dobkin and Sauder 2004).

Healthy shrubsteppe habitat has diminished greatly over the last 200 years (Dobkin and Sauder 2004). Human-caused impacts have contributed to extraordinary fragmentation and degradation across their widespread distribution (Knick et al. 2003, Dobkin and Sauder 2004). Livestock grazing has affected 99 percent of the Intermountain sagebrush shrubsteppe, and it has severely altered more than 30 percent. These changes have altered the form and function of shrubsteppe throughout the Intermountain West by facilitating the spread of invasive plants, thus increasing the severity of disturbance (i.e., wildfire) and accelerating the fragmentation and loss of shrublands (Knick and Rotenberry 2002).

In Wyoming, the composition of plant species in sagebrush habitats has changed from historic conditions with the invasion of exotics such as cheatgrass (Cervoski et al. 2001). Wyoming sagebrush habitats have also undergone considerable fragmentation due, in part, to extensive oil and gas exploration and development in sagebrush dominated landscapes (Knick et al. 2003).

Sagebrush in Colorado occurs at elevations of approximately 1,200 to 3,050 m (4,000 to 10,000 ft) and exists in a variety of climatic conditions, including low-elevation semidesert habitats and moist, cool, mountainous areas. Perhaps 30 percent of Colorado's sagebrush shrublands were altered between 1900 and 1974 (Braun et al. 1976), and the ecological integrity of these shrublands has been compromised by the invasion of exotic (e.g., cheatgrass) or native (e.g., pinyon-juniper) plant species, conversion to agricultural, residential, and other developed land types, and changes in natural fire regimes (Biedleman 2000).

Habitat availability relative to occupied habitat

This information has not been specifically reported. However, sage sparrows are often missing from what appears to be suitable habitat (Martin and Carlson 1998). This could indicate that there may be more habitat available than is occupied during a given breeding season. Alternatively, other unknown habitat characteristics that are important could be missing (Martin and Carlson 1998) including minimum patch size. The influences of patch dynamics, succession, and temporal effects on habitat availability and occupancy are unknown.

Food habits

The sage sparrow is categorized as a ground-foraging omnivore. Foods taken during the breeding season include adult and larval insects, spiders, seeds, small fruits, and succulent vegetation that are mainly gleaned from the ground near or under the edges of shrubs, or from the lower stems or leaves of shrubs (Martin and Carlson 1998). The proportion of particular food items taken likely depends on availability; sage sparrows will opportunistically exploit temporarily abundant food (Wiens and Rotenberry 1979, Martin and Carlson 1998). Sage sparrows drink available water occasionally, but apparently they obtain most of their water from vegetation and insects (Martin and Carlson 1998).

Diet varies depending on the season. This may reflect the fact that food resources are highly temporal in semiarid environments and dependent on climatic conditions. They ingest a lot of seeds in April and again in July and August (Rotenberry 1980, Martin and Carlson 1998). A wide variety of arthropods are eaten in May and June, primarily coleopteran (Coleoptera), orthopteran (Orthoptera), and lepidopteran (Lepidoptera) larvae (Wiens and Rotenberry 1979, Rotenberry 1980, Martin and Carlson 1998). Larger prey items are consumed early in the season, gradually declining in size from April through August (Rotenberry 1980, Martin and Carlson 1998). Information on winter food use comes from observations of *canescens* and *nevadensis* along the lower Colorado River. Meents et al. (1982) found that in fall, the sage sparrow's diet consisted of 44 percent animal and 56 percent seeds. In winter, it shifted to 13 percent animal and 87 percent seeds (Martin and Carlson 1998).

Nestling diet has also been studied. Food items fed to *nevadensis* nestlings are small; 73 percent were less than 0.05 cm^3 (Petersen and Best 1986, Martin and Carlson 1998). In southeast Idaho, 59 percent of the diet consists of spiders, butterflies and moths, true bugs, and leafhoppers. Flies, grasshoppers, bees and wasps, beetles, and barklice (Psocoptera) were also fed to nestlings (Petersen and Best 1986, Martin and Carlson 1998).

Increasing precipitation during the preceding winter, which increases ecosystem productivity the following spring, was strongly correlated with increases in hatching rates in Oregon. This implies that sage sparrows respond to resource availability at the time of egg formation (Rotenberry and Wiens 1991). No studies have related food resources in fragmented and unfragmented shrubsteppe habitats to differences in nest success or clutch size.

Breeding biology

The nesting season of the sage sparrow begins with their arrival on nesting grounds in the spring (from February to April). Males generally begin establishing territories shortly after arrival. Nest site selection likely begins with pair formation or soon after they arrive in breeding areas. Some *nevadensis* individuals arrive in breeding areas already paired (Rich 1980b, Martin and Carlson 1998). In the Uinta Basin of Utah, Green (1981) observed a pair that took 12 days to select a nest site (Martin and Carlson 1998). The breeding season extends from mid-April to early August, with most nesting activity concentrated between April and late July.

Construction of the first nest, by the female, takes approximately one to eight days to complete (Martin and Carlson 1998). Egg laying likely begins soon after nest completion, but in one instance the first egg was laid eight days after the nest was complete (Martin and Carlson 1998). Sage sparrows lay one egg per day, with an average clutch size of three to four eggs. In Idaho, first egg dates range from 6 April to 16 June (Martin and Carlson 1998).

Incubation begins when the last egg is laid and lasts 10 to 16 days (Martin and Carlson 1998). The female normally incubates the eggs, but occasionally the male will incubate when the female leaves the nest unattended. Eggs hatch within 24 hours of piping; usually a remaining egg in the clutch hatches 24 to 36 hours after the rest of the viable eggs have hatched. During one year in Utah, seven nests produced clutches with three eggs each, and only one egg failed to hatch (Green 1981, Martin and Carlson 1998). Sage sparrows will often renest soon after the loss of the first nest. *Amphispiza belli nevadensis* usually double-broods and occasionally has three broods (Martin and Carlson 1998).

Both parents brood and feed the nestlings, which typically fledge at 9 to 10 days of age (Petersen and Best 1986, Martin and Carlson 1998). Both parents have been observed feeding fledglings, whose tail and flight feathers are not fully developed at fledging, for up to two weeks (Martin and Carlson 1998).

Demography

Genetic issues

Allozyme analysis of the five subspecies indicates that the *belli* and *canescens* races are each other's closest relatives. Subspecies apparently do not hybridize, and populations of *canescens* and *nevadensis* show no intergradation where subspecies meet at the northern end of the White Mountains in California (Johnson and Cicero 1991, Martin and Carlson 1998). Within *nevadensis*, there is a low average nucleotide difference of 0.1 percent, indicating little genetic difference with the *nevadensis* subspecies (Johnson and Cicero 1991, Martin and Carlson 1999).

The extent of dispersal of *nevadensis* within its breeding range and the extent to which populations are currently isolated are both unknown. Knick and Rotenberry (2002) expect that adult shrubsteppe passerine breeding birds might exhibit strong site tenacity and return after migration to the same breeding territory as the previous year. In contrast, young birds may seek new areas either following fledging or upon returning from migration (Knick and Rotenberry 2002).

Considering *nevadensis*' somewhat contiguous distribution, their migratory habit, and their suspected ability to disperse, there is little reason so far to suspect that small breeding populations are suffering genetic consequences. Still, sage sparrows evolved in (and presumably are adapted to) landscapes dominated by sagebrush that were homogeneous over large spatial scales (Knick and Rotenberry

2002). Continued fragmentation of these landscapes, with increased isolation of breeding populations and reduction in numbers, may have genetic consequences not yet manifested.

Recruitment, survival, immigration, age at reproduction

Sage sparrows breed annually, starting at one year of age, and they normally breed each year until death (Martin and Carlson 1998). There is limited information regarding the proportion of males that successfully acquire mates among years and sites. At one site in Idaho, over a 5-year period, an average of 92 percent of male sage sparrows succeeded in acquiring mates (Petersen and Best 1987a).

Mean clutch size for *nevadensis* is 3.28 ± 0.61 SD (range = 1 - 4, n = 61; Martin and Carlson 1998), and clutch size apparently varies regionally. In Washington, Oregon, and Nevada 70 percent of the nests contained three eggs, and mean clutch size was 3.06 ± 0.06 SD (n = 53; Rotenberry and Wiens 1989, Martin and Carlson 1998). Mean clutch size in a study in Idaho was 2.8 ± 0.4 SD (range = 2 - 3, n = 13; Reynolds 1981, Martin and Carlson 1998). Also in Idaho, Petersen and Best (1987a) reported the average clutch size during a 5-year period to be 3.3 ± 0.1 SE; mean clutch size varied annually on the control (unburned) sites. In Utah, seven nests contained clutches of three eggs (Green 1981, Martin and Carlson 1998). In the northern Great Basin, clutch size was not significantly correlated with precipitation, yet 34 percent of the variation in the number of eggs laid was explained by weather during the period of egg formation (Rotenberry and Wiens 1991).

Reynolds (1981) found the average number of *nevadensis* hatchlings produced per nest in Idaho was 2.6 (range = 1 to 3, n = 11), and the average number of fledglings produced per nest was 1.3 ± 1.3 SD (range = 0 to 3, n = 15; Martin and Carlson 1998). Petersen and Best (1987a), also in Idaho, found the number of sage sparrow young fledging from each successful nest averaged 2.6 ± 0.1 SE. Fledgling success can vary annually. Reynolds (1981) had a high fledgling success in his first year of study, but loggerhead shrikes (*Lanius ludovicianus*) depredated almost all nests in a second year. In Oregon, the number of chicks and the number of fledglings was negatively affected by daytime high temperature (Rotenberry and Wiens 1989).

Using the Mayfield estimate (Mayfield 1975), daily survival estimates (eggs and nestlings combined) on burned and unburned sites in Idaho, from 1980 to 1984, ranged from 0.903 ± 0.018 SE to 0.995 ± 0.005 SE (n = 12 - 24; Petersen and Best 1987a). In the northern Great Basin, from 1976 to 1977, across three sites, daily survival estimates were, respectively, 0.96 ± 0.02 SD (n = 15), 1.00 ± 0.01 SD (n = 11), and 0.75 ± 0.07 SD (n = 11) (Rotenberry and Wiens 1989). The overall probabilities of nest success for the same three sites in this study were 0.39, 1.00, and 0.001, respectively (Rotenberry and Wiens 1989). Within one of these sites, from 1976 to 1980, the probability of nest success varied significantly across years. In these five years, the probability of nest success was 1.00, 1.00, 0.66, 0.17, and 0.73, respectively (Rotenberry and Wiens 1989). There are no estimates of annual fecundity or lifetime reproductive success (Martin and Carlson 1998).

There is limited information regarding life span and survivorship. A 6-year old *nevadensis* was found in one study (Wiens 1985, Martin and Carlson 1998). Also, for *nevadensis*, 55 percent of 46 males returned to a previous breeding site, and the female return rate was 25 percent (n = 82; Petersen and Best 1987b). These rates represent a lower limit, as they do not take into account individuals that may be alive and breeding elsewhere (Rotenberry et al.1999).

