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Disturbance as Restoration in the Intermountain Sagebrush Steppe: Effects on Non Target Bird Species

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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)

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2008

ABSTRACT

Disturbance as Restoration in the Intermountain Sagebrush-Steppe:

Effects on Non-target Bird Species

by

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Utah State University, 2008

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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

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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.

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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 $< 2\text{-}4$ 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 (α = 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).

<div align="center">LITERATURE CITED</div>

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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
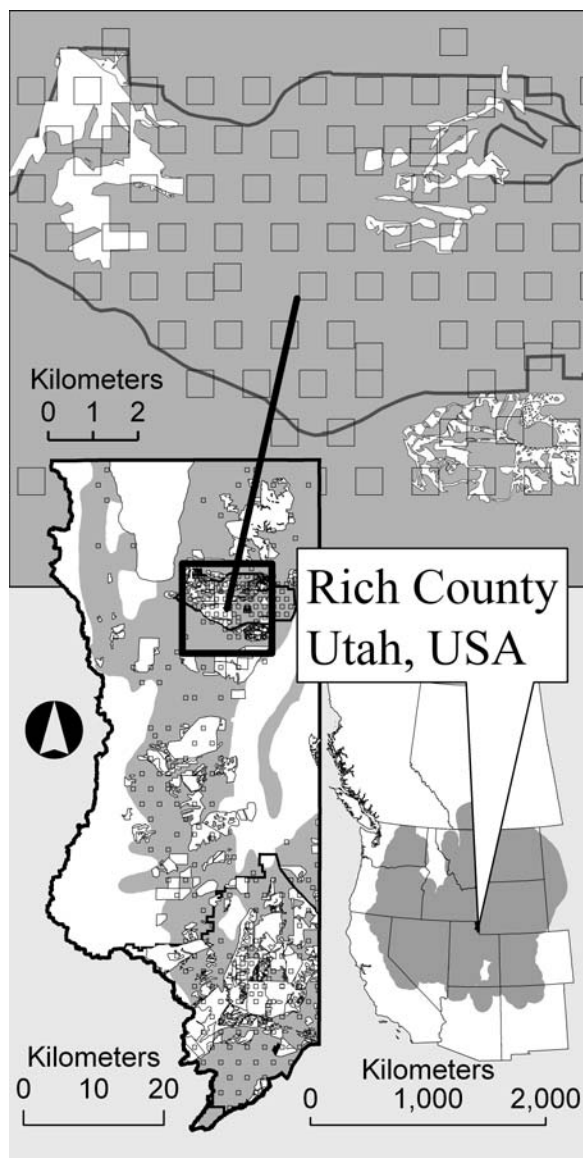
Figure 2.2 (a). Least square mean estimates plotted for species by treatment age effects for extirpation (presence/absence) analysis models. Due to model estimation and convergence issues when occupancy is close to 100% (i.e., BRES in T+1 and T+4, and VESP in T+3, see Table 2.1), no SE's are shown for 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).

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).

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

(1250 m spacing) were randomly selected to establish 18 36-ha nest monitoring plots (600 m x 600m) within current or planned vegetation treatment areas in each of three large study allotments: Duck Creek (DC), Big Creek (BC), and Deseret Land and Livestock (DL) (Table 3.1, Fig. 3.1). Treatments occurred in portions (pastures) of the DC and DL areas, while the BC plots were used as reference. Each large study area contained 2-6 pastures, and treatments were implemented by pasture. Two pastures were treated between the 2003 and 2004 breeding seasons (no pre-treatment data, and three years post-treatment), one between the 2004 and 2005 breeding seasons (one year pre-treatment data, and two years post-treatment), and one between the 2005 and 2006 breeding seasons (two years pre-treatment data, and one year post-treatment). Reference sites (Table 3.1) were drawn from untreated sagebrush-steppe areas that were at least 1000 m away from the nearest experimental treatment. Using the tessellation grid point as the Southwest corner, nest plots were laid out using flagging every 50 m.

