DISTURBANCE AS RESTORATION IN THE INTERMOUNTAIN SAGEBRUSH-STEPPE: EFFECTS ON NON-TARGET BIRD SPECIES

by

Russell E. Norvell

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology
(Wildlife Ecology)

Approved:

Thomas C. Edwards, Jr. Major Professor	Frank P. Howe Committee Member
Karen H. Beard Committee Member	D. Richard Cutler Committee Member
S. K. Morgan Ernest Committee Member	Ronald J. Ryel Committee Member

Byron R. Burnham
Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan Utah

2008

ABSTRACT

Disturbance as Restoration in the Intermountain Sagebrush-Steppe:

Effects on Non-target Bird Species

by

Russell E. Norvell, Doctor of Philosophy

Utah State University, 2008

Major Professor: Dr. Thomas C. Edwards, Jr.
Department: Wildland Resources

Changes in shrubsteppe passerine bird habitat associations in response to disturbance were investigated at multiple temporal and spatial scales. Spatial measures incorporated the effects of area at different ecological scales (nest site, territory, and landscape) to include ecologically meaningful extents. Temporal measures included seasonal and annual effects, and were designed to detect lagged responses should they occur. Local-to-landscape scale effects of mechanical restoration treatments on local extirpation and abundances of nine species indicated most were insensitive to changes in habitat quality, while abundance models showed only broad declines. Changing the availability of nesting habitat on both the attractiveness and quality of an area at multiple extents confirmed the need for long-term study effects due to lagged responses in expressed preference and changes to nesting habitat quality. Time since treatment affected nest success in two of the four species, yet the changes in habitat quality did not forecast changes in habitat preference as expected. Non-adaptive mismatches seemingly occurred as habitat preferences indicated treatments may create benign-appearing “sink” habitat for species that remained in the area. The umbrella species concept is misapplied at this scale: each species’ response was consistent, but responses varied in scale, timing, and direction among species. Patterns of nest density and nest site descriptions demonstrated population-level movement in response to treatments, suggesting half the focal species moved nest sites to remaining habitat areas. Larger scale responsive movements were observed in the remaining species, both out of and into the nest plot. Descriptions of nesting habitat characteristics for the focal species tested if the selected nesting habitat was consistent between pre- and post-treatment, and determined which habitat characteristics, including distance to disturbance, were related to nest success. Descriptions of nesting habitat characteristics support previous work in terms of structural characteristics. Habitat selection was consistent even when the available habitat was not, implying these species choose sites and are not merely settling randomly. However, selected nesting habitat was not strongly tied to nest success at local scales and nest success was negatively related to landscape qualities that treatments were designed to enhance.

(154 pages)

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. T. Edwards, the Utah Division of Wildlife Resources, the Rich County landowners, the Rich County Coordinated Resource Management group, the NRCS, the BLM, and Deseret Land and Livestock, our hard-working field technicians, my committee members (Drs. K. Beard, R. Cutler, M. Ernest, F. Howe, and R. Ryel), my fellow Rich County researchers, and most of all my wife, Adrienne. I am indebted to you all. This work was supported by grants from the Utah Division of Wildlife Resources, the NRCS, the BLM, the IMJV, and ESMF/SWG. All work was reviewed and conducted under Utah State University's IACUC procedures.

Russell E. Norvell

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

MONITORING OF SHRUBSTEPPE ASSOCIATED PASSERINES IN ACTIVELY MANAGED AND ECOLOGICALLY DYNAMIC RANGELANDS IN RICH COUNTY, UTAH

INTRODUCTION

Shrubsteppe ecosystems: definition and extent

Vast areas of western North America are dominated by shrubsteppe ecosystems (approximately 63 million ha; Beetle 1960, Miller and Eddleman 2001, Adams et al. 2007), providing essential habitat for a wide variety of taxa (Marcot et al. 1997). Shrubsteppe ecosystems of western North America are a blend of sagebrush (*Artemisia* spp.) and a variety of grass species, with the many sagebrush subspecies traditionally grouped by growth form into “low” and “big” communities (West and Young 2000, Miller and Eddleman 2001). The floristic composition of the grasses present and the degree of their ecological dominance varies with latitude, elevation, overstory species, grazing pressure, management, and fire history (Stewart and Hull 1949, Vale 1974, West 1983). Species frequently included in described associations are bluebunch wheatgrass (*Agropyron spicatum* Pursh), Thurber needlegrass (*Stipa thurberiana* Piper), Idaho fescue (*Festuca idahoensis* Elmer), and Great Basin wildrye (*Elymus cinereus*). The “low” group of sagebrush subspecies is dominated by black sage (*A. nova*) and low sagebrush (*A. arbuscula*), often in association with sandberg bluegrass (*Poa sandbergii* Vasey). Other shrubs play important roles in the composition of shrubland areas, including rubber (gray) rabbitbrush (*Ericameria nauseosus*), green rabbitbrush (*Ericameria viscidiflora*), and snowberry (*Symphoricarpos* spp.).

Well over 300 vertebrate species are considered dependent on, or primarily associated with, sagebrush (more generally shrubsteppe) ecosystems; over 100 of these species are birds (Braun et al. 1976, Knick et al. 2003). Best studied of these birds are the sage-grouse (*Centrocercus* spp.), with well over 700 reports and peer-reviewed references on the two species comprising this genus, and recent petitions for listing these species under the U. S. Endangered Species Act (Rowland et al. 2006). Also dependent upon sagebrush ecosystems are the estimated one million people who also derive some portion of their livelihood from the over 400,000 farms and ranches in the western U.S. (Weltz and Dunn 2003). Taken together, declines in shrubsteppe birds and other animal populations, their potential for listing under the Endangered Species Act, tenuous economic sustainability of grazed lands, and limited distribution and abundance of many plants and other taxa make sagebrush habitats, according to some, one of the most imperiled ecosystems in North America (Noss and Peters 1995, Dobler et al. 1996, West 2000). Knick et al. (2003) further warn that “cumulative effects of land-use and habitat degradation raise the greater threat of imminent large-scale collapses of sagebrush ecosystems.”

Disturbance and restoration

The immense scale of this habitat’s extent is matched by the scope of its degradation and outright loss. West (2000) estimated that ca. 4.5 million ha have been converted to intensive agriculture, urban developments, or have been directly impacted by resource extraction, roads, powerlines, and pipelines. In comprehensively studied areas, direct losses to type conversion (including ecological state-change) range from 40-60 percent (Dobkin and Sauder 2004). The overwhelming majority of losses have been due to conversion to intensive agricultural uses (West 1983, West and Young 2000, Miller and Eddleman 2001, Knick et al. 2003) or to vegetative manipulations designed to "control" sagebrush in order to provide forage for livestock (Vale 1974, BLM 1991). While shrublands were not the first areas to be developed by European settlement, they were certainly impacted (Vander Haegen et al. 2000), with grazing impacts said to have "…destroyed the bunch-grass system in 40 years…" (West and Young 2000). The pattern of development predictably prioritized immediate arability, with the most mesic, deepest, and most fertile soils falling immediately to the plow (Noss and Peters 1995, Dobler et al. 1996, Scott et al. 2001).

Sagebrush control, the practice of chaining, crushing, burning, spaying, or otherwise removing or reducing shrubland cover in order to improve grass and forb production for livestock, peaked in the 1970's after treating an estimated 2-6 million ha of shrublands (Vale 1974). The practice continues to a reduced extent today (BLM 1991, 2007, Olson and Whitson 2002).

While fire remains the dominant process structuring shrubsteppe habitats at regional scales, its primary role as the mediator of patch size and seral class has been radically altered through the invasion and establishment of exotic annual understory species such as cheatgrass *Bromus tectorum* (Knick and Rotenberry 1997, Brooks and Pyke 2001).

The synergistic effect between the soil disturbance that allows exotic annuals to establish a foothold — often attributed to overgrazing (Young and Allen 1997, Miller and Eddleman 2001), and the increased fire size, frequency, and intensity that results from the widespread fine fuels that early senescing annual grasses provide (D'Antonio 2000), has combined to convert an estimated 50-60% of the remaining shrubsteppe to areas dominated by exotic annual grasses (West 2000). Fire suppression, however, is believed to have allowed the establishment of “decadent” shrub stands where older, more mature sagebrush becomes ecologically dominant at the expense of understory species (Welch and McArthur 1979).

Second only to habitat loss in determining habitat quality for shrubsteppe birds is the fragmentation of habitat (Reed 1986, Knick and Rotenberry 1997, Laurance 2000, Vander Haegen et al. 2002, Weiss and Reice 2005). Fragmentation effects on bird habitat are thought to be expressed in three ways: area, edge, and isolation (Wiens 1995). All three have been demonstrated to have important consequences for bird use of habitat. Configuration of these elements on the landscape has also been demonstrated to affect bird use of habitat.

Landscape ecology provides a series of metrics (e.g., patch size and shape, patch isolation and dispersion, corridors, matrices and networks) that describe the spatial qualities of a landscape, the distribution, aggregation, and extent of habitat elements in a consistent manner. While the hierarchical nature of landscape spatial qualities is fairly well accepted (Wiens 1999), the underlying processes (e.g. scaling factors), the consequences for biota (e.g., impacts of land cover change), and the integration and interaction of spatial qualities of habitat (e.g., ecological flows) are active areas of research (Wu 2004). No comprehensive assessment of the range of large-scale natural variation in shrubsteppe landscape metrics is available (S. Knick, U.S. Geological Survey, personal communication), in part due to the lack of extant natural landscapes to measure. Intermediate scales of landscape investigation have been widely investigated, but are typically only applied at local scales (Knick and Rotenberry 1995, 1997).

Widespread and intensive grazing on western rangelands has led to significant changes in the structure and composition of vegetative communities (Olson and Whitson 1996, Young and Sparks 2002). Knick et al. (2003) note that "virtually all sagebrush lands are managed for livestock," leading to calls for a meaningfully scaled series of exclosures (Bock and Bock 1999) to realistically test management assumptions and impacts. At intermediate levels of grazing intensity, however, plant diversity at local and landscape scales may be augmented or maintained by reducing overall dominance and facilitating heterogeneity which may allow other less competitive plants to persist (Rambo and Faeth 1999). Heavy and long term grazing can lead biosimplification, as many shrubsteppe areas did not develop with large herbivores as an historic perturbation. Intensive or long-term grazing in such areas leads to greater uniformity in species composition, physical structure and organization, and considerable aboveground herbaceous biomass reduction. Intensive grazing regimes have also led to disturbed soil substrates, altered water and nutrient cycles that have facilitated the invasion of non-native plant species, many of which are considered unpalatable to both domestic and wild ungulate species (Olson and Whitson 2002), and thereby further concentrating grazing pressure on native plants.