Summary of lifecycle model findings (prepared with David B. McDonald)

We created a lifecycle graph and constructed a two-stage matrix population model for the sage sparrow (details in **Appendix A**). When substantial data are available for a species, demographic modeling can be used to predict population growth rates (λ)? under various environmental, demographic, and genetic conditions, providing a measure of the stability (e.g., population viability) of the wildlife population being modeled. However, in cases where data are limited, such as for the sage sparrow, λ cannot and should not be estimated. Yet, modeling exercises (e.g., sensitivity and elasticity analyses) can provide valuable information regarding certain aspects of the population biology of the species of interest. For example, these analyses can improve our understanding of how important specific vital rates are to λ, our ability to identify those vital rates that are the most important for researchers to focus their efforts, and our ability to quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates.

Here, we present a summary of our model results and direct readers to **Appendix A** for the complete methodological considerations and technical analyses.

The matrix population analysis was produced with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001). Our first exercise was to conduct a sensitivity analysis. Sensitivity is the effect on λ of an absolute change in the vital rates (i.e., survival and fertility). The vital rate to which λ was most sensitive for the sage sparrow was first-year survival (36.5 percent of total). Nearly as important was adult (i.e, >1 year old) survival (34.1 percent of total). Thus, our major conclusion from the sensitivity analysis is that survival rates are most important to population viability. Next, we conducted the elasticity analysis. Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivity analysis. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. The elasticities have the useful property of summing to 1.0. Elasticity analyses for sage sparrow indicate λ was most elastic to changes in adult survival (e_{22} = 44.8 percent of total elasticity). Next most elastic were first-year survival and adult reproduction ($e_{21} = e_{12}$ = 24.3 percent of total elasticity), and reproduction by first-year birds was relatively unimportant (e_{11} = 6.6 percent of total elasticity). The sensitivities and elasticities for sage sparrow were generally consistent in emphasizing survival transitions. Thus, survival rates, particularly for adults, appear to be the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Finally, we constructed a stochastic model to simulate the effect of environmental variation on λ. The stochastic model produced two major results. First, high levels of stochastic fluctuations affecting survival had the greatest detrimental effects, and second, varying adult survival had the greatest detrimental effects. These results indicate that populations of sage sparrow are vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance) when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. The sage sparrow, however, may have little flexibility in reducing variability in first-year survival, which has a relatively high elasticity. Variable early survival, and probably fertility, is likely to be the rule rather than the exception.

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in this demographic analysis. The most important "missing data elements" in the life history of sage sparrow are for survival transitions, which emerge as vital rates to which λ is most sensitive as well as most elastic. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations.

Summary of major conclusions from matrix projection model:

- ❖ Survival accounts for 71 percent of the total "possible" sensitivity, fairly equally distributed between first-year and "adult" survival. Any absolute changes in survival rates will have major impacts on population dynamics.
- ❖ "Adult" (e_{22} = 45 percent) and first-year (e_{21} = 24 percent) survival account for almost 70 percent of the total elasticity. Proportional changes in survival rates will have a major impact on population dynamics.
- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of survival rates to population dynamics.
- ❖ Reformulation of a matrix analysis with improved data might substantially change some of the values, but would be unlikely to radically revise the major emphases presented here.

Ecological influences on survival and reproduction

Territory size did not increase significantly over the short term in areas where vegetation was removed (Wiens et al. 1986, Lovio 1995, Martin and Carlson 1998), perhaps due to territory fidelity or tenacity (Martin and Carlson 1998). During the two years following vegetation removal, sage sparrow abundance gradually decreased (Wiens and Rotenberry 1985).

Food availability and weather apparently can affect final reproductive success (i.e., the number of fledglings produced). In a 5-year study in the Great Basin, sage sparrows achieved significantly greater final reproductive success in wetter, presumably more biologically productive years, with greater food resources. Increased precipitation during the preceding winter, which increases ecosystem productivity the following spring, led to higher hatching success. Hatching rate was positively associated with rainfall during incubation and negatively associated with night-time low temperature. The number of chicks and the number of fledglings appeared to be negatively affected by daytime high temperature; nests averaged fewer chicks, and thus fewer fledglings, when daily maxima were relatively high (Rotenberry and Wiens 1991).

Predation is the major cause of nest mortality, and predation rates are apparently affected by fragmentation of shrubsteppe habitat. Predation on artificial and natural nests of shrubsteppe birds was higher in fragmented sites than in continuous shrubsteppe sites in eastern Washington, likely due to an increase in Corvid populations associated with agricultural and other human-modified habitats. Also, nests might be more difficult to locate in extensive stands of shrubsteppe than in fragmented sites (Vander Haegen et al. 2002).

Spacing, defense and size of area, and population regulation

Males occupy breeding territories that are generally non-overlapping. The intensity of territorial defense may be affected by differences in density- with more defense behaviors occurring at higher densities. Territories of *nevadensis* vary in size and shape (Martin and Carlson 1998). In two studies in Idaho, mean territory sizes were 4.43 ha ± 1.86 SD (range 1.06 to 7.06, n = 8; Rich 1980a) and 0.81 ha ± 0.21 SD (n = 16; Reynolds 1981). In Oregon and Nevada, mean territory size ranged from 0.65 to 5.81 ha (Wiens and Rotenberry 1985), and in Utah it was 1.53 ha ± 0.23 SD (range 1.21 to 1.79, n = 7; Green 1981). Territory boundaries can change slightly from day to day, and territory shifting appears to be adaptive to increasing territory size. Territory sizes regulate populations when suitable habitat is fully saturated at optimum densities (Martin and Carlson 1998). Sage sparrow reproductive success has been correlated with bird population densities: the average numbers of chicks and fledglings produced by sage sparrows were negatively associated with the average density of Brewer's sparrows (both $r = -0.87$, $P = 0.04$; Rotenberry and Wiens 1989).

Dispersal

There are no data on the extent of initial dispersal from the natal site of *nevadensis*. Sage sparrows that have fledged or successfully bred at a given site demonstrate a strong probability of returning to the same site in succeeding years (Martin and Carlson 1998).

Spatial characteristics of populations

BBS data indicate that this species has undergone declines throughout much of the West (Martin and Carlson 1998), including regions within USFS Region 2 (**Table 1**). In particular, the Southern Rockies region shows significant declines. Rangewide, sage sparrows show reduced abundance at the periphery of their range (**Figure 2**). Sage sparrows can be thought of as habitat specialists, in that they only occur in sagebrush shrubland habitats, and bird specialists may be poorly equipped to tolerate conditions beyond those experienced in the core of their geographic range (Brown 1995, Pavlacky and Anderson 2001).

Factors limiting population growth

Because *nevadensis* populations are affected by events that lie beyond the domain of demographic studies so far conducted (Knick and Rotenberry 2002), elucidating the processes that regulate population size, causes of population declines, and effects of habitat loss and fragmentation on *nevadensis* is problematic. It is not known to what extent processes operating in wintering areas regulate population size in breeding areas. Nevertheless, it is thought that territory sizes regulate populations in breeding areas when suitable habitat is saturated at optimum densities (Martin and Carlson 1998).

Nest predation is the major cause of nest mortality and appears to account for the majority of variation in local reproductive success (Martin and Carlson 1998). Levels of nest predation vary significantly both geographically and temporally. In three geographically separate sites in Oregon, in 1976-1977, the percentage of nests depredated was 0 (n = 11), 40 percent (n = 15), and 90 percent (n = 11). Temporally, at one site in Oregon, from 1976-1980, annual nest predation ranged from 0 to 54 percent. Annual variation in daily nest survival rates for this same time period in Oregon ranged from 0.93 ± 0.03 SD to 1.00 ± 0.01 SD. During this study, reproductive success was reduced due to predation during high densities of ground squirrels (Rotenberry and Wiens 1989).

There is some evidence that, at least in part of the sage sparrow's range, nest success is lowered due to increased nest predation by predators associated with agricultural and other human-modified habitats in fragmented landscapes (Vander Haegen et al. 2002). Yet, Knick and Rotenberry (2002) found that individual productivity or probability of predation was not directly related to fragmentation at the level of individual territories. They postulate larger regional patterns of fragmentation may be more important in affecting range-wide dynamics.

Predators also take adults, but predation is likely insufficient to depress population sizes. The impact of predation outside the breeding season is unknown.

The impact of brown-headed cowbird (*Molothrus ater*) parasitism on sage sparrow populations is affected by the timing of breeding. The overall rate of parasitism of sage sparrows in the Columbia River Basin, Washington was <10 percent (Vander Haegen and Walker 1999), because most nesting attempts by the host species were started before cowbirds arrived on the study areas (Knick and Rotenberry 2002). When parasitized, some nests were abandoned by the host (Reynolds 1981, Friedman and Kiff 1985, Martin and Carlson 1998), while in others sage sparrows fledged cowbird young or attempted to raise them (Gaines 1988, J. T. Rotenberry personal communication *in* Martin and Carlson 1998).

Weather can influence productivity and thus affect population growth. Increased precipitation during the preceding winter was strongly correlated with an increase in the hatching rate of sage sparrows in Oregon. Short-term weather conditions (i.e., rainfall, nighttime low temperature, daytime temperature) also affect productivity (Rotenberry and Wiens 1991).

Community ecology

Predators and relationship to habitat use

Nest predation is the primary cause of nest failure and is likely to be an important factor in sage sparrow life history traits and habitat use (Rotenberry and Wiens 1989). Specific differences in sage sparrow habitat use as they relate to the presence/absence and abundance of specific predators have not been reported.

The common raven (*Corvus corax*) is a documented nest predator (Martin and Carlson 1998). Black-billed magpies (*Pica hudsonia*), Townsend's ground squirrels (*Spermonphilus townsendii*), snakes, long-tailed weasels (*Mustela frenata*), and chipmunks (*Eutamias* spp.) are also potential predators of eggs and nestlings (Rotenberry and Wiens 1989, Vander Haegen et al. 2000). An intense, episodic predation of nests was attributed to an outbreak of Townsend's ground squirrels. The irruption of ground squirrels appeared to be triggered by a pattern of a drought year followed by two relatively wet years, and nest predation peaked when ground squirrels were most abundant (Rotenberry and Wiens 1989). Adult predators are likely the common avian predators. Loggerhead shrikes have been observed successfully and unsuccessfully attacking adult sage sparrows (Reynolds 1979, Martin and Carlson 1998). A merlin (*Falco columbarius*) was seen chasing an adult (Martin and Carlson 1998), and sage sparrow bones have been found in a great horned owl (*Bubo virginianus*) pellet (Bond 1940, Martin and Carlson 1998).

One study in eastern Washington (Vander Haegen et al. 2002) examined predation on artificial and actual nests of birds in fragmented and continuous shrubsteppe sites. They found that the predation rate for artificial nests and real nests was greater in fragmented than in continuous shrubsteppe landscapes, a result likely attributable to increased predation by black-billed magpies and common ravens. Small mammals were photographed at nests in both fragmented and continuous landscapes, whereas corvids were photographed depredating nests almost exclusively in fragmented habitats. Corvids in shrubsteppe often are associated with agricultural and other human-modified habitats, and Vander Haegen et al. (2002) found a significantly greater abundance of magpies in fragmented landscapes. Ravens were common in both landscapes, and they depredated nests in continuous shrubsteppe. However, the authors suggest that nests may be more difficult to locate in extensive stands of shrubsteppe than in fragmented sites.