Each year, trained nest surveyors were randomly assigned one reference and one treated nest plot in which to locate and monitor nests of the four target species: Brewer's sparrow (BRES), sage sparrow (SAGS), sage thrasher (SATH), and vesper sparrow (VESP). Surveyors were precluded from having both plots in the same allotment, and returning surveyors did not monitor their plots from previous year to ensure observer error was randomized. Nest searching and monitoring were conducted only during appropriate weather conditions. Data were collected during the approximately 100-day breeding season (late April to early August), with sampling starting 0.5 h after dawn and ending at 12:00 h. To increase observer efficiency and minimize bias, each observer

searched one-half of a nest plot on each visit, searching the other half on the subsequent visit. All known nests were monitored on every visit. Nests were located using a combination of systematic searches, behavioral cues, and physical evidence. Daily nest search maps derived from annotated GPS tracks were kept showing route(s) taken, nests found, and location of active and probable territories. Daily maps were also used to determine where additional search effort was needed to achieve uniform search effort.

When a nest was located, a flag or cairn was placed 10 m east of the nest with the nest ID number and species code. Nests were coded with a unique identifier. The nest UTM coordinates were recorded from a handheld GPS unit and a nest card filled out. Care was taken to minimize time spent at the nest to limit disturbance, and a variety of approaches and exits from the nest were used to minimize human scent around the nest. Nests were not checked when being observed by suspected nest predators (e.g., corvids). Nests were checked no more than every other day and no less often than every fourth day, depending on the nest stage (building, laying, incubating, nestling, or fledgling) (Martin and Geupel 1993). A nest found under construction was left alone for several days to minimize disturbance and the likelihood of abandonment. Nests close to transition events (hatching, fledging) were checked every other day to increase accuracy of recorded hatching and fledging dates. Nest searches were completed before monitoring of known nests each day because birds are most active from 0600 to 1000, and observation of bird behavior is the key to locating nests.

Monitoring data for each nest included species, nest age, number and age of eggs and nestlings, the number of brown-headed cowbird (*Molothrus ater*) eggs and nestlings,

and the nest's fate. Our criteria for coding nest fate are given in Table A.1 in the Appendix. After nesting activities concluded, vegetation data were collected. Vegetation data were collected each year around the active nests as well as at randomly selected points and whether the sample was within the aerator footprint. Two methods were used to estimate local cover variables. Estimates of forb, bare ground, and rock cover were calculated using a three 0.5 m^2 Daubenmire frames (placed at the point and 2 m from the point in two randomly selected cardinal directions). For woody shrub cover, a point-centered quadrat method was utilized.

Statistical methods

Nest density, our measure of habitat preference, was calculated as the mean number of nests standardized by the area of the nest plot. Mean nest density values for each species were used in four multi-factor (two-way) nested ANOVA models. Factors were survey year (YEAR) and number of breeding seasons since treatment (TRTAGE). Assumptions of normality and homogeneity of variance were examined using normal probability plots, bi-plots, and Bartlett's test. All analyses were run using R (R Development Team 2008).

Mean daily nest survival rate (DSR) was used as the measure of habitat quality. A multi-model inference framework (Burnham and Anderson 2002) was used to estimate DSR for each species using the nest survival model found in program MARK (White and Burnham 1999, Version 5.1 2007). All DSR analyses were performed independently by species, as we assumed there was no interaction in DSR models between the species

considered here. Potential models of DSR were ranked and compared using ΔAICc (as per Burnham and Anderson 2002). Models ≤2 AICc units from the best model were considered to be competing models, those that were between 2-4 AICc units from the best model were considered plausible models, and models >4 AICc units were considered poor models and were disregarded. Competing models in the final set were averaged as they were considered to be equally credible.

Variables considered in the DSR models included both temporal and habitat variables. For temporal variables, we used year (YEAR, 2004:2006), treatment age (TRTAGE, 0-3 years old), and circannual effects. Circannual effects were modeled as a linear trend model of within-year change (T), a quadratic trend model of within-year change (TT), and the estimated of age of the nest on the first day of the survey season (NESTAGE) (Rotella et al. 2004). Habitat variables included six vegetation cover variables: three extents of shrub cover, and three ground cover variables considered important to nesting habitat quality for our focal species. The three measures of shrub cover were intended to correspond to landscape, territory, and nest-scale extents where the region within a 1000 m radius was considered "landscape" scale (SHRBLAND), within a 50 m radius considered "territory" scale (SHRBTERR), and within a 4 m radius considered "nest" scale (SHRBNEST). A single set of pooled shrub categories capturing big sagebrush and tall (>10 cm) shrub forms was used for all extents. Using a GIS, SHRBLAND was estimated by intersecting 1000 m radius buffers with 30 m pixel based vegetation cover maps created from SWReGAP (Prior-Magee et al. 2007) and summing areas of appropriate vegetation categories. Hand-digitized vegetation maps created from