Recent reviews of sagebrush ecosystems (Connelly et al. 2000, Knick et al. 2003, Crawford et al. 2004) estimate that of the remaining shrubsteppe areas over half have a “significant” non-native annual grass understory, or have been wholly converted to an exotic annual grass-dominated system through the combined but largely indirect effects of human activities. This form of habitat degradation is widespread in the more xeric sites of the Great Basin, but is ubiquitous throughout sagebrush-dominated landscapes (Miller and Eddleman 2001, Knick et al. 2003). Of the exotic invasive species, cheatgrass is among the best studied. It has been invading shrubsteppe ecosystems for at least a century (Young and Allen 1997), frequently establishing dense stands after wildfire or ground disturbance. Cheatgrass has an earlier phenology than most native grasses, and by senescing early, leaves fine fuels that shorten fire intervals and creates a synergy of effect that leads to a persistent altered ecological state wholly dominated by cheatgrass (Brooks and Pyke 2001).

Research and management paradigms

Rangeland management, in theory and practice, has been dominated by a Clementsian model of habitat succession from its formative years (Briske et al. 2003, 2006). The traditional range model has been a linear one: a spatially-unspecific and scale-free description of shrubsteppe plant communities existing along a single axis defined by the bare ground at one end and a climax equilibrium community at the other.

Movement along this axis was driven by in one direction by succession, and grazing in the other. The equilibrium state has typically been defined as a grassland/savanna community: an anthropogenically determined fire-climax, rather than climactic-climax, vegetation community (Briske et al. 2003, 2006). A key feature of the range model is the dialectical pairing of secondary succession and grazing impacts, where management impacts are seen as temporary reversals of progressive succession of the system toward its climax state. Criticisms of the range model have centered on this aspect, and although the range model has been effectively debunked in the research literature (Allen-Diaz and Bartolome 1998, Briske et al. 2003, 2006), it remains a pervasive element framing justifications of current and proposed rangeland management actions. The increasingly obvious, and public, failure of traditional rangeland models to either accurately describe current conditions or predict vegetation change (Laycock 2003) spurred the development and rapid adoption of the state-and-transition model (Briske et al. 2006) now currently in vogue.

The state-and-transition conceptual model may be described as an ecological surface, with multiple-stable state “basins” bordered by transition “thresholds” where induced change in state is a non-linear function of the impetus. States are described in terms of vegetative communities (e.g., grassland, shrubland); transitions in terms changes in ecological structure (e.g., pattern) or function (e.g., process). The model does not assume equilibrium conditions as a climax model endpoint (Wiens et al. 1985a), though change within basins is typically described as linear, successional transition toward the “local” ecological climax community specific to that basin. The conceptualization of the state-and-transition model appears to have been formulated as a descriptive, or phenomenological model, and currently lacks explicit linkages to underlying ecological theory, traditional measures of rangeland health, or practical applications (Briske et al. 2003, 2006).

The main benefit of the state-and-transition approach is to place descriptions of rangeland communities in a non-linear, non-equilibrium, and dynamic conceptual framework, reconciling the dissonance between assessments of rangeland condition and descriptions of rangeland health. However, while re-scaling rangeland condition observations to an improved anthropogenic scale may suffice as a management model, it lacks the breadth necessary for an ecological modeling approach. For example, transitions between states are couched in management time frames, such that any state change longer than is tractable by rangeland managers are termed “irreversible” (Briske et al. 2003, 2006). Both rangeland condition and rangeland health are subjective concepts with their roots in Clementsian conceptualizations and resource extraction mindsets that posit a facilitative linkage between livestock effects and ecological processes. Critics of public land grazing imply that in cases where the “ecological site potential” (NRCS 2001) is not amenable to grazing, management plans often dictate a “Desired Vegetative Condition” that justifies grazing activity, and therefore “restoration” toward grassland states (http://www.publiclandsranching.org/). While any system can be manipulated toward political ends, the state-and-transition model does empirically describe observed patterns of state change, despite its lack of clear linkage to theory.

Bird-habitat relationships: patterns and processes

Shrubsteppe-dependent birds are defined here as those whose life histories are inexorably intertwined with shrubsteppe vegetation (Braun et al. 1976, Knick et al. 2003). In this work, I will examine the effects of habitat alterations designed to improve brood rearing habitat for the greater sage-grouse (*Centrocercus urophasianus*) while improving livestock foraging conditions by focusing on three regionally declining (Sauer et al. 2007) shrubsteppe-dependent species: sage thrasher (*Oreoscoptes montanus*), sage sparrow (*Amphispiza belli*), Brewer's sparrow (*Spizella breweri*) and one grassland species, the vesper sparrow (*Pooecetes gramineus*).

While the concept of the ecological niche has been tracked back to Aristotle, current usage of the term ecological niche is more frequently attributed to Joseph Grinnell. Similarly, Hutchinson (1957) is credited with formalizing the definition to include the range of physical and biological properties required for a species to survive and reproduce, the "n-dimensional hypervolume." Underlying the modern definition of ecological niche is the competitive exclusion principle (Hardin 1960), whereby two species cannot coexist if they overlap extensively in their resource requirements. Explanations of how species in communities coexist when they have at least partial overlap in their "fundamental niche" (i.e., the theoretical breadth of system conditions under which a species can survive in the absence of competitors) have led to the description of "realized niche" spaces for species that demonstrate the minimization or avoidance of competition (e.g., MacArthur 1958). While competition is thought to be major ecological force structuring bird communities, it is not consistently apparent.

Effects of disturbance on bird habitat selection

The mechanisms of disturbance effects on shrubsteppe birds are not well described beyond local levels and short-term effects (Knick et al. 2003). At broad scales declines in bird abundance and diversity have been noted; proposed mechanisms include increases in predation and parasitism resulting from fragmentation. Reductions in species diversity due to habitat fragmentation and loss may take a long time to be expressed since strong natal philopatry and breeding area fidelity exists in many bird species. In theory, after a disturbance event, increased fragmentation in the remaining habitat areas reduces an individual's ability to assess habitat quality, resulting in the non-optimal selection of habitat (*sensu* Ideal Free Distribution or Ideal Despotic Distribution; Fretwell and Lucas 1969) that in turn leads to a depressed population growth rate and lowered extinction thresholds.

Disturbance impacts on my four focal species can be best judged in the context of their selected habitat. Sage thrashers are noted for their sensitivity to patch area and are almost entirely dependent on sagebrush habitat during the breeding season (Reynolds et al. 1999). Disturbance effects tend to reduce patch size and seral class and are likely to have negative effects on local sage thrasher breeding habitat (Vander Hagen et al. 2000). Sage sparrows are similarly sensitive to loss of contiguity, and to increased fragmentation as well (Martin and Carlson 1998, Vander Haegen et al. 2000). Exotic annual grasses are also known to compromise breeding habitat (Dobler et al. 1996, Knick and Rotenberry 1997, Martin and Carlson 1998, Vander Haegen et al. 2000). While Brewer's sparrows are though to be less sensitive to patch size and contiguity issues, they appear sensitive to proportion of shrub cover at local and landscape scales (Petersen and Best 1985, Karl et al. 2000). Vesper sparrows are predominantly a grassland-associated species that readily inhabits small openings in shrublands caused by disturbance and fragmentation (Jones and Cornely 2002). They are also declining nationally, presumably due to habitat loss and degradation in grassland areas (Jones and Cornely 2002).

Habitat selection: dynamic and scale dependent process

In management terms, a species “habitat” is roughly equated with its fundamental niche; whereas a bird’s specific selection of, say, breeding habitat, is more likely to provide an expression of its realized niche. In this paradigm, habitat selection has become understood to be a hierarchical and scale-dependent process (Hilden 1965, Johnson 1980, Cody 1985, Hutto 1985). Each level in the hierarchy represents the suite of possible options, and each selection limits subsequent suites of options available at finer levels. Within the distribution of a given habitat type (such as shrubsteppe, where the broad selection of the habitat itself is implicit in definition of shrubsteppe-dependent) lie the physical dimensions that define the scales in the hierarchy of choice: regional, landscape, and local scale. Whereas habitat selection can be considered a continuous process (e.g., Rotenberry and Wiens 1998), here I am only examining selection of breeding habitat.

Embedded within the physically scaled hierarchy of options are the elements of choice defined by a species life history: breeding territory, foraging patches, and nesting area. These behaviorally defined elements are the most frequent scales on which choice is measured, but interpretation of the results (typically patterns of distribution) depends heavily upon the assumed heuristic model of selection (Van Horne 1983, Jones 2001), the scale of measurement (Wiens 1989, Knick et al. 2003), the history of the area (Knick and Rotenberry 2000), and the history of the individual (Wiens et al. 1986). There are also questions about the ability of habitat selection (occupancy) models to resolve important differences in habitat quality. This difficulty is largely due to the challenge of modeling inherently highly variable survivorship and productivity parameters. Further, if habitats are not saturated (Wiens 1977, 1993, Wiens et al. 1985b, 1986,), then attempts to assess habitat quality using abundance or occupancy as a surrogate measure will be frustrated (e.g., Van Horne 1983).

The process of habitat selection is constrained from the often assumed, but rarely tested (Jones 2001), Ideal Free Distribution (Fretwell and Lucas 1969) by many factors: territorial behaviors (leading to Ideal Despotic Distribution), imperfect assessment of quality, limiting search costs, patchy distribution of habitat elements or quality within searched areas, the prior experience of the individual, and the availability and use of proximate cues to habitat quality ("public information," e.g., conspecific attraction). Habitat selection is based on a set of cues that signify habitat suitability (Cody 1985). Suitability is defined through a series of continuous, threshold, or combination models that may not pan out for the individual since environmental variability also constrains success. For example, "marginal" habitat may be expressed as a function of time, e.g., becoming "unsuitable" in a dry year, rather than as a continuous or discrete spatial aspect.