Vander Haegen et al. (2002) did not find an association between patch size and predation rate among their fragment sites. They suggested that predators associated with agricultural lands may move easily through adjacent shrubsteppe (Rotenberry 1998), and the mere presence of agricultural fields or developed lands in the landscape may play a larger role than the size of the fragment in predation on sage sparrow nests by magpies and other generalist predators.

Competitors

Some information suggests that Brewer's sparrows may be competitors of sage sparrows. Brewer's sparrows of either gender will chase sage sparrows that come within a few meters of the nest site (Rotenberry et al. 1999). The average number of chicks and fledglings produced by sage sparrows was negatively associated with the average density of Brewer's sparrows (both r = -0.87, P = 0.04) (Rotenberry and Wiens 1998). Resources may have been depressed by densities of Brewer's sparrows to the point that it affected reproduction during the breeding season.

Brown-headed cowbirds

The sage sparrow is a host for the brown-headed cowbird. Prior to European-American settlement, they were probably largely isolated from cowbird parasitism, but they are now vulnerable as cowbird populations increase throughout the West and where the presence of livestock and pastures, land conversion to agriculture, and fragmentation of shrublands create contact zones between the species (Rich 1978, Rothstein 1994).

Parasites and disease

Sage sparrows are hosts to body parasites including chewing lice (Mallophaga) (Malcomson 1960, Martin and Carlson 1998). In Bonneville Basin, Utah, they are parasitized by philopterid lice (*Bruela lautiuscula* and *Penenirmus* sp.) and trombiculid mites (*Euschongastia radfordi* and *Neoschongastia americana*) (Martin and Carlson 1998). Nestlings are parasitized by fly larvae; in Oregon botflies (Oestridae) were found in young that had died (Martin and Carlson 1998). In southeastern Idaho, 14 percent of 102 broods were parasitized by flesh flies (Petersen et al. 1986), and the tarsi of the parasitized chicks were shorter than normal near the end of the nestling period (Martin and Carlson 1998). Avian pox was found on the feet and legs of only one of more than 250 birds banded in Riverside County, California (Martin and Carlson 1998). Information on disease in sage sparrows is lacking, and evidence of symbiotic and mutualistic interactions has not been reported.

Envirogram

An envirogram is a tool used to depict the proximal and distal causes/components that affect a species' chance to survive and reproduce (**Figure 5**). Within the envirogram model, the environment comprises everything that might influence an animal's chance to survive and reproduce. The environment consists of the "centrum" and the "web". Only those things that are the proximate causes of changes in the physiology or behavior of the animal are placed in the "centrum". These are recognized as directly-acting components of the environment. Everything else acts indirectly, through an intermediary or a chain of intermediaries that ultimately influence the activity of one or other of the components in the "centrum". All of these indirectly acting components are placed in the "web" (Andrewartha and Birch 1984).

Within the "centrum", the directly acting components are classified into four subdivisions according to the response of the animal to the component and the consequent reaction of the component to the animal. The four subdivisions are "mates", "resources", "predators", or "malentities". The names "resources" and "mates" refer to well-understood colloquial meanings. "Malentities" differ from "predators" in that they are components that directly affect the animal, causing a decrease in life expectancy or fecundity, but the consequent component activity decreases or does not change. "Predators" also cause a decrease in life expectancy or fecundity in the animal, but unlike "malentities", the consequent component activity increases.

An envirogram depicts the relationships described above. It consists of a dendogram whose branches trace pathways from distal causes in the web to proximate causes in the centrum.

CONSERVATION

Threats

Influence of management activities or natural disturbances on habitat quality and availability

For many decades, range scientists believed that grasslands originally dominated the Intermountain West and that sagebrush invaded because of heavy grazing. As a result, numerous management actions were undertaken to clear sagebrush from areas. More recently it has become evident that sagebrush shrublands, not grasslands, dominated the basins of the Intermountain West, and that the boundaries of sagebrush habitats were generally the same as they are today. Furthermore, it is now recognized that sagebrush habitats provide important habitat to many plant and animal species. In fact, many sagebrush birds, including the sage sparrow, live nowhere else (Paige and Ritter 1999).

Unfortunately, although sagebrush remains widespread in the west, sagebrush habitats are threatened throughout their range. The synergistic pattern of ground disturbance (due to excessive livestock grazing, failed agriculture, and intentional eradication of sagebrush), altered fire frequency and intensity, and increased dominance of exotic vegetation has caused the fragmentation and loss of this habitat to the point that it is one of the most endangered ecosystems in North

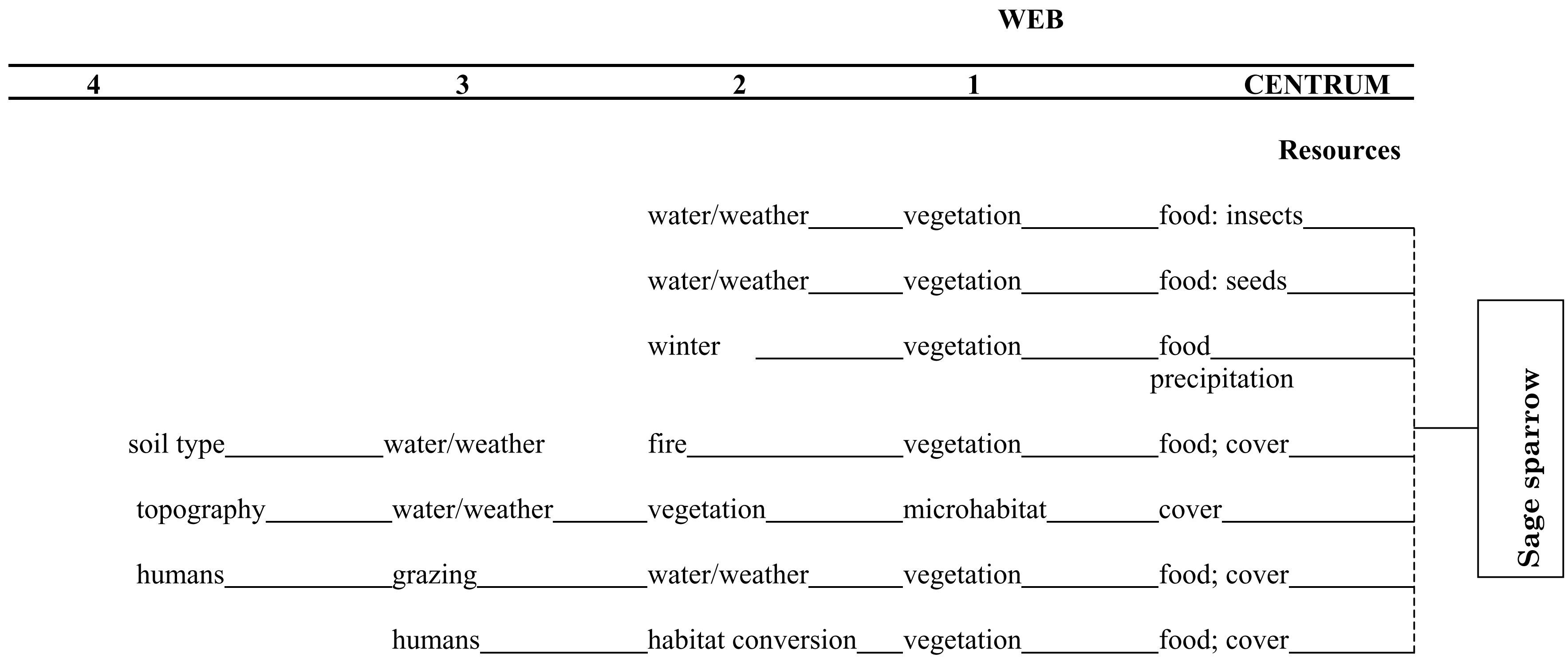

Figure 5a. Resources centrum of the envirogram for the sage sparrow.

WEB

Sage sparrow

4	3	2	1	CENTRUM: Malentities
humans	grazing	water/weather	vegetation	fecundity, densities
humans	grazing	soil; vegetation	disturbance	fecundity, densities
humans	sagebrush eradication	fragmentation	vegetation	fecundity, densities
humans	oil/gas development	fragmentation	disturbance	fecundity, densities
humans	agriculture	exotic annual grasses	fragmentation/ habitat loss	population decline
water/weather	vegetation	food; cover	winter distribution	winter survival
	water/weather	vegetation	microclimate	nest phenology
	water/weather	vegetation	habitat selection	distribution
	humans	agriculture	fragmentation/ habitat loss	population decline
	humans	prescribed fire	vegetation	fecundity, densities
	humans	pesticides	food; cover	fecundity, densities
		humans	pesticides	densities, mortality
		humans	grazing	nest mortality

Figure 5b. Malentities centrum of the envirogram for the sage sparrow.

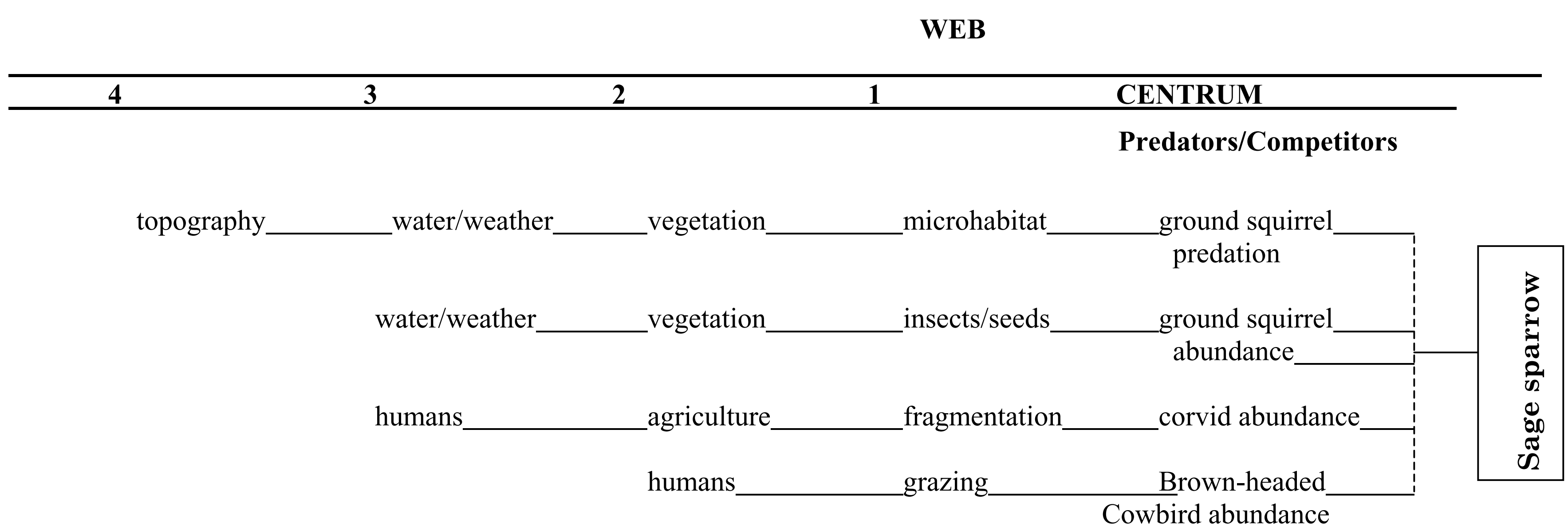

Figure 5c. Predators/competitors centrum of the envirogram for the sage sparrow.