1-m color NAIP (NAIP 2004, 2006) imagery were used for the creation of SHRBTERR estimates. Cover of shrubs at nest scale, SHRBNEST, was estimated as the mean of the data collected in the field at each point. The three estimates of ground cover (grass – CVRGRASS, forb – CRFORB, and bare ground/rock - CVRBARE) were estimated similarly to and at the same extent as SHRBNEST.

We evaluated the relative support for 13 *a priori* models of factors affecting DSR (Table 3.2). Individual models were structured to evaluate the relative support for combinations of temporal and habitat variables considered important to nest survival of our focal species in disturbed landscapes; these were grouped into three analysis sets. We made each analysis set ecologically consistent, working down from relatively coarse factors to increasing fine grained models of space and time (Fig. 3.2). The first set compared factors including year (YEAR), age of treatment (TRTAGE), and two interaction terms (additive and multiplicative models). The second set modeled circannual effects as linear (T) and quadratic (TT) season-long trends, and as the nest's age on the first day of the survey season (NESTAGE). The third set compared support for models including estimates of shrub cover at three extents and measures of ground cover at nest extents.

Following procedures similar to those of Anthony et al. (2006), Farnsworth et al. (2006) and Dinsmore et al. (2002), analysis was performed sequentially on sets to keep the number of models considered from becoming too large. This was accomplished by using the top performer from each previous set as the additive base model for each subsequent set such that the initial selection of models including relatively coarse factors

constrained the selection of subsequent models. For example, the best model from the first set (Fig. 3.2, Set One, coarse factors) serves as both the null and additive base model for the next (circannual factors); the best model from the Set Two (circannual factors) becomes the null and additive base model for Set Three (habitat cover variables). Because we were interested ultimately in the degree of relative support for individual covariates, and not simply the most robust estimate of DSR, only the final set was model averaged using Akaike weights (Burnham and Anderson 2002).

RESULTS

Vegetation alteration

Vegetation cover variables were measured on the 18 unique nest monitoring plots at 2,073 sample points representing used and available nesting habitat from 2004–2006. Cover variables were used to describe active nest sites for each of the four focal species. Treatment prescriptions ranged from 28–62% by pasture, but the aerial extent of the treatment "footprint" as implemented ranged from 13–36% (mean 23%) of the pasture, and from 23–40% (mean 29%) of the potentially treatable areas in each pasture. This difference largely reflects the area of the reserved vegetation "islands". The change in mean percent cover within 2, 50, and 1000 m of randomly selected points in treated sites was -13.4, -2.5, and -3.9%, respectively. Mean shrub cover at all three extents ranged between 41.1% and 82.3%, reflecting the relatively intact surrounding vegetation in the county. Both mean percent forb and mean percent bare ground increased with treatment,

2.5% and 5.7%, respectively.

Nest density

A total of 1,788 nests of the four focal species were located and monitored over the course of the study. Some of the nests located (up to 20% in a given plot or year) never showed any sign of activity and were presumed to have failed prior to laying or to be remnant nests from prior years. These inactive nests were not included in calculations of nesting density for the four focal species, for which the total number of active nests was 1,516. Across all species and years, the mean failure rate due to predation was relatively high at 43%, while losses due to weather were small, averaging less than 2%. Because both the number and the size of nest plots varied with survey year, the nest densities indexing habitat attractiveness were standardized to number of nests located per unit area (40 ha) to facilitate comparison (Table 3.3).