Thus, environmental variability that falls outside the range of “normal” change in the habitats may be termed “disturbance” (Picket et al. 1989).

Even species whose successful habitat preferences evolved in dynamic landscapes can be maladapted to disturbance regimes when these regimes fall outside range of “normal” variation, where “normal” can be defined by the historical range (e.g., Baker 2006), the range of spatial heterogeneity (e.g., Knopf et al. 1990), or the set of theoretical conditions that promote continuity if not necessarily constancy (Picket et al. 1994) and change more rapidly than the species can track (e.g., Donovan and Lamberson 2001). Maladaption may be subtly and inconsistently expressed through habitat selection strategies (e.g., random, philopatric, quality, presence, or success; Doligez et al. 2003). In simulations, not all strategies are equal and success depends on the degree of consistency of the change itself (Doligez et al. 2003).

The assessment of the effects of habitat change has been the focus of several studies of shrubsteppe bird-habitat associations (Wiens and Rotenberry 1985, Wiens et al. 1986), and throughout these studies the scale of habitat selection assessment has been critical to the interpretation of the results (Wiens et al. 1987a, 1987b). Different scales of investigation can often give different answers, and comparisons that assume equivalence can lead to confusion. In addition, locally selected elements of habitat do not always aggregate well into regional models of selection. Similar to patterns of community diversity, habitat elements important at fine scales may be swamped by landscape and regional influences (D'Antonio 2000). This sensitivity to scale has led to calls for hierarchically integrated approaches to be used in determining the appropriate physical and ecological scales for habitat assessment (Knick et al. 2003).

In this work, I recognize that bird-habitat associations are dynamic and scale dependent, and that the interpretation of observed patterns is filtered through model assumptions. Effective assessment in dynamic systems requires robust estimates of the range of natural and anthropogenic variability across the landscape. With these elements in mind, I designed my research to assess: (1) how habitat loss and fragmentation influence productivity, density of breeding adults, size of home range, and the probability of parasitism and/or predation (Knick et al. 2003); (2) how counts of singing males relate to productivity and survivorship across landscapes (Knick et al. 2003); and (3), how productivity and survivorship themselves vary across landscapes. This last element will provide an estimate of spatially defined fitness (e.g., source/sink dynamics), and potentially insight into the mechanisms of population trend (Knick et al. 2003).

STUDY OBJECTIVES

My work consists of three primary research objectives:

1. To describe the effects of sagebrush steppe restoration treatments on non-target passerine bird species landscape occupancy and abundance;
2. To describe the effects of sagebrush steppe restoration treatments on the nesting habitat preferences and nesting habitat quality of four sagebrush-steppe passerines; and

3. To describe the fine scales habitat characteristics of used vs. available nesting habitat, and to examine the relationship of these to the nest success of four sagebrush-steppe birds.

The first objective assesses the effects of vegetation restoration treatments, intended to increase forage production and greater sage-grouse brooding habitat, on the persistence and abundance of shrubsteppe-associated passerine bird species. The treatments are hundreds to thousands of hectares in size, and occur in stages, with each stage treating one-to-many pastures in various allotments. Typical prescriptions call for approximately 75% treatment by area, utilizing a pasture aerator to retain a substantial shrub component in treated areas, as well as the existing understory plants. By measuring the relative change over time in bird abundance and occupancy in a case-control and Before-After-Control-Impact design framework (Underwood 1994, Stewart-Oaten and Bence 2001), I will describe and model the pattern of impact and recovery on nine shrubsteppe-associated birds: three sagebrush-steppe obligate, three steppe-associated, and three non-sagebrush-steppe associated. This allows me to examine the utility of the “umbrella species” concept at this scale via the consistency of responses of each grouping.

My second objective is to describe, and model, the scale-specific effects of treatments on the nesting habitat preferences and nesting habitat quality of four sagebrush-steppe birds: three sagebrush-steppe “obligates” and one steppe-associated species. Examining the rate at which affected nesting habitat is preferentially selected, relative to its demonstrated quality, allows for a critical examination of the potential for creating “sink” habitat. By further incorporating explicit representations of scale into these models, I will be able to explore the relationship between treatment and habitat quality at landscape, territory, and nest-site scales.

My third objective is to describe the fine-scale habitat variables preferentially selected by four sagebrush-steppe birds in a used vs. available approach, and then to model the relationship of these fine-grained variables to individual nest success. This is necessarily a spatially and temporally discrete research target focused on specific treated areas, and as such it will require a consistent application of relatively fine-grained effort at large extents.

A collateral benefit will be a full and scaled description of the variables important to the creation and maintenance of patterns in the distribution, abundance, and demography of shrubsteppe passerine birds. With these, I can better judge which patterns of change and scales are most important and amenable to monitoring.

Satisfying the need for an effective and efficient means of monitoring and assessing change in shrubsteppe bird assemblages is a tacit research objective. The broad ecological context model derived from the first objective, taken in combination with the spatial examination of nesting habitat and quality from the second, and the fine-grained assessment of nesting habitat description from the third, provides a unique research setting in which to test of a set of shrubsteppe bird monitoring methods. By comparing their relative efficiencies across scales, and their abilities to resolve important qualities of the diverse underlying patterns, I will have a means of eventually assessing the suitability and efficacy of each method, singly and in combination, and across spatial scales, for common monitoring goals.

LITERATURE CITED

Adams, A. A. Y., S. K. Skagen, and J. A. Savidge. 2007. Population-specific demographic estimates provide insights into declines of lark buntings (*Calamospiza melanocorys*). Auk **124**:578-593.

Allen-Diaz, B. and J. W. Bartolome. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. Ecological Applications **8**:795-804.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin **34**:177-185.

Beetle, A. A. 1960. A study of sagebrush - the section *Tridentata* of *Artemesia*. Wyoming Agricultural Experiment Station, Laramie, Wyoming, USA.

BLM. 1991. Final environmental impact statement: vegetation treatment on BLM lands in thirteen western states. USDI Bureau of Land Management, Wyoming State Office, Cheyenne, Wyoming, USA.

BLM. 2007. Vegetation treatments using herbicides on Bureau of Land Management lands in 17 western states programmatic EIS (PEIS). USDI Bureau of Land Management, Washington, D.C., USA.

Bock, C. E. and J. H. Bock. 1999. Response of winter birds to drought and short-duration grazing in southeastern Arizona. Conservation Biology **13**:1117-1123.

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin **88**:165–171.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. Journal of Applied Ecology **40**:601-614.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. Rangeland Ecology & Management **59**:225-236.

Brooks, M.L., and D.A. Pyke. 2001. Invasive plants and fire in the deserts of North America. Pages 1–14 *in* K.E.M. Galley and T.P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, Florida, USA.

Cody, M. L., editor. 1985. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin **28**:967-985.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Synthesis paper - ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management **57**:2-19.

D'Antonio, C. M. 2000. Fire, plant invasions, and global changes. Pages 65-93 *in* H. A. Mooney and R. J. Hobbs, editors. Invasive species in a changing world. Island Press, Washington, D.C., USA.

Dobkin, D. S. and J. D. Sauder. 2004. Shrubsteppe landscapes in jeopardy. Distributions, abundances, and the uncertain future of birds and small mammals in the Intermountain West. High Desert Ecological Research Institute, Bend, Oregon, USA.

Dobler, F. C., J. Eby, C. Perry, S. Richardson, and W. M. Vander Haegen. 1996. Status of Washington's shrub-steppe ecosystem: extent, ownership, and wildlife/vegetation relationships. Washington Department of Fish and Wildlife, Wildlife Management Program, Olympia, Washington, USA.

Doligez, B., C. Cadet, E. Danchin, and T. Boulinier. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Animal Behaviour **66**:973-988.

Donovan, T. M. and R. H. Lamberson. 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. Ecology **82**:1170-1179.

Fretwell, S. D. and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica **19**:16-36.

Hardin, G. 1960. The competitive exclusion principle. Science **131**:1292-1297.

Hilden, O. 1965. Habitat selection in birds. Annales Zoologici Fennici **2**:53-75.

Hutchinson, G. E. 1957. Concluding remarks. Population studies: animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology **22**:415-427.

Hutto, R. L. 1985. Habitat selection by nonbreeding migratory landbirds. Pages 455-476 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, New York, New York, USA.

Johnson, D. H. 1980. The comparison of useage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk **118**:557-562.

Jones, S. L. and J. E. Cornely. 2002. Vesper sparrow (*Pooecetes gramineus*). The birds of North America online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA.

Karl, J. W., P. J. Heglund, E. O. Garton, J. M. Scott, N. M. Wright, and R. L. Hutto. 2000. Sensitivity of species habitat-relationship model performance to factors of scale. Ecological Applications **10**:1690-1705.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor **105**:611-634.

Knick, S. T. and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. Conservation Biology **9**:1059-1071.

Knick, S. T. and J. T. Rotenberry. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (USA). Landscape Ecology **12**:287-297.

Knick, S. T. and J. T. Rotenberry. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. Ecology **81**:220-227.

Knopf, F. L., J. A. Sedgwick, and D. B. Inkley. 1990. Regional correspondence among shrubsteppe bird habitats. Condor **92**:45-53.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends In Ecology & Evolution **15**:134-135.

Laycock, W. A. 2003. Lessons from the past: have we learned from our mistakes? Arid Land Research and Management **17**:359-367.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forest. Ecology **39**:599-619.

Marcot, B. G., M. A. Castellano, J. A. Christy, L. K. Croft, J. F. Lehmkuhl, R. H. Naney, R. E. Rosentreter, R. E. Sandquist, and E. Zieroth. 1997. Terrestrial ecology assessment. U S Forest Service General Technical Report PNW **405**:1497-1713.

Martin, J. W. and B. A. Carlson. 1998. Sage sparrow (*Amphispiza belli*). The birds of North America online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA.

Miller, R. F. and L. E. Eddleman. 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Oregon State University, Oregon Agricultural Experiment Station Technical Bulletin **151**.

Noss, R. F. and R. L. Peters. 1995. Endangered ecosystems. a status report on America's vanishing habitat and wildlife. Defenders of Wildlife, Washington, D.C., USA.

NRCS. 2001. Component potential ecosystem conversion guidelines and diagnostics. USDA Natural Resources Conservation Service Rule 7 CFR Part 636.