America (Noss and Peters 1995, Knick and Rotenberry 2002). These changes have potentially compromised the viability of species obligate to the sagebrush ecosystem. Nationally, grassland and shrubland birds show the most consistent population declines over the last 30 years of any group of bird species. Across the United States the populations of 63 percent of shrubland and shrub-dependent birds are declining (Paige and Ritter 1999). In the Intermountain West, more than 50 percent of grassland and shrubland bird species show downward population trends (Sauer et al. 1996b). In Region 2, sage sparrows have apparently declined in abundance in the Wyoming Basin and show significant downward population trends in the Southern Rockies region.

In many areas of the West, the influences of management activities and disturbances of sage sparrow habitat have led to large scale conversion of shrublands to grassland habitats dominated by exotic annuals. Sagebrush habitats managed by the USFS in Region 2 have suffered only minimally from invasion of exotics and altered fire regimes (C. Quimby 2004 personal communication). Yet, over its geographic range, a large portion of the sage sparrow's habitats has been impacted. The conversion of landscapes to exotic annual grasslands with high fire frequencies has resulted in changes in the avian composition from communities composed of shrubland obligates (such as the sage sparrow) to those composed of grassland species (such as meadowlarks [*Sturnella* spp.] and horned larks [*Eremophila alpestris*]) (Knick and Rotenberry 1997). Sagebrush habitat has been found to support more species, to have a greater bird density, and to have a greater individual density for most species than cheatgrass habitat types (Schuler et al. 1993). This conversion process likely will result in loss of bird species richness and decreased numbers of shrubland-obligate species, including the sage sparrow (Knick and Rotenberry 2002). Correspondingly, the bird species perhaps in the most need of conservation attention are those most typical of undisturbed shrubbesteppe, including sage grouse (*Centrocercus* spp.), Brewer's sparrows, sage sparrows, black-throated sparrows (*Amphispiza bilineata*), and sage thrashers (*Oreoscoptes montanus*) (Rotenberry 1998, Paige and Ritter 1999).

The threats to sage sparrows and their habitat are widespread across their range, occurring at all spatial scales, from local to landscape to geophysical scales. There are probably other as yet unknown factors contributing to their decline, including factors in wintering areas and the cumulative effects of habitat disturbance and fragmentation. Many of these threats are interrelated and synergistic, have led to large-scale changes in habitat, and have likely contributed to the reported declines of sage sparrows.

Threats to the sage sparrow's habitat interact in complex ways, making it difficult to separate and prioritize them. We have attempted to order them according to their severity, from the threats that contribute to long-term habitat loss to those that contribute to habitat degradation.

Habitat loss, fragmentation

Large-scale reduction and fragmentation of native shrublands have occurred and continue to occur, and may be largely responsible for declines in sage sparrows observed on BBS routes (Rotenberry 1998). Habitat loss and fragmentation are attributable to a number of activities, including land conversion to tilled agriculture; urban and suburban development; development of road and power-line rights of way; and range improvement programs that remove sagebrush through fire, herbicide application, and/or mechanical treatment, and then replace sagebrush with annual grassland to promote forage for livestock. The pace of loss and fragmentation has accelerated because of complex interactions among agriculture, livestock grazing, and invasion of exotic plants, especially cheatgrass. Modeling predicts the loss of more than half of the remaining shrublands (Rotenberry 1998, Rotenberry et al. 1999).

The sage sparrow belongs to a group of species that are most typical of undisturbed shrubsteppe and appear to be especially sensitive to the negative effects of habitat fragmentation (Knick and Rotenberry 1995, Rotenberry 1998). Fragmentation of sagebrush shrubsteppe degrades habitat quality for sage sparrows. Increases in the amount and proximity of agricultural areas in the landscape have been linked with higher rates of nest predation, the primary cause of sage sparrow nest failure. In the Rocky Mountain Region, the increased fragmentation of sagebrush shrublands by agriculture and development are likely resulting in increased exposure of breeding sagebrush bird species, including the sage sparrow, to nest predators. Fragmentation also increasingly breaks up breeding populations into smaller demes, and reduces sagebrush patch sizes below the minimum suitable for sage sparrow occupancy.

Agriculture

The predominant impact of agricultural development is direct habitat loss due to conversion of shrubland areas to grasslands and croplands, and the subsequent fragmentation of once contiguous shrublands. These losses are long-term in that most agricultural areas, including entire landscapes, are unlikely to be returned to shrublands in the foreseeable future (Dobler et al. 1996, Vander Haegen et al. 2000, Knick and Rotenberry 2002). In addition to outright habitat loss, agricultural development has a less obvious but destructive role in the introduction and spread of alien plants into natural habitats; this may now be the most serious threat to these habitats (Rotenberry 1998). Agricultural areas, and associated roads, serve as continually renewable sources for immigrant alien species of plants (Janzen 1986, Alberts et al. 1993, Rotenberry 1998). Furthermore, agricultural areas apparently extend the landscape-level distribution of brown-headed cowbirds, which parasitize avian broods, and corvids, such as common ravens and American crows, which can be major predators of nests of songbirds (Marzluff et al. 1994, Rothstein 1994, Rotenberry 1998, Vander Haegen et al. 2000).

Invasion of exotic annual grasses and the effects on fire frequency and intensity

Agricultural development, livestock grazing, off-road vehicle use, and road building disturb the soil, which promotes germination of annual plant seeds and thus promotes the invasion of exotic annual plants into otherwise undisturbed areas. This process has resulted in perhaps the greatest impact on western shrublands: the establishment of the invasive, exotic cheatgrass. Cheatgrass first appeared in the early to mid-1800s, probably as a contaminant in grain seed (Mack 1981), and it quickly spread among agricultural areas and along roads and railroads. It spread into otherwise undisturbed shrublands through widespread livestock grazing and the disturbance of the soil surface.

Cheatgrass now occupies millions of hectares of western rangelands, has greatly increased fire frequency, and has substantially, and perhaps permanently, altered postfire successional pathways (Whisenaut 1990, Rotenberry et al. 1999). Its principle impact has been to alter the fire ecology of shrubsteppe ecosystems. Cheatgrass provides a continuous surface cover of relatively fine fuel that carries fire into and over much larger areas than likely occurred historically (Whisenant 1990; www.ut.blm.gov/FireRehab). It matures and dries earlier than native bunchgrass, increasing the chance of fire earlier in the season (Knick and Rotenberry 1997). Also, because it does not catch and hold snow like a diverse perennial stand of vegetation, the site becomes drier (desertification; www.ut.blm.gov/FireRehab). In fact, shrublands infested with cheatgrass are 20 times more likely to burn than those without (Stewart and Hull 1949, Whisenant 1990).

With increasing probability of fire, the establishment of cheatgrass reduces the average fire-return intervals to less than five years, and reduces the chances for sagebrush and native bunchgrasses to regenerate (Whisenant 1990). Post-fire survivorship of cheatgrass is high because it is a winter annual that matures and sets seed by the onset of summer fires, which shatter the seed heads. Conversely, native perennial grasses mature in the summer and have low survivorship after fires. The establishment of cheatgrass in an area makes it more likely to burn again. Thus, once cheatgrass becomes a part of an ecosystem, it is very likely to remain a part of that ecosystem (Rotenberry 1998). Another non-native grass, crested wheatgrass, has also had a role in fundamentally altering the native grass-forb community in many areas of sagebrush shrubsteppe (Whisenant 1990, Rotenberry et al. 1999).

Unlike cheatgrass and other non-native annual grasses, sagebrush after a fire must be re-established by wind-dispersed seeds or by seeds in the soil. A second fire within five to eight years can destroy any viable sagebrush seeds in the seed bank, and subsequent recovery of sagebrush can only come from other living sagebrush. Sagebrush seeds disperse about 30 m from a seed source (Meyer 1994, Paige and Ritter 1999). Additionally, sagebrush may take several years to mature before producing seed. Thus, repeated, frequent fires can eliminate sagebrush entirely as cheatgrass becomes established and creates uniform annual grasslands perpetuated by large, frequent fires and void of native plant communities (Whisenant 1990, Paige and Ritter 1999). Restoring native plants is then extremely difficult, if not impossible (West 1988, Paige and Ritter 1999), and the exotic plant-dominated landscapes that replace native vegetation are uninhabitable for native shrubsteppe-dependent species (Dobkin and Sauder 2004) such as the sage sparrow.

Although cheatgrass and the increased fire frequency associated with its invasion are threats to sagebrush habitats and the species dependent on them, complete fire suppression can also be a threat to healthy sagebrush ecosystems. In some areas, fire suppression and the loss of fine fuels to livestock grazing has resulted in much longer fire-return intervals and has altered the dominant process (i.e., fire) that controlled the shifting temporal and spatial mosaic of grasslands and shrubland characteristic of these landscapes (Dobkin and Sauder 2004).

Within Region 2, sagebrush habitats have not suffered from altered fire regimes due to invasive annual plants to the same extent as has occurred in the Intermountain West (C. Quimby 2004 personal communication) Nonetheless, cheatgrass has become established in some areas of the Rocky Mountain Region, and the invasion of exotics such as cheatgrass should be considered a threat to Region 2's sagebrush ecosystems.

Prescribed fire

Prescribed fire can represent a threat to sage sparrows if it is implemented over large areas. Burning over large areas to eradicate sagebrush is detrimental to sage sparrows because it removes shrub cover, fragments large tracts of sagebrush, and can reduce patch size to levels not used by sage sparrows. It can also promote changes in the vegetative community and increase the frequency or severity of fires, further altering vegetative composition and structure. Although there is disagreement over 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 last 150 years (Dobkin and Sauder 2004). Altered fire frequencies in combination with the ubiquity of livestock grazing continue to drive the loss of native plant community structure and composition upon which shrubsteppe birds depend.

Mining and oil/gas development

Energy development and natural resource extraction directly alter sagebrush habitats at the site of operation (Braun et al. 2002, Knick et al. 2003). Associated road networks, pipelines, and power transmission corridors fragment habitat and/or create soil conditions that facilitate the spread of invasive species (Braun 1998, Gelbard and Belnap 2003, Knick et al. 2003). The cumulative effects of energy development have not been assessed. The density of sagebrush-obligate birds within 100 m of roads constructed for natural gas development was 50 percent lower than at greater distances (Ingelfinger 2001, Knick et al. 2003). Increased numbers of corvids and raptors associated with powerlines also increase the potential impact of predation on sagebrush-breeding birds (Knick et al. 2003). As permitting for oil and gas exploration and development continues to accelerate within the Rocky Mountain Region, these types of development are potential threats to the integrity of sagebrush ecosystems. Much of the oil and gas development in Wyoming and Colorado occurs in sagebrush habitats.