Nest density varied consistently among survey years, with mean nest densities averaging 2.4-fold higher in 2005 than either 2004 or 2006. This was true for all species in both reference and treatment plots. The effects of treatment age were less consistent by species (Fig. 3.3). Mean Brewer's sparrow nest densities were more than twice as large as vesper sparrows, the next most abundant species. Nest densities for Brewer's sparrow were significantly affected by annual effects (df $= 2$, F $= 5.79$, $p = 0.01$), but not treatment age (df $= 3$, F $= 0.11$, $p = 0.95$). Sage sparrows had the lowest mean nesting densities overall. For this species nest densities were not notably affected by annual effects (df $= 2$, F $= 1.14$, $p = 0.33$), and were indistinguishable in reference and treatment

sites in the first year post treatment (df = 3, F = 0.55, p = 0.65). However, no sage

sparrow nests were located in any treatment plot older than 1 year, and thus no

assessment of treatment age was possible. Nest densities of sage thrasher remained

moderate but relatively unchanged by annual effects (df = 2, F = 2.12, p = 0.14) or by age

of treatments (df = 3, F = 0.08, p = 0.97). Vesper sparrow nest densities varied more than

any other species but sage sparrow, and did so without apparent relationship to year (df =

2, F = 0.45, p = 0.64). Treatment age was significantly and positively related to vesper

sparrow nest densities (df = 3, F = 2.88, p = 0.05).

Nest survival

Models included in the final confidence set for each species are shown in Table

3.4, and an example of a specific DSR analysis pathway (vesper sparrow) is shown in

Fig. 3.4. There was little consistent support for individual model or variable influence on

nesting success among our four focal species (Table 3.4). Daily nest survival rates for

sage thrasher and vesper sparrow were best modeled by the constant ($S_{(.)}$) model, whereas

Brewer's sparrow and sage sparrow DSRs were best modeled using unique combinations

of temporal, within-season time variation, and vegetation cover variables.

In terms of Set One models evaluating coarse factors, Brewer's sparrow nest

success was best explained by a multiplicative interaction model between survey year and

age of treatment (YEAR*TRTAGE). This same model was the best model in Set Two

(evaluating the relative support for models including within season time effects),

indicating a lack of support for within-season time variation in nest survival. The best

model of Brewer's sparrow DSR in Set Three (evaluating models that include cover variables at multiple extents) was (YEAR*TRTAGE) + SHRBNEST. The SHRBNEST cover variable improved model fit but was not individually influential on DSR, and hence was considered a "helper" variable like all other cover variables for Brewer's sparrow. All six models in the final set differed by <2.3 ΔAICc, indicating there is relatively even support for all models including habitat cover extents, irrespective of the ground cover form (e.g., shrub, forb, or bare ground) or the extent at which shrub cover was measured (SHRBLAND, SHRBTERR, or SHRBNEST).

The model with the greatest relative support for factors affecting sage sparrow DSR in Set One was the null model S(.), but given that the S(YEAR) model was an equally valid model (ΔAICc = 0.8), we chose to use the latter because it was more informative. The best model in Set Two was the additive model of year plus quadratic time effects model (YEAR+TT), which, when also evaluated against the null S(.) model, garnered over 90% of the relative support in Set Two. The best sage sparrow DSR model in Set Three (including vegetation cover extents) was an additive model reflecting the importance of year, within-season quadratic time trend, and bare ground cover (YEAR+ TT+CVRBARE). The large within-year quadratic trend in DSR indicates extremely low nest success in the early and late portions of the breeding season; the large effect of year was due to increased nest success rate in 2005. The combination of year + within-year quadratic trend in DSR essentially reflects the duration of the effective breeding season; thus, not only was sage sparrow nest success higher in 2005, but their effective breeding season was also longer. The effect of bare ground cover on nest success was large and

positive, but not significant. Like Brewer's sparrow, however, all six models in Set

Three were within 2.5 ΔAICc implying relatively even support for all models including

cover variables.

Similar to the sage sparrow, the null ($S_{(.)}$) model was the best model in Set One

for sage thrasher DSR. However, we again used the survey year alone (YEAR) as it was

an equally plausible yet more informative choice (ΔAICc = 3.2). However, the null

model was again the (marginal) best in model Set Two, and so both the null and the

survey year alone models were retained in the final model evaluation Set Three. In Set

Three, the null model and an additive model with year and forb cover (CVRFORB) were

the only two with support from the data.