Olson, R. A. and T. D. Whitson. 1996. Improving wildlife habitat quality on sagebrush rangelands with Spike 20P herbicide. Down to Earth **51**:7.

Olson, R. A. and T. D. Whitson. 2002. Restoring structure in late-successional sagebrush communities by thinning with Tebuthiuron. Restoration Ecology **10**:146-155.

Petersen, K. L. and L. B. Best. 1985. Brewer's sparrow nest-site characteristics in a sagebrush community. Journal of Field Ornithology **56**:23-27.

Picket, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos **54**:129-136.

Picket, S. T. A., J. Kolsa, and C. G. Jones. 1994. Ecological Understandings. Academic Press, San Diego, California, USA.

Rambo, J. L. and S. H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology **13**:1047-1054.

Reed, J. M. 1986. Vegetation structure and vesper sparrow territory location. Wilson Bulletin **98**:144-147.

Reynolds, T. D., T. D. Rich, and D. A. Stephens. 1999. Sage thrasher (*Oreoscoptes montanus*). The birds of North America online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA.

Rotenberry, J. T. and J. A. Wiens. 1998. Foraging patch selection by shrubsteppe sparrows. Ecology **79**:1160-1173.

Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation **129**:323-335.

Sauer, J. R., J. E. Hines, and J. Fallon. 2007. The North American breeding bird survey, results and analysis 1966 - 2006. USGS, Laurel, Maryland, USA.

Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: do they capture the full range of America's biological diversity? Ecological Applications **11**:999-1007.

Stewart-Oaten, A. and J. R. Bence. 2001. Temporal and spatial variation in environmental impact assessment. Ecological Monographs **71**:305-339.

Stewart, G. and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum*) - an ecologic intruder in southern Idaho. Ecology **30**:58-74.

Underwood, A. J. 1994. On beyond BACI - sampling designs that might reliably detect environmental disturbances. Ecological Applications **4**:3-15.

Vale, T. R. 1974. Sagebrush conversion projects: an element of contemporary environmental change in the western United States. Biological Conservation **6**:274-284.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893-901.

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, USA. Conservation Biology **14**:1145-1160.

Vander Haegen, W. M., M. A. Schroeder, and R. M. DeGraaf. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor **104**:496-506.

Weiss, J. M. and S. R. Reice. 2005. The aggregation of impacts: using species-specific effects to infer community-level disturbances. Ecological Applications **15**:599-617.

Welch, B. L. and E. D. McArthur. 1979. Feasibility of improving big sagebrush (Artemisia tridentata) for use on mule deer winter ranges *in* J. R. Goodlin and D. K. Northington, editors. Arid land plant resources Vol. 1. International Center for Arid and Semi-Arid Land Studies, Texas Tech University, Lubbock, Texas, USA.

Weltz, M. A. and G. Dunn. 2003. Ecological sustainability of rangelands. Arid Land Research And Management **17**:369-388.

West, N. E., editor. 1983. Western intermountain sagebrush steppe. Elsevier, Amsterdam.

West, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pages 15-26 *in* Entwhistle, P. G., A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof, compilers. Proceedings: sagebrush steppe ecosystems symposium. Bureau of Land Management Publication No. BLM/ID/PT-001001+1150, Boise, Idaho, USA.

West, N. E. and J. A. Young, editors. 2000. Vegetation of intermountain valleys and lower mountain slopes. 2nd edition. Cambridge Univ. Press, New York, NewYork, USA.

Wiens, J. A. 1977. On competition in variable environments. American Scientist **65**: 590-597.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

Wiens, J. A. 1993. Fat times, lean times and competition among predators. Trends In Ecology & Evolution **8**:348-349.

Wiens, J. A. 1995. Habitat fragmentation - island vs landscape perspectives on bird conservation. Ibis **137**:S97-S104.

Wiens, J. A. 1999. Landscape ecology: the science and the action. Landscape Ecology **14**:103-103.

Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985a. Boundary dynamics - a conceptual framework for studying landscape ecosystems. Oikos **45**:421-427.

Wiens, J. A. and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North-American shrub-steppe locality. Journal of Applied Ecology **22**:655-668.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1985b. Territory size variations in shrubsteppe birds. Auk **102**:500-505.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments - shrubsteppe birds and habitat alteration. Ecology **67**:365-376.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987a. Habitat occupancy patterns of North-American shrubsteppe birds - the effects of spatial scale. Oikos **48**:132-147.

Wiens, J. A., B. Van Horne, and J. T. Rotenberry. 1987b. Temporal and spatial variations in the behavior of shrubsteppe birds. Oecologia **73**:60-70.

Wu, J. G. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology **19**:125-138.

Young, J. A. and F. L. Allen. 1997. Cheatgrass and range science: 1930-1950. Journal of Range Management **50**:530-535.

Young, J. A. and B. A. Sparks. 2002. Cattle in the cold desert. University of Nevada Press, Reno, Nevada, USA.

CHAPTER 2

DISTURBANCE AS RESTORATION IN SAGEBRUSH-STEPPE: EFFECTS ON EXTIRPATION AND ABUNDANCE OF NON-TARGET BIRD SPECIES

INTRODUCTION

Anthropogenic disturbance is considered both a tool for restoration and an agent of habitat fragmentation, degradation and loss. Restoration frequently targets a limited number of species, yet disturbance-as-restoration for these species may equate to habitat degradation or loss for others. For example, studies by Rich (2002) and Rowland (2006) suggest that greater sage-grouse (*Centrocercus urophasianus*) serves as a good umbrella for sagebrush-steppe species, given overlapping distributions at regional scales, yet this idea has not been tested empirically at landscape-to-local scales. Consideration of the role of anthropogenic disturbance on non-target species is critical as we move toward a more holistic and ecologically sound approach to restoration.

Current sagebrush-steppe restoration approaches using mechanical vegetation treatments differ from past practices in several ways. First, they are not the large, uniform, systemic conversions that have earned considerable negative attention for over 30 years (Braun et al. 1976, Knick et al. 2003). They seek to avoid conversions that facilitate invasive weeds or lead to seeded monocultures, and generally embrace a more ecologically dynamic view of succession (Briske et al. 2006). Treatments are believed to improve the health and integrity of the sagebrush-steppe ecosystem for all sagebrush-steppe species, increasing resistance and resilience to disturbance and invasion by creating a diversity of ages of shrub patches (McAdoo et al. 2004). Prescriptions frequently call for the application of disturbance at endemically-scaled durations, intensities, and scopes (White and Walker 1997, Hemstrom et al. 2002, BLM 2005, Baker 2006). While there is agreement that disturbance-mediated processes are important to the long-term maintenance of sagebrush-steppe habitats for many species (Sousa 1984, Brawn et al. 2001) the appropriate extents, grains, types, and intensities leading to comprehensive conservation are not clear. The ultimate success of this approach to restoration relies on the validity and utility of the umbrella species concept (Lambeck 1997, Rowland et al. 2006), where the inferred ecological niche of one-to-several species is used as the goal of restoration. Given all of these considerations, while current restoration approaches are vastly improved, they do not necessarily equate to treatments that promote sagebrush-steppe bird community stability, integrity, or individual species population growth.

The idea that sagebrush-steppe obligate bird species have a consistent and uniform response to disturbance is central to the utility of the umbrella species approach at landscape-to-local scales. Prior work is equivocal, however. Some studies indicate shrub-associated and steppe-associated species groupings show similar reactions to treatment (Knopf et al. 1990, Knick and Rotenberry 1997, Rich et al. 2002) while others imply species-specific responses to restoration are more likely given the delayed effects seen in studies of other treatment types (e.g., fire, chemical; Best 1972, Wiens and Rotenberry 1985, Wiens et al. 1986, Petersen and Best 1987, Howe et al. 1996). These delayed effects have been described as lagged responses, with the magnitude of the response and lag's duration based on a combination of a species' minimum patch size tolerance, differing "grain" of habitat needs (or perception), and differing degrees of natal and site fidelity. If the umbrella species concept is useful in sagebrush-steppe habitat restoration at landscape-to-local scales, target and non-target species would react to treatments in neutral or positive ways.

In our work, we examined the effects of restoration on non-target species by investigating the landscape-level effects of mechanical restoration vegetation treatments (hereafter restoration) on the local extirpation probabilities and abundances of nine sagebrush-steppe passerines. We refer to these nine species as non-target species since restoration efforts in our area were designed to benefit target and umbrella species (e.g., greater sage-grouse, domestic livestock, and ungulates) with assumed collateral benefits to habitat quality for other species, including the nine we studied. We assumed local density of the birds was a reliable surrogate measure of local habitat quality, and explored the effects of restoration treatments on bird species presence and densities using a case-control approach applied at a landscape scale.

In two study sites in Rich County, Utah, USA, we followed current restoration protocols for sagebrush-steppe designed to reduce shrub cover by 80% in 40-60% of a treated area. Our design sought evidence to support or refute the existence of treatment effects at what we felt were meaningful ecological scales: assessing local (10's of ha) treatment effects using large (grain) samplers intensively deployed across a landscape-scale (1000's of ha) context. Bird responses were then compared to untreated reference sites located throughout the county. Drawing on the species-specific literatures, we expected treatment effects to: 1) be large; 2) be negative for shrub-associated species and positive for steppe-associated species; 3) propagate beyond the treatment "footprint" itself; and 4) be expressed at species-specific lags from treatment dates. We also expected these effects to be grossly expressed at a community level through local extirpation of area-sensitive sagebrush-steppe-obligate species as a group, and more subtly as effects on densities of individual species.

METHODS

Study area

We sampled bird abundance across all sagebrush-steppe areas of Rich County, Utah, USA (roughly 70% of the county, or 179,411 ha), and in two intensive study areas, Duck Creek Allotment (hereafter DC) and Deseret Land and Livestock (DL) (Fig. 1). Experimental treatments to reduce shrub cover occurred in the DC and DL study sites. All bird sampling was done during the 2004-2006 breeding seasons.