Livestock grazing

Livestock grazing has impacted much of the sagebrush habitat across the range of the sage sparrow. The effects of livestock grazing in shrubland habitats are complex, depending on grazing intensity, season, duration, and the extent of alteration to native vegetation. Livestock grazing impacts sagebrush habitats in several interrelated ways. Its greatest impact is soil disturbance that promotes the germination of annual plant seeds and thus promotes the invasion of exotic annual plants into otherwise undisturbed areas. Livestock grazing can lead to other changes in the plant community. Because much of the western shrublands did not evolve under grazing pressure from large ungulates such as bison (*Bison bison*), the impact due to livestock grazing has been detrimental to native vegetation (Mack and Thompson 1982, Rotenberry 1998, Paige and Ritter 1999). As cattle graze sagebrush habitats, they first select grasses and forbs and avoid browsing on sagebrush, which can have a toxic effect on the microorganisms in their rumen (Young 1994). Even light grazing can put pressure on the herbaceous plants favored by livestock (West 1996). Thus, grazing disturbs the soil and results in selective removal of plant biomass, altering competitive relationships among species. Where grazing removes the herbaceous understory altogether, the balance is tipped in favor of unpalatable species, allowing sagebrush to spread and creating dense sagebrush stands with a sparse understory of annuals and unpalatable perennials (Tisdale and Hironaka 1981). While it is not clear that this situation would be detrimental to sagebrush-dependent species, it ultimately discourages livestock use. This has, throughout this century, led to destruction of sagebrush habitats as range managers used fire, herbicides, chaining, and other methods to remove dense sagebrush stands and re-establish grass forage, often reseeding with introduced grass species.

Livestock grazing also destroys the crust that usually forms on the soil and, thus, adversely influences water infiltration, erosion, and nitrogen fixation (Harper and Marble 1988, Rotenberry 1998). This destruction can have long-term effects: recovery from grazing that includes a well-developed crust community can take a decade or more, depending on the type of disturbance, the presence of inoculants from nearby crust communities, and the occurrence of invasive weeds (Belnap 1993, St. Clair and Johansen 1993, Kaltenecker 1997, Paige and Ritter 1999). The extent to which soil crusts have been impacted by grazing within Region 2 has not been reported.

In addition to its indirect effects, livestock grazing can also directly affect sage sparrows during nesting. Livestock trample and disturb nests, resulting in nest failure. Also, the presence of livestock (particularly cattle and horses) can increase the abundance of brown-headed cowbirds, potentially impacting sage sparrow productivity (Robinson et al. 1995). There is no reported information on cowbird brood parasitism of sage sparrows in Region 2.

Recreation

Recreation activities such as camping, hiking, biking, and off-road driving can degrade sagebrush habitats. These activities tend to be concentrated near roads and campgrounds. Thus, the threat from such activities depends on the extent of roaded areas and developed recreational sites. Recreationists may trample plants and biological soil crusts, and increase the incidence of fire, weed invasion, and road kills (Paige and Ritter 1999).

Conservation Status of the Species in Region 2

Sufficient evidence exists to suggest that the sage sparrow should be considered a species of high conservation concern in Region 2. Although it has a wide distribution across western North America, population declines are widespread. Populations have declined across both the Wyoming Basin and Southern Rockies regions, which together encompass the areas of Region 2 occupied by the sage sparrow (Sauer et al. 2003). In the Intermountain West, more than 50 percent of grassland and shrubland bird species show downward population trends (Sauer et al. 1996a).

Sage sparrow life history traits and ecology evolved within a habitat that once experienced little if any change within the home range and life span of an individual. They appear to be maladapted for living in a system with rapid, extensive loss and fragmentation due to interrelated and synergistic threats (Knick and Rotenberry 2000, Knick and Rotenberry 2002), and they are vulnerable to land use and habitat management practices within the region. There is evidence that fragmentation and changes in habitat patch size affect habitat suitability; sage sparrows are often absent from tracts of native habitat that otherwise appear suitable (Knick and Rotenberry 1995, Rotenberry 1998) and may not meet minimum patch size requirements. High site fidelity in concert with habitat fragmentation may confound species presence or absence in many locations (Dobkin and Sauder 2004).

While population declines are fairly well documented, linkages between habitat variability (due to habitat management) and population viability are poorly understood. How habitat fragmentation influences productivity, density of breeding adults, size of home range, or probability of predation or brown-headed cowbird parasitism is not understood (Knick et al. 2003). Our limited understanding of shrubland bird ecology is almost entirely derived from site-specific studies of fine-scale management actions that mostly address short-term effects (e.g., changes in abundance rather than demographic changes) immediately following treatment (Knick et al. 2003). Models developed using site-specific information often do not perform well in regions or times outside of the sampling space (Rotenberry 1986, Knick and Rotenberry 1998, Knick et al. 2003). Additionally, the cumulative effects of habitat variability due to habitat management at different spatial and temporal scales are unknown.

Generally, habitat destruction, degradation, and fragmentation are the chief threats to sage sparrow populations. Agricultural conversion, frequent fire, livestock grazing, and “range improvements” (e.g., shrub removal, exotic grass plantings, etc.) all negatively influence sage sparrow populations. Additionally, these factors frequently promote other impacts, such as predation and nest parasitism (Dobkin and Sauder 2004). The extent to which management activities of the USFS in Region 2 impact sage sparrows versus threats on other areas within the landscape, managed by other entities, is unknown.

Despite the unknowns associated with sage sparrow ecology and response to threats, it is evident the sagebrush habitats on which it depends have been altered by land use, spread of invasive plants, and disrupted disturbance regimes beyond a threshold at which natural recovery of these habitats is likely (Knick et al. 2003). The threats to sagebrush ecosystems are numerous and continue to impact these ecosystems. Some threats (e.g., fragmentation due to road building, recreational use) can be expected to increase in the region. While the likelihood of extirpation within Region 2 is low because of its widespread distribution, considering the long-term declines in Region 2, and its specific habitat requirements and ecological characteristics, this species should be a high conservation concern. Action must be taken to increase our knowledge of the conservation status of this species to enable appropriate management action.

Potential Management of the Species in Region 2

Implications and potential conservation elements

In Region 2, long-term declines in sage sparrow populations indicate that existing landscape conditions and management activities negatively affecting this species. The overriding essential element for the conservation of the sage sparrow is healthy sagebrush shrubsteppe. Non-native grasses and agricultural and urban conversion now dominate much of western shrublands, making it is especially important to sustain the remaining native sagebrush communities in a healthy state to support native wildlife, including sage sparrow populations (Paige and Ritter 1999, Rotenberry et al. 1999). Conservation of the sage sparrow in Region 2 will require a renewed emphasis on creating the necessary landscape matrix and habitat conditions needed to support this species.

At a regional scale, the maintenance of sage sparrows depends on the existence of extensive tracts of sagebrush shrubsteppe and associated habitat physiognomy. At the home range scale, the occurrence and abundance of sage sparrows depends on high sagebrush cover, large patch size, spatially similar patches, low disturbance, and little fragmentation. Habitat components that have been positively correlated with sage sparrow densities (i.e., greater sparrow abundance with increasing amount of the specific element) are the amount of big sagebrush, shrub cover, patches of bare ground, and above-average shrub height. The minimum patch size and the degree of patch isolation required for breeding have not been determined; Knick and Rotenberry (2002) found that equal probabilities of sage sparrow occupancy were possible with different combinations of ground cover of sagebrush and patch size. For example, a patch that has high ground cover and is small may have the same probability of being occupied as a larger patch that has a lower amount of ground cover. Sage sparrows do appear to be area-sensitive; isolated stands of sagebrush smaller than 130 ha were not occupied by sage sparrows in eastern Washington (Paige and Ritter 1998).

Because sagebrush habitats and their dominant disturbance processes vary across Region 2, a simple set of strategic guidelines for sage sparrow management will not work. In general, management of sagebrush landscapes should attempt to mimic the historic natural disturbance regime (Samson and Knopf 1994). The creation and maintenance of this habitat condition is best accomplished by managing multiple large patches of sagebrush habitat through different or rotating management schemes that ensure the long-term availability of large patches with low disturbance and no fragmentation. Management activities that eliminate or fragment sagebrush over large areas can lead to significant declines in sage sparrow abundance (Wiens 1985, Wiens and Rotenberry 1985, Weins et al. 1986, Rogers et al. 1988, Martin and Carlson 1998). Any further conversion of shrublands to agricultural, resource extraction, urban, or suburban development, and its fragmenting effects, can be expected to adversely affect sage sparrow distribution and abundance. Conserving native sagebrush habitats will take concerted efforts to prevent the replacement of native understory plants with exotics, including the careful management of the disturbance factors that facilitate the spread of exotic plants (i.e., livestock grazing, road building, and agricultural development). In areas dominated by cheatgrass, efforts will be needed to reduce soil disturbance, reduce fine fuels, and determine and re-establish natural fire cycles.

Given the sage sparrow's association with unfragmented landscapes of sagebrush and the complexity of disturbance processes, desired conditions may be best managed using a flexible regional scheme that incorporates management approaches based not only on the size and use of the local reserve, but also on the management of nearby reserves and adjacent land use. For example, grazing within the landscape matrix surrounding a reserve that is ungrazed can impact sage sparrows within the reserve by promoting the invasive plants and brown-headed cowbirds. Strategies that encompass public and private lands within the landscape and assess cumulative effects over large spatial and temporal scales will be the most successful in ensuring healthy sage sparrow habitats.

Besides a paradigm shift in habitat management, the successful conservation of the sage sparrow and other sagebrush shrubsteppe birds will require new and innovative strategies that go beyond basic habitat management. Sagebrush habitats within Region 2 are relatively healthy and represent important reserves for the conservation of sagebrush-dependent species. However, these lands alone are unlikely to ensure the long-term population viability of this species. There is a significant need to develop partnerships between landowners and state and federal managers that are actively involved in the conservation of sagebrush habitats important to birds. Participation by private landowners may be accomplished through incentive-based programs to conduct agricultural and grazing practices in a manner beneficial to wildlife, but with a reasonable economic cost. Finally, a greater effort is needed to educate the public on the conservation value of healthy, intact sagebrush habitats.

Tools and practices

Inventory and monitoring

Inventory and monitoring populations and habitat. Public lands are managed with an overriding constraint that species, ecosystems, and processes be sustained on the landscape while allowing a variety of other activities to be conducted (Hutto and Young 2002). To ensure that these are being sustained, species population trends must be tracked, and the effects of natural and human-caused disturbances must be measured. It is not feasible to monitor every species or every aspect of an ecosystem.