The best Set One model for vesper sparrow DSRs was the null model, with age of

treatment (TRTAGE) an equally viable and more informative alternative (ΔAICc = 2.7).

Both were retained in Set Two, where there was little support for any specific within-

season time effects. In the third set of model evaluations there was little change in the

relative support for the null and the age of treatment models, implying little relationship

with vegetation cover variables.

DISCUSSION

We perturbed a relatively intact sagebrush-steppe system using a relatively light

intensity and widely distributed form of disturbance to gain insight into restoration's

potential for positive or negative impacts, and to better understand the relationship

between habitat preference and habitat quality. Our results support the idea that

restoration is likely to have diverse and often unintended consequences. Our results also showed that the relationship between habitat preference and habitat quality was not as we had predicted. Changes in habitat quality did not successfully forecast changes in habitat preference, even after considering lagged responses in expressed preference and changes to apparent quality. Nor were the responses to treatment similar among shrubsteppe-obligate species uniform: each species response was consistent between plots and over time, but responses to treatment varied among all species in scale, in timing, and in direction.

Each species was uniquely affected by our treatments in at least one spatial and temporal scale specific to that species, although environmental variability remained a dominant factor for all species in this system. For vesper and sage sparrows, the two species that responded to treatments at the plot scale, both showed evidence of a threshold-type response, with abrupt changes in nest density after a time lag. However, Brewer's sparrow and sage thrasher, the two species that did not exhibit a response among plots, showed evidence of within plots responsive movement by remaining on plot after treatment, implying that shrubsteppe habitat was not saturated for these two bird species here. They simply moved to the undisturbed islands and peninsulas within the treatment areas. Overall, our data confirm that the relationship between habitat preference and quality is more subtle than may be described by relatively coarse abundance-based methods. These relationships appear to be complex, as predicted by Wiens et al. (1987), and scale-dependent, as described by Chalfoun and Martin (2007).

As such, we found that habitat quality measured at any single scale was not a reliable predictor of habitat preference.

At what scale do sagebrush-steppe birds move in response to vegetation treatments? Our study design allowed us to formally ask this question only at the plot level scale. Movement at this scale translated into either no change in mean nest densities (Brewer's sparrow and sage thrasher) or a dramatic change (sage sparrow and vesper sparrow), depending on the scale of response relative to the size of our nest plots. Brewer's sparrow and sage thrasher showed no change in mean nest density per plot. They instead "packed" into the remaining islands and peninsulas of habitat in treated plots. These two species moved only small distances, side-stepping the treatment footprint, as demonstrated by their unchanged nest densities. This small-scale packing supports the idea that shrubsteppe habitat is not saturated, and reveals a resilience to patchily distributed, low intensity disturbance for these two species. By contrast, sage sparrows did not nest in any treatment plot older than 1 year. Prior to treatment, sage sparrows were not as uniformly distributed or abundant as were the other focal species, but the relationship we observed between nesting activity and treatment age was consistent in every plot occupied and in all three years. Our single steppe-associated species, the vesper sparrow, did respond as expected to treatment with increased mean nest densities per plot, although the response took three years. Both sage sparrow and vesper sparrow exhibited these changes in preference relatively abruptly and at different temporal lags, suggesting these two species exhibit threshold-type responses to treatment, albeit with different time lags.

Not all sagebrush-steppe obligate species exhibited the expected decreased nest densities over time, although nest densities of the steppe-associated species (vesper sparrow) eventually increased as expected. Sage sparrows reacted with a threshold-form response in the expected direction, either abandoning treated plots older than 1 year or nesting in such low densities as to be essentially undetectable. A lag in response time for sage sparrow was expected, although it was shorter (1 yr vs. 2-3) than has been reported elsewhere (Wiens and Rotenberry 1985, Wiens et al. 1986). This shorter lag suggests that sage sparrows in our study region may be less philopatric than reported elsewhere (Knick and Rotenberry 2000, Vander Haegen 2007), and hence less susceptible to losses from "sink" habitat conditions created by fragmentation in the landscape than are the other three focal species. If habitat quality is indeed largely controlled through predation rates as posited by Martin (1993) and others (Nagy and Holmes 2004, Tewksbury et al. 2006), and if these rates are, in turn, positively related to anthropogenic habitat fragmentation and loss at landscape scales, then strong philopatry may lead to undue persistence in "sink" breeding habitat.