Rich County is located at the intersection of the Wyoming Plateau, Great Basin, and Columbia Plateau ecoregions (Omernick 1987, Bailey et al. 1994). The shrubsteppe vegetation in the county consists principally of big sagebrush (*Artemisia tridentata*, subspecies *tridentata*, *vaseana*, and *wyomingensis*). A variety of other shrub species can be locally important, including rubber rabbitbrush (*Ericameria nauseosa*), green rabbitbrush (*Chrysothamnus viscidiflorus*), Utah serviceberry (*Amelanchier utahensis*), antelope bitterbrush (*Purshia tridentata*), and the "low" sagebrushes (*A. arbuscula, A.*

nova). Study area elevation ranges from 1806 m to 2820 m (mean 2131 m). Climate is typical of western North American high-cold desert in terms of temperature (annual mean 13.0 ºC, mean annual range -16.6–28.8 ºC, 17 year average) and moisture (20–35 cm annually); the majority of annual moisture falls from October to December in the form of snow, and from April to May in the form of brief but intense rainstorms (Western Regional Climate Center 2007).

Study design and field methods

Our approach was embedded in a common tessellated sampling design (Stevens 1997, Nusser et al. 2004). We used a random start to anchor the systematic tessellated grid across all shrubsteppe areas in Rich County, and used grid panel center points (hereafter grid points) to establish sample locations. Four grid panels were used (P1: 10 000 m, P2: 5000 m, P3: 2500 m, and P4: 1250 m) to define sample point spacing intervals. Using the point as the origin (usually the SW corner), 2400-m long line transects were surveyed in four 600-m legs along cardinal bearings (i.e., describing a square: north, then east, south, then finishing to the west). Perpendicular distances for all birds seen or heard to the transect line were measured using laser rangefinders, pacing, and GPS. Surveys were conducted by trained observers during appropriate weather conditions in the breeding season (May to June), and restricted from 0.5 hr after dawn and before 1000 hr in order to maximize data quality (Ralph et al. 1993, Buckland et al. 2001). If a transect had >30% non-shrubsteppe vegetative cover (e.g., due to a misclassified image, or subsequent conversion to crops or housing), then the orientation was pivoted clockwise on the grid point and attempted again. If none of the four possible rotations met minimum coverage qualifications, then the sample point was discarded (~ 23% discarded across all panels and years). Samples in 2004 were based on a limited random sample of all possible P3 points; in 2005 and 2006 we sampled all P2 points countywide in random order, and all P4 points within 2.5 km of the restoration treatments.

Mechanical restoration treatments using a Lawson pasture aerator were applied in a case-control design at the DC site (9221 ha total, 8930 ha of shrubsteppe), while experimental treatments were applied in a BACI design (Underwood 1991) at DLL (53 987 ha total, 43 151 ha of shrubsteppe). Each of these two intensive study areas contained defined pastures grazed by domestic livestock. Our experimental treatments mimicked current mechanical restoration treatments applied to sagebrush-steppe, using a 60% prescription (by area) actual aerator footprint within "treated" pastures, with the remaining 40% of sagebrush-steppe vegetation left as islands and peninsulas. Untreatable areas (e.g., steep slopes) identified in the course of treatment were subtracted from treatment areas.

To control for annual differences in bird population responses to treatments, and to account for annual variations in vegetation response to treatments, experimental treatments were staggered across study years. Two pastures were treated in 2003 (i.e., no pre-treatment data and three years post-treatment), one in 2005 (i.e., one year pre-treatment and two years post-treatment), and one in 2006 (two years pre-treatment and one year post-treatment). Line transects associated with treatments were defined as those with >20% of transect treated, and were coded by the number of breeding seasons since treatment (Table 2.1). Reference samples were drawn from all untreated sagebrush-steppe areas of the county, and from untreated areas within the DC and DL intensive study areas.

Not all passerine birds observed in sagebrush-steppe habitats are obligates. We excluded from analysis *a priori* all species that were not directly using the habitat (e.g., birds flying overhead), and species whose habitat use was not consistent with local breeding. We excluded *a posteriori* those species for which reliable density estimates could not be made with these data. Excluded species comprised <8% of all observations. Following Braun et al. (1976) and Knick et al. (2003), we categorized the remaining nine species into three groups: Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*), and sage thrasher (*Oreoscoptes montanus*) as "sagebrush-steppe-obligate" species; vesper sparrow (*Pooecetes gramineus*), green-tailed towhee (*Pipilo chlorurus*), and horned lark (*Eremophila alpestris*) as "sagebrush-steppe associated"; and gray flycatcher (*Empidonax wrightii*), mourning dove (*Zenaida macroura*), and western meadowlark (*Sturnella neglecta*) to be "non-sagebrush-steppe associated" species.

Statistical methods

Estimates of abundance per line transect were modeled for all nine species. These were used in all subsequent comparisons of individual species and assemblage responses to treatment and treatment age. Survey year and site were considered random effects. We used distance sampling (Buckland et al. 2001) to account for the native differences in detectability (p) by species, and for potential bias in detectability due to observer, survey weather, vegetation, and seasonality. These estimates were then evaluated in a two-stage conditional generalized linear mixed modeling framework (Cunningham and Lindenmayer 2005, Min and Agresti 2005).

Two central hypotheses were tested. In the first, a binomial data distribution model of species presence as a function of the number of breeding seasons since restoration was fit to the data, and to evaluate local extirpation effects due to restoration. In the second, a log-normal data distribution model was fit to the density data, where density > 0, to investigate treatment effects on species abundance. This two-stage approach addressed data distribution concerns by fitting generalized linear mixed models with appropriate data distribution models to the two datasets. All analyses were done using SAS 9.3.1 (SAS Institute Inc. 2007).

We used program Distance 5.0.2 (Thomas et al. 2005) to find the best approximating model (Buckland et al. 1997) of detectability-corrected density, using model selection approaches described in Burnham and Anderson (2002). All density analyses were completed by species, as we assumed *a priori* there are differences in detectability by species, and that no interaction in detectability existed among the species. We recognize that distance sampling for estimating abundance precludes a community-wide analysis due to insufficient data for rare species, but feel the benefits of obtaining unbiased estimates of abundance for the dominant species – and hence facilitating fair comparisons between them – outweighs the limited analytic reach.

Estimates of density per transect were calculated for each species, and in each analysis the relative influences of several classes of potential covariates on detectability were examined and included in the density model if appropriate. Covariates considered in each analysis included: observer (ID), location (treatment, site), weather (temperature, wind, and sky codes), time (survey year, seasonality, and time of day), and observation type (audial only, visual only, both). Models of detectability were ranked and compared using ΔAIC_c (Akaike 1973). Models ≤ 2 AIC_c units greater than the best model were considered to be competing models, those that were < 2-4 AIC_c units were considered plausible models, and models > 4 AIC_c units were considered poor models and were excluded from further consideration. Results from competing models (e.g., where model uncertainty existed) were averaged.

RESULTS

Summary statistics: density estimation and local extirpation

Over 24,400 observations were used to model detectability and estimate density for the nine selected species. Detectability and density estimates were constructed for each line transect location in each year. The number of independent line transects classified as either reference or mechanically-treated surveyed in each year was: 24 in 2004, 205 in 2005, and 210 in 2006. Many of these locations were re-surveyed each year (162 were considered spatially independent line transect locations across all years, 33 of these were surveyed in two or more years). Not all species were observed in all years by restoration treatment combinations. The most commonly observed species were Brewer's and vesper sparrows, followed by sage thrasher (Table 2.1). All other species were observed in roughly 20% to 30% of the treatment transects. Density estimates were again highest for Brewer's sparrow, followed by vesper sparrow and horned lark (Table 2.2).

A total of seven spatially independent transects were surveyed both before and after treatment. No species was lost from any avian assemblage sampled by these seven transects. The total number of transects transitioning from present to absent, or absent to present, with increasing years since treatment (BYR) for each species are shown in Table 2.3. Species categorized as sage-steppe obligates appeared to increase occupancy with increasing BYR, those categorized as sagebrush-steppe associated species were mixed, as were the species considered steppe-associated.

Generalized linear modeling: extirpation model

For the analysis of occupancy, each sample was coded as present or absent for each of the nine selected species. The binomial data distribution model fit the data (-2 Log Likelihood = 1593, Pearson χ^2 = 1402, DF = 1374), and met methodological assumptions as assessed by convergence criterion, visual inspection of residual plots, and model stability. Survey year was eventually excluded from the analysis because of convergence issues in the density estimations and standard errors for two species, Brewer's and vesper sparrow.

Years since treatment (BYR in tables) had no apparent effect on local extirpation (P = 0.78), though important differences between species were obvious, reflecting different county-wide species distribution patterns unrelated to mechanical treatments (Table 2.4). The predicted interaction between treatment age and survey year was not supported (P =

0.99). No consistent differences in extirpation probability magnitudes or patterns between sagebrush-steppe-obligate, sagebrush-steppe-associate, and non-sagebrush-steppe-associate species were observed (Fig. 2.2a). While considerable annual variation occurred, there is no apparent trend or evidence of expected threshold behaviors observed in these data.

Generalized linear modeling: abundance model

Model fit of the log-normal abundance data was good (-2 Res Log Likelihood = 2080, Pearson χ^2 = 577, DF = 0.75). Seven outliers were removed (two Brewer's sparrows, one vesper sparrow, and four western meadowlarks) to ensure model assumptions as assessed by convergence criteria and residual analysis were met. Treatment age had a significant depressive effect on abundances ($\alpha = 0.05$, $P = 0.03$), though the effect size was small (Table 2.5). No obvious pattern of effects was seen by species groupings (sagebrush-steppe obligate status), nor were there important interactions between BYR and individual species: the expected lagged treatment effects were not seen (Fig. 2.2b). Most species abundances, regardless of sagebrush-steppe-obligate status, varied with treatment age, decreasing in the first year post-treatment and then staying depressed.

DISCUSSION

No species was locally extirpated by our treatments at the resolution and duration of our study, and the negative short-term impacts on abundance were less dramatic than expected. We predicted restoration treatments would negatively affect shrubsteppe-obligate bird extirpation and abundances generally, but sage sparrows and sage thrashers most severely (due to demonstrated patch size sensitivity) and Brewer's sparrows the least (Petersen and Best 1985, Rotenberry and Wiens 1998, Vander Haegen et al. 2000). Other shrub-specialists (but not sagebrush-specialists) that have not shown patch-size sensitivity (i.e., gray flycatcher and green-tailed towhees) were also expected to react negatively to restoration treatments, but in direct proportion to the loss of extent of nesting habitat. The steppe-associated study species (vesper sparrow, horned lark, western meadowlark, and mourning dove) were expected to increase proportionally to treatment extent, as there is no data to suggest an expected lag in colonization. Mechanical treatments of up to 40/60 percent treated/untreated prescription had no apparent effect on local persistence of birds in the shrubsteppe landscape through the first four years post-treatment, and their effects on passerine densities overall were limited to a small but significant depressive effect.