Monitoring selected birds can, in some ecosystems, be a cost-effective method of assessing ecosystem integrity. Birds can be good indicators of ecosystem health because they tend to have dynamics that parallel those of the ecosystem; they are sensitive enough to provide an early warning of change and to provide continuous assessment over a wide range of stresses. Birds also have dynamics that can be linked to either natural cycles or anthropogenic stressors. In addition, bird populations are distributed over wide geographical areas and/or are often relatively numerous, so they can be accurately estimated, have costs of measurement that are not cost prohibitive, have a low impact to measure, and can provide measurable results that are repeatable with different personnel. Because of the relative ease of detection of songbirds such as the sage sparrow, both individual species and communities can be monitored. Thus, birds can serve as informative organisms for measuring natural and anthropogenic changes and for guiding and measuring management and restoration actions.

Prior to monitoring, an inventory of the biological resource of concern is generally conducted. Bird inventories seek to identify species presence/absence, range, distribution, and relative abundance, and they can provide a baseline for monitoring. Bird monitoring programs are generally developed on this baseline inventory. Commonly, monitoring programs fit into one of two categories: those designed to monitor long-term population trends and those designed to monitor the effects of land management actions. The goals of the monitoring program will affect the methods used. The current Partners in Flight landbird monitoring strategy (Bart and Ralph 2001) recommends integration of long-term monitoring programs and short-term assessments of habitat associations and land-use effects (Hutto and Young 2002).

Species inventory. The initial step in monitoring is conducting an inventory. A species inventory generally consists of conducting systematic surveys to identify the presence and abundance of a species within an area and to document the variables associated with its occurrence, such as habitat type and characteristics. Because information from monitoring can figure so prominently in landbird conservation, it is essential that managers use techniques that can provide "reliable information" (Romesburg 1981). Bird counting techniques that have been used for long-term monitoring can be divided into two groups: methods that use counts or maps of bird detections as an index to relative abundance and detection sampling methods that employ empirical modeling techniques to estimate bird density (Rosenstock et al. 2002). The second group of techniques (i.e., detection sampling) was developed with the recognition that some birds are missed during sampling, making it necessary to incorporate some method of estimating how many birds are missed. These techniques are similar to index counts, but they have an analytic component that models variation in species' detection to yield direct estimates of density. In practice, the field methods used for detection sampling techniques are basically the same as those used in index counts such as unlimited distance point counts, except that for each bird heard or seen during the count, the horizontal distance from the observer to the bird is estimated.

There are limitations of detection sampling methods even with the best-trained and most highly skilled observers. In many surveys, for example, the majority of birds are heard but not seen, and the observers estimate the distance to a tree or bush or other object where they think the bird is hiding rather than the bird's actual location. Also, distances cannot be estimated accurately in many situations because of habitat complexity, ventriloqual bird voices, or other reasons. Another drawback to distance sampling is that more than 100 detections are required to develop a good detection function for each species, such that multiple surveys of the same area may be required for all but the most common species in order to get adequate sample sizes (Fancy and Sauer 2002). Thus, detection sampling such as distance sampling is often inappropriate for rare species. However, distance sampling can be easily conducted in appropriate habitats (where distances can be reliably measured or estimated), including sagebrush steppe habitats. Density estimates can then be calculated for species detected in sufficient numbers to enable modeling detectabilities.

To conduct robust sampling over the spatial and temporal scales that we view as necessary for adequately monitoring sage sparrows, distance sampling can be used to detect estimates and describe the sources of variation. Recording distance can be facilitated by the use of a laser range finder. These are easy to use in shrubland habitats that have few trees to obscure the view between the observer and the bird. This method would be relatively easy to use for inventorying sage sparrows, and sage sparrows are likely to be detected in sufficient numbers to enable modeling detectabilities and estimating density (personal observation).

Point count areas for sampling can be established in a variety of ways, depending on the resources available to conduct the inventory. Points can be placed systematically across the landscape or randomly within the landscape. Sampling can also be stratified (e.g., the area is stratified by habitat and random points are selected within each habitat type). In general, there is a trade-off between how many points can be surveyed and how many times each point is surveyed; the greater the number of points, the fewer the number of surveys conducted at each point. There is an advantage to surveying each point more than once in that a greater proportion of the overall breeding season is covered, increasing the probability of sampling during a period when a particular species' breeding behavior, such as territorial calling and singing, increases its probability of detection.

Population monitoring. Existing programs to monitor distribution and population trends of birds across large areas, such as the BBS (Robbins et al. 1986, Peterjohn and Sauer 1999) and the CBC (Root 1988) may not adequately sample many of the species associated with sagebrush ecosystems (Saab and Rich 1997). Even though a high proportion of BBS routes contain sagebrush habitats, the proportional area of sagebrush sampled relative to other habitats along the survey route is far lower. Consequently, Breeding Bird Surveys likely capture neither the large-scale habitat features nor the smaller-scale dynamics in the matrix of habitat configurations available to shrubsteppe birds. In addition, surveys based on road networks may limit our ability to sample population distributions and to estimate abundance over the matrix of available landscapes (Anderson 2001), even though the internal bias due to presence of dirt-tracked or little used roads on bird counts in sagebrush habitats may not be significant (Rotenberry and Knick 1995, Knick et al. 2003). Survey designs need to be based on standard sampling methods for habitats and birds that incorporate local efforts into a broader program in a hierarchical design to address the multi-scale gradients in habitat and bird dynamics (Knick et al. 2003). We suggest using the distance sampling method to monitor long-term population trends in sage sparrows.

These methods fail to provide data on the primary demographic parameters or vital rates (productivity and survivorship) of landbirds. Monitoring the vital rates of sage sparrows, using methods such as constant effort mist-netting or the Breeding Biology Research and Monitoring (BBIRD) protocols (standardized protocols used in a national program for monitoring breeding productivity and habitat conditions for non-game birds; Martin et al. 1997), would make possible the construction of demographic models to assess the viability of populations, aid efforts to identify management actions to reverse population declines, and facilitate evaluating the effectiveness of those remedial management actions. This is because environmental stressors and management actions affect vital rates directly and usually without the buffering or time lags that often occur with population trends. Moreover, habitat- and landscape-specific data on vital rates provide a clear index of habitat and landscape quality and can identify population sources and sinks (Fancy and Sauer 2000).

To assess breeding habitat conditions and nest success and to estimate densities at small scales, the BBIRD protocol (Martin et al. 1997), which was designed to monitor breeding productivity and habitat conditions for non-game birds using standardized sampling, or modifications of it, are often used. Sage sparrows are relatively good subjects for monitoring nest success; several studies (e.g., J.T. Rotenberry, J.A. Wiens, and colleagues in eastern Oregon; L.B. Best, K.L. Peterson, T. Reynolds, and T.D. Rich in southeastern Idaho; W.M. Vander Haegen and colleagues in eastern Washington) were able to acquire relatively large sample sizes of nests within and across sites.

In addition, the technique of constant-effort mist netting and banding (also incorporated in BBIRD protocols) is a tested and proven method for collecting information on vital rates of landbirds. Annual indices of productivity and adult population size can be obtained from analyses of data on the numbers of young and adult birds captured; annual estimates of adult survival rate, adult population size, proportion of residents in the adult population, and recruitment into the adult population can be obtained from modified Cormack-Jolly-Seber analyses of mark-recapture data (Fancy and Sauer 2000).

Inventory and monitoring using focal species. The use of focal species has a number of advantages and disadvantages. The following comments are taken from Chase and Geupel (2003). Advantages of using focal species include the following:

- planning and managing for the habitat requirements of every species present in a planning unit is often impractical, if not impossible.

- knowledge of the needs of individual species can help to direct ecosystem or landscape level planning (Wilcove 1993, Simberloff 1998).

- the legal protection assigned to species in the United States (rather than to higher levels of biodiversity, such as habitats, ecosystems, or landscapes) sets up a funding and incentive structure that is species-specific (Noss 1990).

- some species are simply much more amenable to monitoring and research than others, a consideration that is crucial given real-life time, logistical, and funding constraints (Chase and Geupel 2003).

There are a number of problems associated with some uses of focal species as well (Landres et al. 1988, Lindenmayer et al. 2002).

- the use of indicator species to assess population trends of other species has been criticized on the grounds that individual species have unique ecological requirements (Taper et al. 1995). Empirical studies have shown that population responses to habitat change often cannot be extrapolated from one species to another, even within the same guild (Landres et al. 1988), or from one population to another of the same species (O'Conner 1992).

- the use of focal species to delineate habitat reserves also may be questionable if focal species do not reliably co-occur with a large proportion of other species in the area of interest (Andelman and Fagan 2000). This assumption is often difficult to test rigorously given our incomplete knowledge of species distributions. For example, Andelman and Fagan (2000) tested the effectiveness of several focal species approaches using species distribution databases from three geographical areas, and they found that most approaches performed poorly. However, these databases contained incidence records only for species with special legal status. The authors were unable to test the effectiveness of schemes that include "non-listed" as well as "listed" focal species and could not evaluate the effect that protecting focal species would have on other "non-listed" species.

- using species as indicators of habitat quality is only valid if research shows that the density or demographic parameters of focal species are reliably linked to specific habitat, population, or community attributes. Population density alone is known to be an unreliable indicator of habitat quality, even for a single species (Van Horne 1983).

Clearly, focal species should be chosen based on explicitly defined criteria, and empirical research and monitoring are needed to validate the assumption that other species are receiving protection as a result of the protection of a focal species (Landres et al. 1988, Noss 1990). As this has become more widely recognized, more empirical tests of focal species approaches have appeared in the literature, with mixed results (e.g., Andelman and Fagan 2000, Chase et al. 2000). A focal species approach should not be the only conservation strategy adopted in a given region and the effectiveness of all restoration programs should be rigorously tested (Lindenmayer et al. 2002, Chase and Geupel 2003).

Threatened and endangered species are sometimes suggested to be good focal species. These species may be especially sensitive to changes in habitat attributes of concern, but they may not meet the other criteria for effective focal species. For example, the presence of a threatened species, such as the California gnatcatcher (*Polioptila californica*), often does not indicate the presence of a more diverse or distinctive ecological community (Chase et al. 2000) or the presence of other sensitive taxa (Rubinoff 2001). In some cases, managing for the habitat requirements of an endangered species may not benefit all other species present, and it may even be detrimental to some species or habitats of conservation concern (Launer and Murphy 1994). Also, endangered species that occur at low densities or have regulatory status pose more sampling problems, which may make monitoring less reliable and more expensive (Landres et al. 1988, O'Conner 1992). Even when an endangered species appears to be a good umbrella for co-occurring species, it can be risky to focus conservation emphasis on a single species. If the species can be shown to be more flexible in its breeding requirements than was thought, or if it is found to be genetically indistinguishable from other, less-threatened populations, the justification for protection of its habitat may be undermined (Chase and Geupel 2003).