Our second objective was to assess both time and scale-sensitivity in the relationship between treatment and habitat quality. Our results indicate there are unique sets of factors with several commonalities influencing nest success for these species. For all our focal species, daily nest survival rates in untreated areas were at the low end of the range reported in the literature (Martin and Carlson 1998, Reynolds et al. 1999, Rotenberry et al. 1999, Jones and Cornely 2002). Both Brewer's sparrow and vesper sparrow nest survival rates were negatively related to treatment age, but sage sparrow and

sage thrasher nest survival rates were not. These data suggest that treatment decreases local habitat quality for Brewer's sparrow and vesper sparrow and that these two species persistence in treated areas has the potential to be maladaptive. The lack of a similar relationship with treatment age for sage sparrow and sage thrasher was unexpected, however, and especially so for sage sparrow given the lack of evidence of nesting on any older treatment plots. While sage sparrows were the only species to show the influence of within-season time effects, habitat quality was defined by low early and late season nest success for sage sparrow.

Habitat quality of all three shrubsteppe-obligate species was influenced by nest-scale vegetation, and only the sage thrasher was not influenced by shrubsteppe extent at territory scales. No species was influenced by landscape scale shrubsteppe extents; at this scale there was no significant difference between treated and reference plots. However, landscape contexts for both treated and reference plots were very similar and hence our study context had little scope of potential differences. Smaller scale aspects of DSR models were not necessarily consistent with gross expectations at first glance. Brewer's sparrow DSR increased with decreasing shrubsteppe extent at territory scales, which in our study system translates to areas with less than completely uniform shrub cover. It may also indicate a preference by Brewer's sparrow for slightly more open or at least aggregated habitat at this scale (Chalfoun and Martin 2007). This context influenced all our models, for in contrast to many prior studies in this habitat type, our system was initially quite intact with shrubsteppe cover at territory scales ranging from 55-100% (study-wide mean 82%).

Our final objective was to determine if changes in habitat quality forecast changes in habitat preference. The two species to show variation in nest density at the plot scale related to treatment age were the sage sparrow and the vesper sparrow. Daily survival rate did not forecast changes in nest density for either of these species however. Sage sparrow DSR was unrelated to treatment age and, once year and seasonal effects were accounted for, estimates of DSR did not change significantly between different aged treatments. Vesper sparrow DSR was related to treatment age, but showed a negative relationship, supporting Chalfoun et al.'s (2002) metanalysis indicating that the observation of decreased nest success in fragmented landscapes was related to broad scale predation rates rather than habitat patch structure or composition. A relationship may have been masked by low sample size, high variability, or the relative insensitivity of our nest survival analysis.

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Table 3.1. Number and area (ha) of nest monitoring plots in each treatment age

category[1]. Eighteen unique nest plots were studied: 10 were sampled in every year,

four others were sampled in two consecutive years, and two were each only sampled

in 2004 and 2006. Plot size (ha) was reduced each year for logistical reasons; as a

result all analyses are first standardized on area searched, then on number of plots per

survey year. All but two of the plots monitored in 2004 were monitored in every

subsequent year, and all plots in 2006 but one were monitored in both prior nesting

seasons. Note that: 1) experimental treatments had not aged into the T+2 and T+3 age

categories until 2005 and 2006 respectively, 2) the reference category includes pre-

treatment data, and 3) all plots in all years are treated as independent replicates.

YEAR	Reference	T+1	T+2	T+3	Total
2004	9 (324)	3 (108)	—	—	12 (360)
2005	12 (432)	2 (72)	4 (144)	—	18 (648)
2006	4 (64)	2 (32)	2 (32)	3 (48)	11 (176)

[1] T+ (1:3) columns indicate the number of breeding seasons since mechanical

treatment of vegetation, i.e., if a vegetation treatment occurred prior to the 2005 breeding

season but after the 2004 breeding season, then nest monitoring data collected in the 2005

breeding season were considered to be T+1 samples (e.g., the first breeding season post-

treatment).