Specifically, the extirpation model showed no support for the hypothesis that treatment, or treatment age, accounted for significant variation in the observed pattern of local extirpation, yet large differences between patterns of species occurrence were observed. Our coarse filter measure of community integrity, extirpation probability, was not influenced by treatment age, and treatments had no discernable effect on community composition measured at extents from 50-450 ha (the area sampled by a single sampler up to the extent of the largest single treatment studied). Nor did this model support such effects on either "sagebrush-steppe-obligate" birds as a group, or upon the nine species we examined individually. Thus, no species was extirpated from treated areas.

Similar to the extirpation model, there was little evidence from the abundance model for the large, negative treatment effects we had expected. While treatment effects were in the expected direction and were statistically significant, the magnitude of the effects (approximately 9% decrease per year across all species) was more of a subtle deflection than a precipitous pitch. While abundance did change slightly for our species of study, like the extirpation model, species in shrubsteppe-obligate management categories did not track together.

Strengthening these conclusions is the landscape scale context in which these results were evaluated. Utilizing the entire extent of sagebrush-steppe vegetation in the county (approximately 179,411 ha) as our reference condition provided the most conservative ecological context in which to evaluate potential treatment effects. While it was also the most "noisy" statistical approach to defining a comparative standard, given the lack of observed treatment effects and the lack of important structure in the extirpation model residuals, there is no reason to imply that a large magnitude or extensive treatment effect was masked. Further, while the overall dataset was unbalanced in terms of design matrix cell totals, there was sufficient balance within cells to avoid gross prevalence issues (Fielding and Bell 1997).

Despite the lack of gross treatment effects, we saw little consistent response to treatment or treatment age at the extents and grains studied in either the extirpation or abundance models. This provides little evidence to support the utility of the "umbrella species" management paradigm (Rowland et al. 2006, Wiens et al. 2008) in terms of local-to-landscape effects on community composition in terms of extirpation or abundance in the first four years after mechanical treatment. It may be that the use of greater sage-grouse as an umbrella for these nine species is more effective at regional scales than at landscape or local scales (Wiens et al. 2008), and that applying them at a local grain across a single landscape is not equivalent to a regional correspondence analysis (Knopf et al. 1990, Rich et al. 2002). To date, the holistic management planning perspectives needed to incorporate the differences in species scales and are not widely applied beyond project scales, rarely to landscapes, and have not yet been applied at regional scales (e.g., Wisdom et al. 2005).

LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* Second International Symposium on Theory, Budapest, Hungary.

Bailey, R. G., P. E. Avers, T. King, and W. H. McNab, eds. 1994. Ecoregions and subregions of the United States, with supplementary table of map unit descriptions, compiled and edited by W. H. McNab and R. G. Bailey. Pages scale 1:7,500,000. USFS, Washington, D.C., USA.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin **34**:177-185.

Best, L. B. 1972. First year effects of sagebrush control on two sparrows. Journal of Wildlife Management **36**:534-544.

BLM. 2005. Draft programmatic environmental impact statement and environmental report for vegetation treatments on public lands administered by the Bureau of Land Management in the western United States, including Alaska. Pages 496. USDI Bureau of Land Management, Washington, D.C., USA.

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin **88**:165–171.

Brawn, J. D., S. K. Robinson, and F. R. Thompson. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics **32**:251-276.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. Rangeland Ecology & Management **59**:225-236.

Buckland, S. T., D. R. Anderson, K. P. Burham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. 2nd edition. Oxford University Press, New York, New York, USA.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics **53**:603-618.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.

Cunningham, R. B. and D. B. Lindenmayer. 2005. Modeling count data of rare species: some statistical issues. Ecology **86**:1135-1142.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, USA. Conservation Biology **16**:1243-1255.

Howe, F. P., R. L. Knight, L. C. McEwen, and T. L. George. 1996. Direct and indirect effects of insecticide applications on growth and survival of nestling passerines. Ecological Applications **6**:1314-1324.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor **105**:611-634.

Knick, S. T. and J. T. Rotenberry. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (USA). Landscape Ecology **12**:287-297.

Knopf, F. L., J. A. Sedgwick, and D. B. Inkley. 1990. Regional correspondence among shrubsteppe bird habitats. Condor **92**:45-53.

Lambeck, R. J. 1997. Focal species: A multi-species umbrella for nature conservation. Conservation Biology **11**:849-856.

McAdoo, J. K., S. R. Swanson, B. W. Schultz, and P. F. Brussard. 2004. Vegetation management for sagebrush-associated wildlife species Pages 189-193 *in*: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, Wyoming. Proceedings RMRS-P-31. Ogden, Utah, USA: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, USA.

Min, Y. Y. and A. Agresti. 2005. Random effect models for repeated measures of zero-inflated count data. Statistical Modelling **5**:1-19.

Nusser, S. M., W. R. Clark, J. Y. Wang, and T. R. Bogenschutz. 2004. Combining data from state and national monitoring surveys to assess large-scale impacts of agricultural policy. Journal of Agricultural Biological and Environmental Statistics **9**:381-397.

Omernick, J. M. 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). Annals of the Association of American Geographers.

Petersen, K. L. and L. B. Best. 1985. Brewer's sparrow nest-site characteristics in a sagebrush community. Journal of Field Ornithology **56**:23-27.

Petersen, K. L. and L. B. Best. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. Wildlife Society Bulletin **15**:317-329.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Rich, T. D., M. J. Wisdom, and V. A. Saab. 2002. Conservation of priority birds in sagebrush ecosystems. Page 589-606 *in* Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191. 2005, Asilomar, California, USA.

Rotenberry, J. T. and J. A. Wiens. 1998. Foraging patch selection by shrubsteppe sparrows. Ecology **79**:1160-1173.

Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation **129**:323-335.

SAS Institute Inc. 2007. SAS/STAT Software. Version 9.1.3. SAS Institute Inc., Cary, North Carolina, USA.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353-391.

Stevens, D. L. 1997. Variable density grid-based sampling designs for continuous spatial populations. Environmetrics **8**:167-195.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and

Marques, T.A. 2005. Distance 5.0, release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, UK.

Underwood, A. J. 1991. Beyond BACI - experimental designs for detecting human environmental impacts on temporal variations in natural populations. Australian Journal of Marine And Freshwater Research **42**:569-587.

USGS. 2003. U.S. Geological Survey. 2003. SAGEMAP: a GIS database for Sage Grouse and shrubsteppe management in the Intermountain West. <http://SAGEMAP.wr.usgs.gov> (21 July 2003).

Vander Haegen, W. M., F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, USA. Conservation Biology **14**:1145-1160.

Western Regional Climate Center. 2007. Western U.S. climate historical summaries, climatological data summaries. Western Regional Climate Center, Reno Nevada, USA.

White, P. S. and J. L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology **5**:338-349.

Wiens, J. A., G. D. Hayward, R. S. Holthausen, and M. J. Wisdom. 2008. Using surrogate species and groups for conservation planning and management. Bioscience **58**:241-252.

Wiens, J. A. and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North-American shrub-steppe locality. Journal of Applied Ecology **22**:655-668.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments - shrubsteppe birds and habitat alteration. Ecology **67**:365-376.

Wisdom, M. J., M. M. Rowland, M. A. Hemstrom, and B. C. Wales. 2005. Landscape restoration for greater sage-grouse: implications for multiscale planning and monitoring. U.S. Forest Service Rocky Mountain Research Station Proceedings RMRS-P **38**:62-69.

Table 2.1. Frequency of occurrence and line transect sample sizes. Number of spatially independent line transects (proportion) at which each species[1] occurred by the number of breeding seasons since restoration treatment (BYR) , Rich County, Utah, USA. Total number of transects sampled in each BYR category are shown in parentheses.

		Number of breeding seasons since treatment				
Species	Reference (45)	T+1 (15)	T+2 (44)	T+3 (37)	T+4 (11)	Total
BRES	43 (0.96)	15 (1.00)	42 (0.95)	46 (0.98)	11 (1.00)	157 (0.97)
GRYF	21 (0.47)	5 (0.33)	22 (0.5)	16 (0.34)	3 (0.27)	67 (0.41)
GTTO	13 (0.29)	5 (0.33)	18 (0.41)	18 (0.38)	4 (0.36)	58 (0.36)
HOLA	25 (0.56)	10 (0.67)	25 (0.57)	28 (0.6)	7 (0.64)	96 (0.59)
MODO	11 (0.24)	4 (0.27)	14 (0.32)	13 (0.28)	3 (0.27)	45 (0.28)
SAGS	14 (0.31)	5 (0.33)	15 (0.34)	15 (0.32)	3 (0.27)	52 (0.32)
SATH	26 (0.58)	13 (0.87)	33 (0.75)	39 (0.83)	8 (0.73)	110 (0.68)
VESP	41 (0.91)	13 (0.87)	42 (0.95)	47 (1.00)	10 (0.91)	154 (0.95)
WEME	16 (0.36)	7 (0.47)	17 (0.39)	23 (0.49)	5 (0.45)	68 (0.42)

[1] Species codes are as follows: Brewer's Sparrow (BRES), Gray Flycatcher (GRYF), Green-tailed Towhee (GTTO), Horned Lark (HOLA), Mourning Dove (MODO), Sage Sparrow (SAGS), Sage Thrasher (SATH), Vesper Sparrow (VESP), and Western Meadowlark (WEME).

Table 2.2. Mean estimated bird densities. Densities (birds/ha) and SE for nine species by number of breeding seasons since restoration treatment (BYR) are shown for reference sites and treatments of four ages; note that cell means do not include 0's from locales where a given species did not occur. Species abbreviations used are given in Table 2.1.