Habitat inventory and monitoring. Designing a monitoring program that includes habitat information with sample locations will facilitate the discovery of habitat associations and make a much more effective monitoring program than one based on long-term population trends alone (Hutto and Young 2002). An integrated approach to monitoring both vital rates and population trends of sage sparrows, and relating them to habitat characteristics across the landscape, is critical for understanding causes of population changes and for identifying, as well as testing, management actions and conservation strategies to reverse population declines (Fancy and Sauer 2000). Therefore, habitat inventory and habitat monitoring should be conducted with a sage sparrow inventory and monitoring program. Vegetation and habitat should be characterized at multiple spatial scales, and measurements of both horizontal and vertical structure should be taken in areas where sparrows are detected and where they are not. Habitat measurements can be coupled with bird inventories to establish species habitat selection within the area of concern. This information can be used as baseline information in subsequent monitoring of long-term avian population trends and the effects of land use and management actions.

The importance of various vegetation features (breeding habitat attributes) will vary according to species. For sage sparrows, important breeding habitat attributes likely include shrub density for different size classes, percent cover, species composition, measures of patch size, and landscape-level measures such as spatial distribution and distance between habitat patches, amount of edge, and amount and distribution of agricultural patches.

Monitoring techniques for measuring sage sparrow habitat attributes are not well established. However, identifying habitat relationships for the sage sparrow may better define key habitat attributes (i.e., shrub density) and therefore aid in establishing monitoring methods for this species. The vegetation data collected can document details that are unavailable through remote sensing and may be useful in terms of classifying each point according to elements that are important to sage sparrows, thus explaining any observed changes in sage sparrow density over time (Young and Hutto 2002). Hutto and Young (1999) found that within only a few years, and long before they ever calculated a species population trend, habitat data revealed potential issues of management concern for many species. Even if point-count data suggest that a species is not so specialized, further examination of the habitat relationships can identify critical management issues.

Emphasis should be placed on monitoring variables that are of potential biological importance (i.e., landscape matrix, patch size, shrub density, prevalence of exotic grasses) for sage sparrows. The regional extent, distribution, and condition of sagebrush shrublands should be quantified using Geographic Information Systems (GIS) techniques. Specific techniques for measuring within-patch bird habitats should include estimates of structural characteristics of the vegetation at different layers, including horizontal cover (e.g., Daubenmire frames; Daubenmire 1959) and vertical structure. Tree and shrub species composition should also be measured. Within-patch habitat can be characterized by measuring habitat variables at sampling points within a patch. These habitat measures can be adapted from the field protocols for national or regional programs such as BBIRD (Martin et al. 1997) and the Northern Region Landbird Monitoring Program (NRLMP) of the USFS (Hutto et al. 1998).

Environmental factors (i.e., fire and grazing) that may affect these vegetation characteristics should also be recorded. It is also highly recommended that photo documentation be conducted where point count stations have been established. Photographic documentation could be used to bolster a habitat relationships database for sage sparrows throughout Region 2 (Hutto and Young 1999).

Management approaches

Population or habitat management approaches. The successful management and conservation of sage sparrow populations will depend on the conservation of healthy sagebrush landscapes and the implementation of management actions to restore and conserve degraded areas. In general, management of sagebrush landscapes should attempt to mimic the natural disturbance regime (Samson and Knopf 1994) in order to approximate naturally occurring landscapes. The maintenance of the largest, most continuous stands of sagebrush that exist within Region 2 will benefit sage sparrows, as will small openings (e.g., <1 ha) of short vegetation surrounded by sagebrush (Paige and Ritter 1999).

Many of the management treatments used by land managers in sagebrush habitats have been to remove sagebrush from large areas for reseeding with non-native grasses (Dobkin and Sauder 2004). These practices have been detrimental to sage sparrows. We suggest a suite of approaches to achieve desired conditions for healthy shrubland ecosystems and sage sparrow populations. Some actions taken to protect or restore particular sites will depend on the characteristics of that particular site or landscape. Thus, the following suggestions will need to be adapted to each particular locale, using the expertise of local managers.

There is a need to identify and protect areas of healthy sagebrush shrubsteppe. Desired environmental conditions include landscapes comprised of all habitats originally, "naturally" occurring (such as a range of seral stages of sagebrush stands, interspersed openings, wet meadows, springs, and healthy riparian habitats) represented across a large area. Practices that permanently convert shrublands to non-native grasslands or agricultural lands should be avoided, as should practices that further fragment areas, such as road building. The cumulative impacts of individual management actions that contribute to fragmentation (e.g., energy development) should be assessed. The creation of edges with converted habitat should be minimized, wherever possible. Burning to eradicate sagebrush over large areas (e.g., >20 to 40 ha) should be avoided, and range fires that threaten to eradicate large areas of sagebrush should be suppressed. Providing for "no net loss of sagebrush habitats" (Paige and Ritter 1999) across landscapes will help to achieve the desired condition of large areas of healthy sagebrush in a landscape that, at least, mimics a natural matrix.

Management should move towards the reestablishment of natural disturbance processes and the careful management of practices that can degrade sagebrush steppe, such as livestock grazing. Disturbed sites should be restored or rehabilitated to native plant communities, if possible. In some areas simply protecting areas from degradation may allow for the reestablishment of native plants. In large disturbed areas, sagebrush and native perennial grasses may need to be reseeded to shorten the recovery time and to prevent dominance by non-native grasses and forbs. Ecologically appropriate native plant species should be used in all shrubsteppe restoration projects (Knick et al. 2003).

Sources of soil disturbance (e.g., road building, off-road vehicle use, heavy grazing) should be minimized to maintain biological soil crusts, which are sensitive to trampling by humans, vehicles, and livestock (Paige and Ritter 1999). Roads that fragment otherwise continuous sagebrush should be closed or re-routed, if necessary. All vehicles should be kept on established roads and trails or confined within areas established specifically for off-road recreation. Travel corridors should be established so as not to influence sensitive sagebrush habitats and species.

No single grazing strategy is appropriate for all shrubland habitats, and grazing management must be tailored to the condition and potential of each grazing unit (Paige and Ritter 1999). Management plans should consider the existing influence of native ungulate grazers, such as elk and deer. Combined ungulate stocking levels should enable the stabilization or increase of native perennial ground cover and reduce disturbance to soil crusts. In addition to properly managing stocking levels, grazing seasons and the distribution and types of grazers should be managed to promote native ground cover and to maintain herbaceous cover for nest concealment (Paige and Ritter 1999). For instance, in stands where cheatgrass and native perennial grasses are mixed, grazing during the dormant period may favor perennial species (Young 1992, Vallentine and Stevens 1994, Paige and Ritter 1999). Managing grazing time and intensity can reduce or eliminate trampling of ground nests and nests in low shrubs such as sage sparrow nests.

Situations that concentrate livestock, such as corrals, feedlots, and watering sites, during the sage sparrow breeding season may increase the impact of brown-headed cowbird brood parasitism on sage sparrow nesting success (Robinson et al 1995). Rotating livestock use to rest units from cowbird concentrations in alternate years may give local songbird populations breeding opportunities without high parasitism pressure (Paige and Ritter 1999).

Substantial direct and indirect human-induced impacts occur on public lands every year. Although many treatment plans recommend monitoring, the vast majority of these treatments occur without deliberate, well-considered, or funded efforts to examine causal effects on either habitat or associated wildlife (Knick et al. 2003). As management action is undertaken to establish desired environmental conditions of sagebrush shrubsteppe and sage sparrow populations, it is critical to develop and implement pre- and post-treatment designs, including controls, to increase the understanding of the cause-and-effect relationships between land use and changes in habitat and bird communities (Petersen and Best 1999, Anderson et al. 2000, Knick et al. 2003).

Information Needs

A recent review written by experts in the field (Knick et al. 2003) discusses the threats that face birds in sagebrush habitats, synthesizes existing information regarding avifauna of sagebrush habitats, and identifies their management and conservation needs. They conclude that little is understood regarding shrubsteppe bird-habitat dynamics. To manage and conserve birds in sagebrush habitats there is an urgent need for more research into four major topics:

- identification of primary land-use practices and their influence on sagebrush habitats and birds
- better understanding of bird responses to habitat components and disturbance processes of sagebrush ecosystems
- improved hierarchical designs for surveying and monitoring programs
- linking bird movements and population changes during migration and wintering periods to dynamics on sagebrush breeding areas.

Knick et al. (2003) found that, 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.

The general breeding distribution of the sage sparrow is relatively well known. Within its geographic distribution, including within Region 2, distribution patterns, habitat associations, and demographic information within a range of habitat conditions are not well known. Without information on habitat associations, reproductive success, adult and juvenile survivorship, and dispersal patterns, it is impossible to understand and predict the effects of different management options and conservation actions on source-sink dynamics (Knick et al. 2003). The sage sparrow appears to be an area-dependent species. Studies that improve our knowledge of how landscape context influences sage sparrows' sensitivity to habitat fragmentation and nest predation and parasitism rates are also needed. These studies will provide information that can guide conservation planners in determining how large sagebrush conservation areas should be, how they should be spatially arranged, and into what type of landscapes they should be placed (Herkert and Knopf 1998).

In order to study the effects of management approaches, such as grazing, 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 are needed (Knick et al. 2003). Long-term studies incorporating a widespread system of exclosures and the ability to control treatment levels are necessary to measure the effects of land use on habitats and birds. Knick et al. (2003) suggest that 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. Establishing such studies and combining them with monitoring at appropriate scales would provide the feedback to evaluate treatment effects and provide the basis for adaptive management strategies (Walters 1986, Morrison 2002, Knick et al. 2003). Such information is critical for identifying causes of population changes and for testing management actions and conservation strategies to reverse population declines.

DEFINITIONS

Bird Conservation Region — ecologically distinct regions in North America with similar bird communities, habitats, and resource management issues within which bird conservation efforts are planned and evaluated, as endorsed by the North American Bird Conservation Initiative (2000).

Physiographic Stratum — Breeding Bird Survey regional areas defined on the basis of similar vegetation, soil, and physiographic features and used in analysis of bird species' population trends and relative abundance.

Physiographic Area — Partners in Flight planning units defined on the basis of biotic communities and bird distribution; used in bird conservation planning.

USDA Forest Service Region 2 — Wyoming, Colorado, South Dakota, Nebraska, and Kansas (**Figure 1**).

U.S. Fish and Wildlife Service Region 6 (Mountain-Prairie Region) — Wyoming, Colorado, South Dakota, Nebraska, Kansas, Montana, Idaho, and Utah.

U.S. Fish and Wildlife Service Region 2 (Southwest Region) — Arizona, Oklahoma, New Mexico, and Texas.