Table 3.2. *A priori* model sets of estimated daily survival rates. Set number indicates the group of models against which a given model is evaluated (see Fig. 3.2). Set 1 evaluated temporal effects: null model, year (YEAR), treatment age (TRTAGE), and interactions. Set 2 evaluated within-season time variation: linear (T) or quadratic (TT) trend models, and the age of nest/date in the season when found (NESTAGE). Set 3 evaluated support for models including vegetation cover: shrub cover at landscape-extent (1000 m radius, SHRBLAND), territory-extent (50 m radius, SHRBTERR), and nest-extent (2 m radius, SHRBNEST); and estimates of nest-extent vegetation cover, and two estimates of ground cover (CVRFORB and CVRBARE)

Set	Model Description	Notation
1	Single Estimate of Daily Survival Rate	$S_{(.)}$
1	Effect of Year (YEAR) only	S_{YEAR}
1	Effect of Treatment Age (TRTAGE) only	S_{TRTAGE}
1	Effect of Year plus Treatment Age (additive model)	$S_{YEAR+TRTAGE}$
1	Effect of Year x Treatment Age (multiplicative model)	$S_{YEAR*TRTAGE}$
2	Effect of best set 1 model plus linear trend (T)	$S_{best1+T}$
2	Effect of best of set 1 model plus quadratic trend (TT)	$S_{best1+TT}$
2	Effect of best of set 1 model plus NESTAGE	$S_{best1+NESTAGE}$
3	Effect of best of set 2 model plus SHRBLAND	$S_{best2+SHRBLAND}$
3	Effect of best of set 2 model plus SHRBTERR	$S_{best2+SHRBTERR}$
3	Effect of best of set 2 model plus SHRBNEST	$S_{best2+SHRBNEST}$
3	Effect of best of set 2 model plus CVRFORB	$S_{best2+CVRGRAS3}$
3	Effect of best of set 2 model plus CVRBARE	$S_{best2+CVRBARE3}$

Table 3.3. Total and mean (SE) nest densities for active nests for the four focal species[1]. These are shown for each treatment category (total number of nest found for all species was 3677, 1788 of these were of focal species). Active nests are here defined as those that held at least one egg, e.g., not those which failed or were predated prior to an observed egg. Note that all mean and SE values are re-scaled to 40 ha.

Species	Reference		T+1		T+2		T+3	
	Total	$\bar{x}$ (SE)	Total	$\bar{x}$ (SE)	Total	$\bar{x}$ (SE)	Total	$\bar{x}$ (SE)
BRES	771	39.2 (1.73)	163	37.2 (3.00)	150	34.0 (2.82)	51	42.4 (5.83)
SAGS	23	1.2 (3.22)	6	1.2 (5.25)	0	0 (—)[2]	0	0 (—)[2]
SATH	127	6.4 (1.89)	30	6.8 (8.09)	29	6.4 (2.00)	6	5.2 (5.00)
VESP	102	5.2 (0.82)	31	7.2 (1.65)	14	3.2 (0.66)	13	10.8 (2.88)

[1] BRES = Brewer's sparrow, SAGS = sage sparrow, SATH = sage thrasher, and VESP = vesper sparrow

[2] No nests for SAGS were located in any T+2 or T+3 plots.

Table 3.4. Relative support for all models of nest daily survival rate. Daily survival rates (DSR) with AIC weights > 0.1 are shown for each of the four focal species: Brewer's sparrow (BRES, effective n = 5273), sage sparrow (SAGS, effective n = 301), sage thrasher (SATH, effective n = 1781), and vesper sparrow (VESP, effective n = 1315). Set number indicates the analysis sets in which it appears. Effective n is the sum of number of samples, nests in this instance, multiplied by the number of intervals over which they were monitored.