Species	Reference	T+1	T+2	T+3	T+4
BRES	1.46 (0.102)	1.82 (0.274)	1.68 (0.183)	1.70 (0.136)	1.56 (0.209)
GRYF	0.09 (0.020)	0.06 (0.026)	0.07 (0.016)	0.08 (0.024)	0.02 (0.012)
GTTO	0.07 (0.022)	0.07 (0.039)	0.07 (0.024)	0.07 (0.019)	0.05 (0.025)
HOLA	0.30 (0.086)	0.17 (0.053)	0.13 (0.031)	0.17 (0.033)	0.13 (0.041)
MODO	0.03 (0.012)	0.05 (0.037)	0.03 (0.008)	0.05 (0.021)	0.04 (0.026)
SAGS	0.06 (0.021)	0.05 (0.033)	0.04 (0.015)	0.04 (0.013)	0.02 (0.012)
SATH	0.09 (0.020)	0.08 (0.019)	0.08 (0.012)	0.08 (0.013)	0.06 (0.020)
VESP	0.62 (0.093)	0.61 (0.116)	0.49 (0.058)	0.47 (0.042)	0.43 (0.074)
WEME	0.03 (0.009)	0.04 (0.014)	0.02 (0.005)	0.03 (0.008)	0.02 (0.008)
Total	0.31 (0.029)	0.33 (0.059)	0.29 (0.033)	0.30 (0.030)	0.26 (0.054)

Table 2.3. Number of transects transitioning from present to absent by species. Only transects surveyed in 2 or more years (n = 33) that went from present to absent, or absent to present are shown. Species abbreviations used are given in Table 2.1.

	Species								
	BRES	GRYF	GTTO	HOLA	MODO	SAGS	SATH	VESP	WEME
P to A	1	9	12	2	8	5	5	1	9
A to P	2	9	6	13	6	8	10	2	11

Table 2.4. Generalized linear mixed model type III tests of fixed effects for the extirpation model (binary data distribution). Results are shown for treatment age (BYR), species (SPP), and their interaction; note that no important effects of treatment age (BYR) are seen on local (transect level) extirpation

Type III Effect	Num DF	Den DF	F Value	Pr > F
BYR	4	1431	0.43	0.7834
SPP	8	1431	7.79	<.0001
SPP*BYR	32	1431	0.38	0.9993

Table 2.5. Generalized linear mixed type III tests of effect sizes for the abundance model (log-normal data distribution). Results are shown for treatment age (BYR), species (SPP), and their interaction. Note that where species are present, there are significant ($\alpha = 0.05$) effects of treatment age are seen on local abundance of the nine species

Type III Effect	Num DF	Den DF	F Value	Pr > F
BYR	4	733	2.66	0.0315
SPP	8	760	141.70	<.0001
SPP*BYRp	32	760	0.70	0.8906

Figure 2.1. Maps of sagebrush steppe extent, study context, and sample locations. Lower right map shows (shaded) extent of sagebrush-steppe vegetation (USGS 2003) in western North America. The lower left map shows the (shaded) extent of shrubsteppe vegetation in Rich County (Lowry et al. 2005), known vegetation disturbances (irregular white polygons) including all treatments types and wildfire since 1981, and sampled locales (black squares) 2004:2006. The mapped extent of shrubsteppe areas includes areas formerly shrubsteppe but now converted to agriculture or housing. The upper map shows a portion of the Duck Creek study area with (shaded) shrubsteppe extent, experimental treatments (white polygons), and sampled locations. Note that line transects are drawn to scale. Sampling intensity in this region was at the 1250 m tessellation grid.

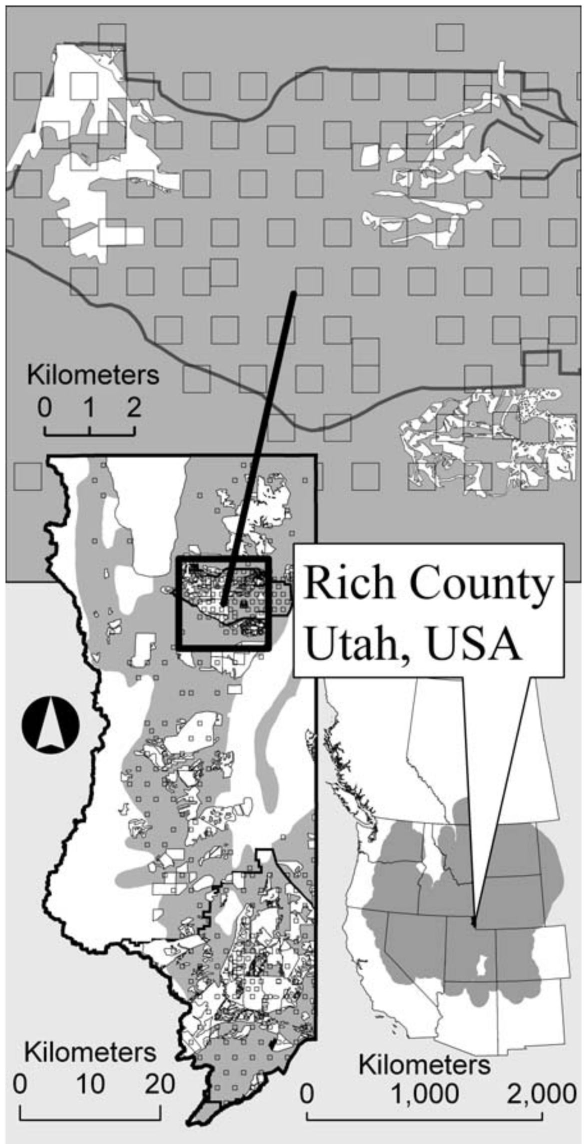

Kilometers
0 1 2
Rich County
Utah, USA
Kilometers
0 10 20
Kilometers
0 1,000 2,000

Figure 2.2 (a). Least square mean estimates plotted for species by treatment age effects for extirpation (presence/absence) analysis models. Due to model estimation and convergence issues when occupancy is close to 100% (i.e., BRES in T+1 and T+4, and VESP in T+3, see Table 2.1), no SE's are shown for the extirpation model. Species categorized as shrubsteppe obligates are indicated with circles and solid lines, shrubsteppe-associated with squares and short dashed lines, and non-shrubsteppe associated species with triangles and dotted lines (symbol fills are varied by species, symbols are offset slightly along the x-axis, and plot a has a break in the Y-axis to enhance figure clarity). While large differences between species can be seen in both plots, coherent patterns by shrubsteppe-obligate status are not seen, nor is there evidence of species-specific threshold responses to treatment age in the first four years after mechanical treatment (with the possible exception of GRYF, a shrub specialist though not unique to sage-steppe regions).

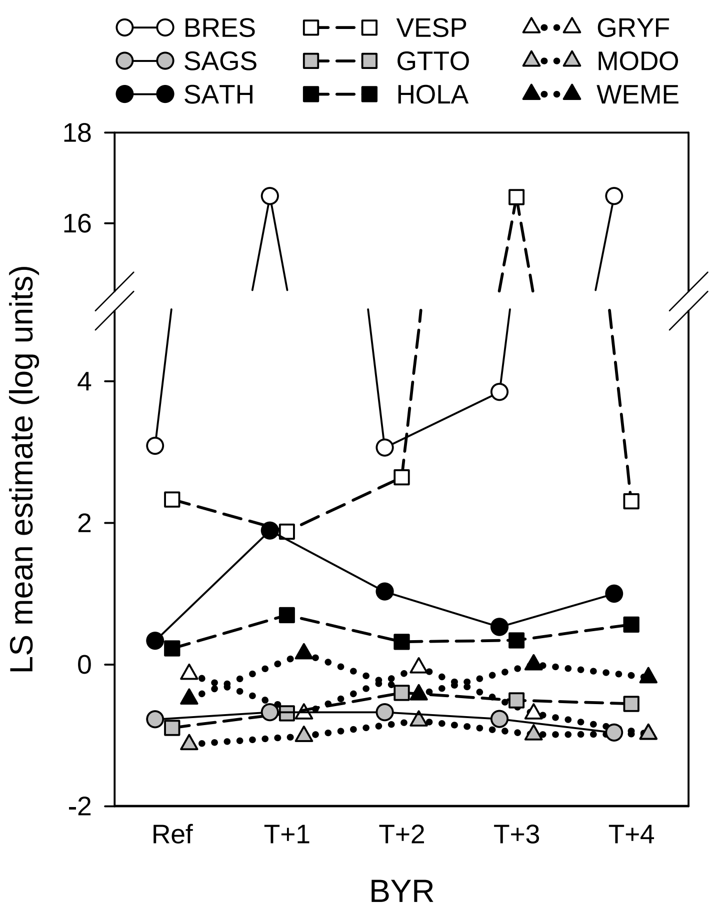
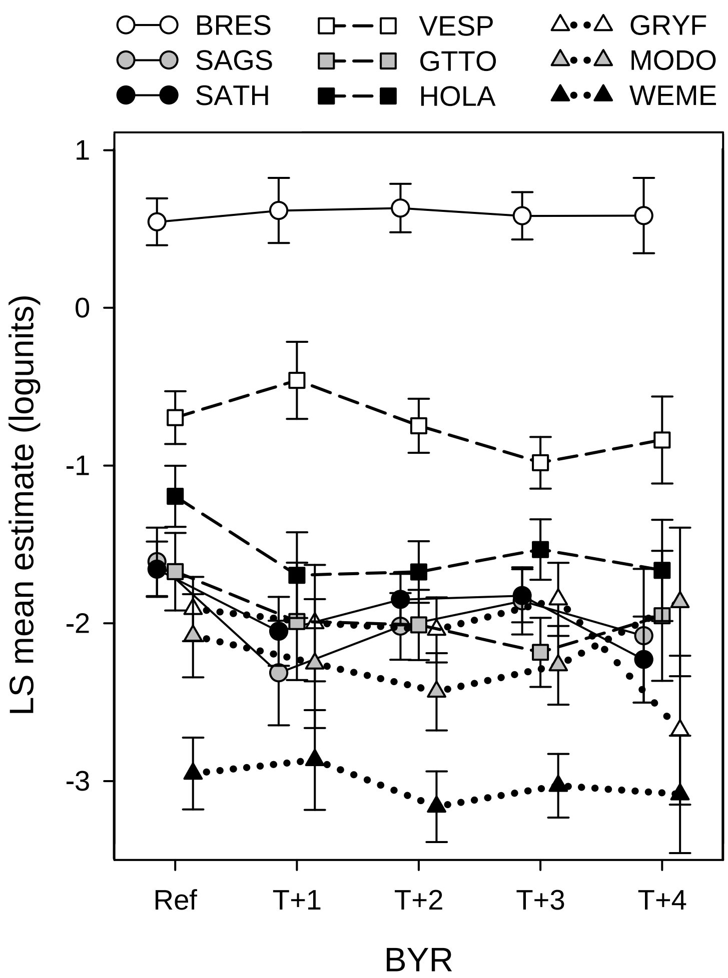

BRES
SAGS
SATH
VESP
GTTO
HOLA
GRYF
MODO
WEME
18
16
4
2
0
-2
LS mean estimate (log units)
Ref
T+1
T+2
T+3
T+4
BYR

Figure 2.2 (b). Least square mean estimates plotted for species by treatment age effects for abundance (present-only) models. Due to model estimation and convergence issues when occupancy is close to 100% (i.e., BRES in T+1 and T+4, and VESP in T+3, see Table 2.1), no SE's are shown for the extirpation model. Species categorized as shrubsteppe obligates are indicated with circles and solid lines, shrubsteppe-associated with squares and short dashed lines, and non-shrubsteppe associated species with triangles and dotted lines (symbol fills are varied by species, symbols are offset slightly along the x-axis, and plot a has a break in the Y-axis to enhance figure clarity). While large differences between species can be seen in both plots, coherent patterns by shrubsteppe-obligate status are not seen, nor is there evidence of species-specific threshold responses to treatment age in the first four years after mechanical treatment (with the possible exception of GRYF, a shrub specialist though not unique to sage-steppe regions).