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Appendix A

Matrix Model Development for the Sage Sparrow

Lifecycle diagram and model development (prepared with David B. McDonald)

The studies of Petersen and Best (1987a) and Martin and Carlson (1998) provided the basis for formulating a two-stage lifecycle graph for sage sparrows (censused at the fledgling stage and "adults"). The scanty data on survival (Petersen and Best 1987a) suggested a minimum "adult" survival rate of 55 percent. Because this estimate did not account for birds surviving but not detected (e.g., those that moved outside the study area), we used an estimate of 65 percent annual survival for adults. We further assumed considerably lower survival in the first year, a value for which we solved by assuming the population growth rate, λ, was 1.003. This "missing element" method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. In addition we assumed that reproduction of first-year birds was half that of "adults" (**Table A1**). The fertility estimate for "adults" was based on the suggestion of two broods per season and 1.3 offspring fledged per nest. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the fledgling number used was half the total annual production of fledglings, assuming a 1:1 sex ratio. From the resulting lifecycle graphs (**Figure A1**), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of entry terms: P_i describing survival rates, and m_i describing number of female fledglings per female (**Table A1**). **Figure A1** shows the numeric values for the matrix corresponding to the lifecycle graph of **Figure A1**. The fertility terms (F_{ij}) in the top row of the matrix include both a term for fledgling production (m_i) and a term for the survival of the mother (P_i) from the census (just after the breeding season) to the next birth pulse almost a year later. The population growth rate, λ, was 1.003, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and it should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

Table A1. Parameter values for the component terms (P_i and m_i) that comprise the vital rates in the projection matrix for sage sparrow.

Parameter	Numeric value	Interpretation
m_1	0.65	Number of female fledglings produced by a first-year female
m_a	1.3	Number of female fledglings produced by an "adult" female
P_{21}	0.329	First-year survival rate
P_a	0.65	Survival rate of "adults"

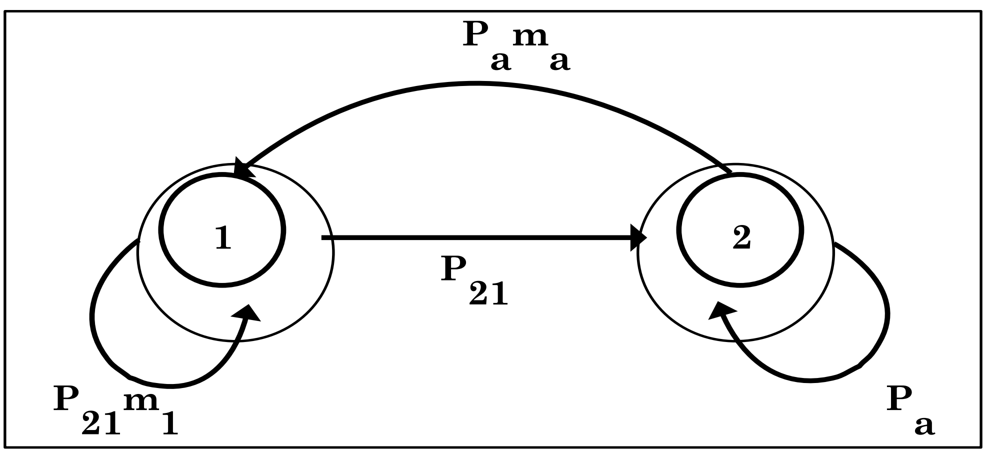

Figure A1. Lifecycle graph for sage sparrow. The numbered circles ("nodes") represent the two stages (first-year birds and "adults"). The arrows ("arcs") connecting the nodes represent the vital rates — transitions between stages, such as survival (P_{ji}) or fertility (F_{ij}, the arcs pointing back toward the first node). Note that the two fertility arcs contain both a term for offspring production (m_i) and a term for the survival of the mother (P_{ij}).

Sensitivity analysis

A useful indication of the state of the population comes from sensitivity and elasticity analyses. Sensitivity is the effect on λ of an absolute change in the vital rates (a_{ij}, the arcs in the lifecycle graph [**Figure A1**] and the cells in the matrix, A [**Figure A2** and **Figure A3**]). Sensitivity analysis provides several kinds of useful information (after Caswell 2001:206-225). First, sensitivities show how important a given vital rate is to λ, which Caswell (2001: 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of survival (P_{ij}) and fertility (F_{ij}) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. To improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the "weak links" in the life cycle of a pest. **Figure A4** shows the "possible sensitivities only" matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible — for example, the biologically impossible sensitivity of λ to the transition from Stage 2 "adult" back to being a Stage 1 first-year bird).

The summed sensitivity of λ to changes in survival (70.6 percent of total sensitivity accounted by survival transitions) was greater than the summed sensitivity to fertility changes (29.4 percent of total). The single transition to which λ was most sensitive was first-year survival (36.5 percent of total). Nearly as important was "adult" survival (34.1 percent of total). The major conclusion from the sensitivity analysis is that survival rates are most important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 to 40 percent). An absolute change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities

	1	2
1	$P_{21}m_1$	P_am_a
2	P_{21}	P_a

Figure A2. Symbolic values for the projection matrix of vital rates of sage sparrow, **A** (with cells a_{ij}) corresponding to the lifecycle graph of **Figure A1**. Meanings of the component terms and their numeric values are given in **Table A1.**

	1	2
1	0.214	0.845
2	0.329	0.65

Figure A3. Numeric values for the sage sparrow matrix corresponding to the lifecycle graph of **Figure A1.**

	1	2
1	0.214	0.845
2	0.329	0.65

Figure A4. Possible sensitivities only matrix, **Sp** for the sage sparrow matrix (blank cells correspond to zeros in the original matrix, **A**). The λ of sage sparrow is most sensitive to changes in first-year survival (Cell s_{21} = 0.74), closely followed by "adult" survival (Cell s_{22} = 0.691).

are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and, thus, partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1 percent). Elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_{ij}) and survival (P_{ij}) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for sage sparrow are shown in **Figure A5**. The population growth rate, λ, was most elastic to changes in "adult" survival (e_{22} = 44.8 percent of total elasticity). Next most elastic were first-year survival and "adult" reproduction (e_{21} = e_{12} = 24.3 percent of total elasticity). Reproduction by first-year birds was relatively unimportant (e_{11} = 6.6 percent of total elasticity). The sensitivities and elasticities for sage sparrow were generally consistent in emphasizing survival transitions. Thus, survival, particularly "adult" survival rates, are the data elements that warrant careful monitoring to refine the matrix demographic analysis.

Other demographic parameters

The stable stage distribution (SSD, **Table A2**) describes the proportion of each stage or age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For sage sparrow at the time of the post-breeding annual census (just after the end of the breeding season), fledglings represent 51.7 percent of the population, and "adults" represent the remaining 48.3 percent of the population. Reproductive values (**Table A3**) can be considered as describing the value of a stage as a seed for population growth relative to that of the first (newborn or, in this case, fledgling) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive production of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by definition, 1.0. An "adult" female is worth 2.4 fledglings. The cohort generation time for this species was 3.8 years (SD = 2.8 years).

Stochastic model

We conducted a stochastic matrix analysis for the sage sparrow. We incorporated stochasticity in several ways (**Table 4A**), by varying different combinations of vital rates, and by varying the amount of stochastic fluctuation. We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation, we used a standard deviation (SD) of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Under Case 1, we subjected the fertility arcs (F_{11} and F_{12}) to high levels of stochastic fluctuations (SD one quarter of mean). Under Case 2, we varied the survival arcs (P_{21} and P_{22}) with high levels of stochasticity (SD one quarter of mean). Under Case 3, we varied only "adult" survival (P_{22}), again with high levels of stochastic fluctuation. Case 4 varied the two survival transitions, like Case 2, but with only half the stochastic fluctuations (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) of the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $log\lambda_S$, according to Eqn. 14.61 of Caswell

	1	2
1	0.066	0.243
2	0.243	0.448

Figure A5. Elasticity matrix, **E** (remainder of matrix consists of zeros) for the sage sparrow matrix. The λ of sage sparrow is most elastic to changes in "adult" survival (e_{22} = 0.448), followed by first-year fertility and survival (e_{12} = e_{21} = 0.243).

Table A2. Stable age distribution (right eigenvector). At the census, 43 percent of the individuals in the population should be fledglings. The rest will be older "adult" females in their second year or older.

Stage	Description	Proportion	Mean age (± SD) Variant 1
1	Fledglings (to yearling)	0.52	0 ± 0
2	"Adult" females	0.48	2.8 ± 2.3

Table A3. Reproductive values (left eigenvector). Reproductive values can be considered as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive value (second-year females) is highlighted.

Stage	Description	Reproductive value
1	Fledglings/first-year females	1
2	"Adult" females	2.4

Table A4. Results of 4 cases of different stochastic projections for the sage sparrow. Stochastic fluctuations have the greatest effect when acting on survival transitions with high stochasticity (Cases 2 and 3).

Input Factors	Case 1	Case 2	Case 3	Case 4
Affected cells	All the F_{ij}	All the P_{ij}	P_{22} ("adult" survival)	All the P_{ij}
S.D. of random normal distribution	1/4	1/4	1/4	1/8
Output values:				
Deterministic λ	1.003	1.003	1.003	1.003
# Extinctions/100 trials	0	77	59	0
Mean extinction time	N.a.	1,213	1,332	N.a.
# Declines/# surviving populations	40/100	18/23	35/41	48/100
Mean ending population size	1.2×10^6	484,507	14,244	450,732
S.D.	4.4×10^6	2.3×10^6	54,893	1.2×10^6
Median ending size	15,856	241	100	11,363
Log λ_s	0.0005	-0.0074	-0.0053	0.0005
λ_s	1.0005	0.9926	0.9947	1.0005
Percent reduction in λ	0.20	0.99	0.78	0.20

(2001), after discarding the first 1,000 cycles to further avoid transient dynamics.

The stochastic model (**Table A4**) produced two major results. First, high levels of stochastic fluctuations affecting survival had the greatest detrimental effects. Low-level stochastic fluctuations (Case 4, SD of one eighth) resulted in no extinctions and 48 declines. High fluctuations in fertility transitions resulted in no extinctions and only 40 declines. Second, varying "adult" survival had the greatest detrimental effects. Case 3, affecting only "adult" survival had 59 extinctions and an additional 35 declines, close to the results for Case 2 (77 extinctions and an additional 18 declines). The difference in the effects of which arc was most important is predictable largely from the elasticities. The population growth rate, λ, was most elastic to changes in the first-year transitions. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. These results indicate that populations of sage sparrow are vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance) when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. The sage sparrow, however, may have little flexibility in reducing variability in first-year survival, which has a relatively high elasticity. Variable early survival, and probably fertility, is likely to be the rule rather than the exception.

Potential refinements of the models

Clearly, improved data on survival rates and age-specific fertilities are needed to increase confidence in any demographic analysis. The most important "missing data elements" in the life history for sage sparrow are for survival transitions, which emerge as vital rates to which λ is most sensitive as well as most elastic. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Using observed correlations would improve on our "uncorrelated" assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models

Survival accounts for 71 percent of the total "possible" sensitivity, fairly equally distributed between first-year and "adult" survival. Any absolute changes in survival rates will have major impacts on population dynamics.

- ❖ "Adult" (e_{22} = 45 percent) and first-year (e_{21} = 24 percent) survival account for almost 70 percent of the total elasticity. Proportional changes in survival rates will have a major impact on population dynamics.

- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of survival and rates to population dynamics.

- ❖ Reformulation of a matrix analysis when improved data are available might substantially change some of the values, but would be unlikely to radically revise the major emphases presented here.