BRES
SAGS
SATH
VESP
GTTO
HOLA
GRYF
MODO
WEME
1
0
-1
-2
-3
LS mean estimate (logunits)
Ref
T+1
T+2
T+3
T+4
BYR

CHAPTER 3

RESTORATION DIFFERENTIALLY AFFECTS NESTING HABITAT PREFERENCES AND HABITAT QUALITY FOR SHRUBSTEPPE-OBLIGATE BIRDS

INTRODUCTION

Understanding the relationship between habitat quality and habitat preference is critical to predicting and assessing impacts from both natural and anthropogenic disturbance. For many taxa, habitat quality is predicted to directly forecast habitat preference (Cody 1985, Pulliam 2000, Boulinier et al. 2001) with both personal knowledge (e.g., prior or direct experience) and public knowledge (e.g., prospective or indirect experience) of habitat quality used to make fitness-maximizing habitat selections (Arlt and Part 2007, Citta and Lindberg 2007). In a multi-species habitat restoration context, anthropogenic disturbance can be used to study the relationship between habitat preference and habitat quality by altering habitat quality and observing responses in expressed habitat preference. Doing so sheds light on whether restoration efforts are improving the overall quality of habitat for the set of species in the affected area, having no effect, or are creating an attractive nuisance. Where the relationship between habitat quality and habitat preference is inverted, lacking, or significantly delayed, selection of a given habitat may be maladaptive, leading to a population "sink" (Pulliam 1988, Misenhelter and Rotenberry 2000, Shochat et al. 2005, Arlt and Part 2007). Here we defined habitat preference as the degree to which restored habitat is selected for nesting, and habitat quality as the relative capacity of these areas to support successful reproduction (Hall et al. 1997, Jones 2001, Johnson 2007). We addressed the question: what effect does changing the availability of nesting habitat have on both the preference for, and quality of, an area at multiple spatial extents?

To answer this, we carried out a series of large (>250 ha) experimental reductions in sagebrush-steppe cover and measured the subsequent nesting responses of four bird species in terms of habitat preferences and habitat quality. We measured habitat preference (via nest density) and habitat quality (using daily nest survival rates) for four species: Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli nevadensis*), sage thrasher (*Oreoscoptes montanus*), and vesper sparrow (*Pooecetes gramineus*). The first three species, widely considered to be "sagebrush-steppe obligates" (Braun et al. 1976), were expected to react negatively to our experimental disturbance and exhibit decreases in nest density and daily survival rates. The fourth, a more general steppe-associated species, was expected to exploit the resulting expansion of nesting habitat and exhibit increases in nest density and daily survival rate.

Our research expectations were based on prior empirical work demonstrating that the relationship between habitat preference and habitat quality is more variable than predicted by theory. Nesting habitat preferences, nesting habitat quality, and the relationship between the two has been shown to vary primarily with three factors: (i) temporal and spatial scale (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Knick and Rotenberry 1995, Vander Haegen et al. 2000, Chalfoun and Martin 2007, Vander Haegen 2007); (ii) covariance with environmental variability over time (Wiens and Rotenberry 1985, Wiens et al. 1987, Rotenberry and Wiens 1991, Van Horne et al. 1997); and (iii) lagged response times due to site fidelity and potentially natal philopatry (Wiens and Rotenberry 1985, Wiens et al. 1986) Prior work in altered systems has also described three potentially confounding elements: (i) nonlinear (threshold-type) responses (e.g., Fahrig 2002); (ii) species-specific area sensitivities (Donovan and Flather 2002, Rodewald and Vitz 2005, Winter et al. 2006); and (iii) temporally and spatially variable habitat saturation (Dunning 1986, Wiens and Rotenberry 1987). All are important factors that guide assumptions, influence interpretation of results, and were considered in our research design.

It is a significant challenge to simultaneously measure responses at spatial scales fine enough to be relevant to the success of an individual nest, yet large enough to be relevant to disturbance regimens. As a result, little information is available describing the relationship between preference for a habitat and the intensity of disturbance, the extent of disturbance, or the distribution of quality for birds (but see Tewksbury et al. 2006, Vander Haegen 2007). Previous work on disturbance effects in sagebrush-steppe was done in settings with complete conversions to non-shrub vegetation types that typically induced threshold responses (i.e., local extirpation). It is not known if similar responses, lagged by philopatry or not, are induced by low-intensity anthropogenic “restoration” disturbances intended to maintain some constant amount of sagebrush-steppe habitat across landscapes.

Specific to sagebrush-steppe systems, prior work has documented lagged responses to disturbance of 1-2 years in duration for sage sparrows and to a lesser degree for Brewer's sparrows (Wiens and Rotenberry 1985, Wiens et al. 1986, Howe et al. 2000, Knick and Rotenberry 2000). The strong site fidelity and apparent natal philopatry observed in shrubsteppe species in general (Martin and Carlson 1998, Reynolds et al. 1999, Rotenberry et al. 1999, Jones and Cornely 2002, Vander Haegen 2007) has been suggested as the proximate cause of these lags. Few studies have addressed this question experimentally, either being too short temporally to detect important lags in response, or not at large enough extents to detect potentially confounding scale-sensitivities. Thus the minimum scales of impact (i.e., time and space) required to trigger a response have not been well investigated.

In arid systems such as sagebrush-steppe, environmental variability can play a dominant role by revealing relationships only in high-stress years (Wiens 1991). If populations under study are not at equilibrium with the system because of external factors, then habitats will not necessarily be saturated and relationships between pattern and process will be more difficult to detect. While the concept of habitat saturation is often raised as a potentially mitigating factor in studies of shrubsteppe disturbances, there is little empirical work to support or refute it.

To address these challenges, our research design sought to affect and measure sagebrush-steppe nesting habitat at extents and time frames central to conservation and restoration efforts. Our study objective focused on four elements of potential response: (i) lagged response times; (ii) scale of responses in terms of habitat quality; (iii) scale of response in terms of habitat preference; and (iv) the relationship between habitat quality and habitat preference. We used nest density as our measure of habitat preference, and compared it among three years and among treatment ages to determine if and when lagged responses to treatments occurred. Tracking changes in nest density also allowed us to assess the scale of response to treatment at the scale of individual study plots. To describe scale-dependent changes to nesting habitat quality induced by vegetation treatment, our estimation of nest success explicitly incorporated the availability of nesting habitat extents at nest, territory, and landscape scales. Because theory predicts that changes in mean daily survival rate of nests should forecast changes in preference if selection is adaptive, i.e., if these species are sufficiently behaviorally plastic to avoid poor quality habitat, our final goal was to determine if changes in habitat quality forecast changes in habitat preference for these four species. Our study should also reveal whether sagebrush-steppe cover reductions used to restore habitat creates "sink" habitat for these species.

METHODS

Study area

Rich County, Utah, USA, is located at the intersection of the Wyoming Plateau, Great Basin, and Columbia Plateau ecoregions (Fig. 3.1). Sagebrush-steppe vegetation comprises roughly 70% of the county (~1790 km^2 of 2560 km^2), and consists principally of big sagebrush (*Artemisia tridentata*, subspecies *tridentata*, *vaseana*, and *wyomingensis*). Locally important shrub species include rubber rabbitbrush (*Ericameria nauseosa*), green rabbitbrush (*Chrysothamnus viscidiflorus*), Utah serviceberry

(*Amelanchier utahensis*), antelope bitterbrush (*Purshia tridentata*), and the "low" sagebrushes (e.g., *A. arbuscula, A. nova*). Locally important grass species include bluebunch wheatgrass (*Pseudoroegnaria spicata*), and Indian ricegrass (*Achnatherum hymenoides*), but little cheatgrass (*Bromus tectorum*). Study area elevation ranges from 1806 m to 2820 m (mean 2131 m). Climate is typical of western North American high-cold desert in terms of temperature (annual mean 13.0 ºC, mean annual range -16.6–28.8 ºC, 17 year average) and moisture (20–35 cm annually); the majority of annual moisture falls from October to December in the form of snow, and from April to May in the form of brief but intense rainstorms (Western Regional Climate Center 2007).

Study design and field methods

Mechanical treatments using a Lawson pasture aerator were implemented in a case-control design. Treatment purpose was to reduce sagebrush cover. The treatment prescription was a 60% aerator footprint within "treated" pastures (fenced subsections of allotments with consistent livestock stocking rates), minus areas untreatable due to steep slopes or rock. The remaining 40% of the vegetation was left as islands and peninsulas. Treatments mimic current sagebrush-steppe restoration practices, which no longer promote type conversion but instead leave remnant patches of untreated sagebrush (e.g., BLM 2007). Treatments were staggered among years to control for annual variations in bird populations, and in vegetation response to treatments.

We used a random start to anchor a systematic tessellated point sampling grid (Stevens 1997) across all sagebrush-steppe areas in Rich County. Tessellation points