Species	Set	Model	ΔAIC_c[1]	w_i[2]	K[3]
BRES	3	$\{S_{((YEAR*TRTAGE)+SHRBNEST)}\}$	0.000	0.22	10
	1,2,3	$\{S_{(YEAR*TRTAGE)}\}$	0.356	0.18	9
	3	$\{S_{((YEAR*TRTAGE)+SHRBTERR)}\}$	1.227	0.12	10
SAGS	3	$\{S_{(YEAR+TT+CVRBARE)}\}$	0.000	0.28	6
	2,3	$\{S_{(YEAR+TT)}\}$	0.429	0.23	5
	3	$\{S_{(YEAR+TT+SHRBTERR)}\}$	0.895	0.18	6
	3	$\{S_{(YEAR+TT+CVRFORB)}\}$	1.745	0.12	6
SATH	1,2,3	$\{S_{(.)}\}$	0.000	0.47	1
	3	$\{S_{(YEAR+CVRFORB)}\}$	3.137	0.11	4
VESP	1,2,3	$\{S_{(.)}\}$	0.000	0.41	1
	1,2,3	$\{S_{(TRTAGE)}\}$	2.770	0.11	4

[1]ΔAIC_c – Delta Akaike's Information Criterion, adjusted for small sample size; [2]w_i – Akaike's Information Criterion weights; [3]k – number of model parameters.
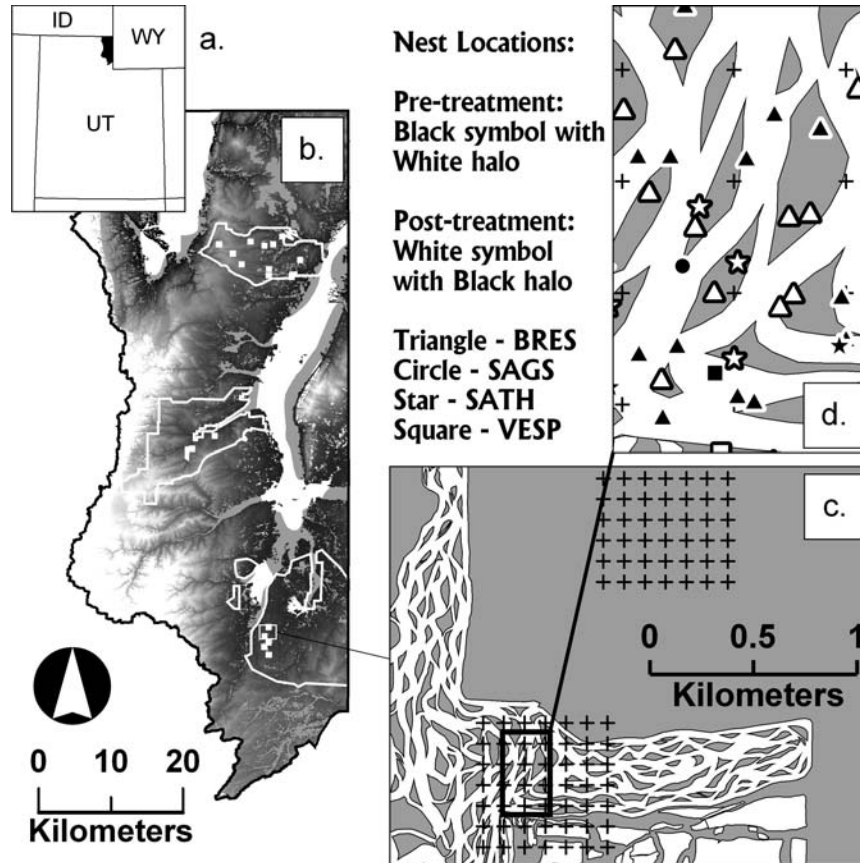
Figure 3.1. Maps of nest grids and nests. Inset map a shows relative the position and size of Rich Co. in North America, inset map b shows the extent of sagebrush-steppe (shaded areas), pasture boundaries, and nest monitoring grid locations (n = 18, white squares) in Rich County, inset map c. shows a close-up of two 36 ha nest monitoring plots (grids of black crosses, 100m spacing) and mosaic treatment design (in white), and inset map d shows nest locations for Brewer's sparrow (triangles), sage sparrow (circles), sage thrasher (stars), and vesper sparrow (squares). Pre-treatment nest locations are black symbols haloed in white, post-treatment nest locations are white symbols haloed in black.

Figure 3.2. Heuristic model of potential DSR analysis flow. Notation follows Table 3.2.
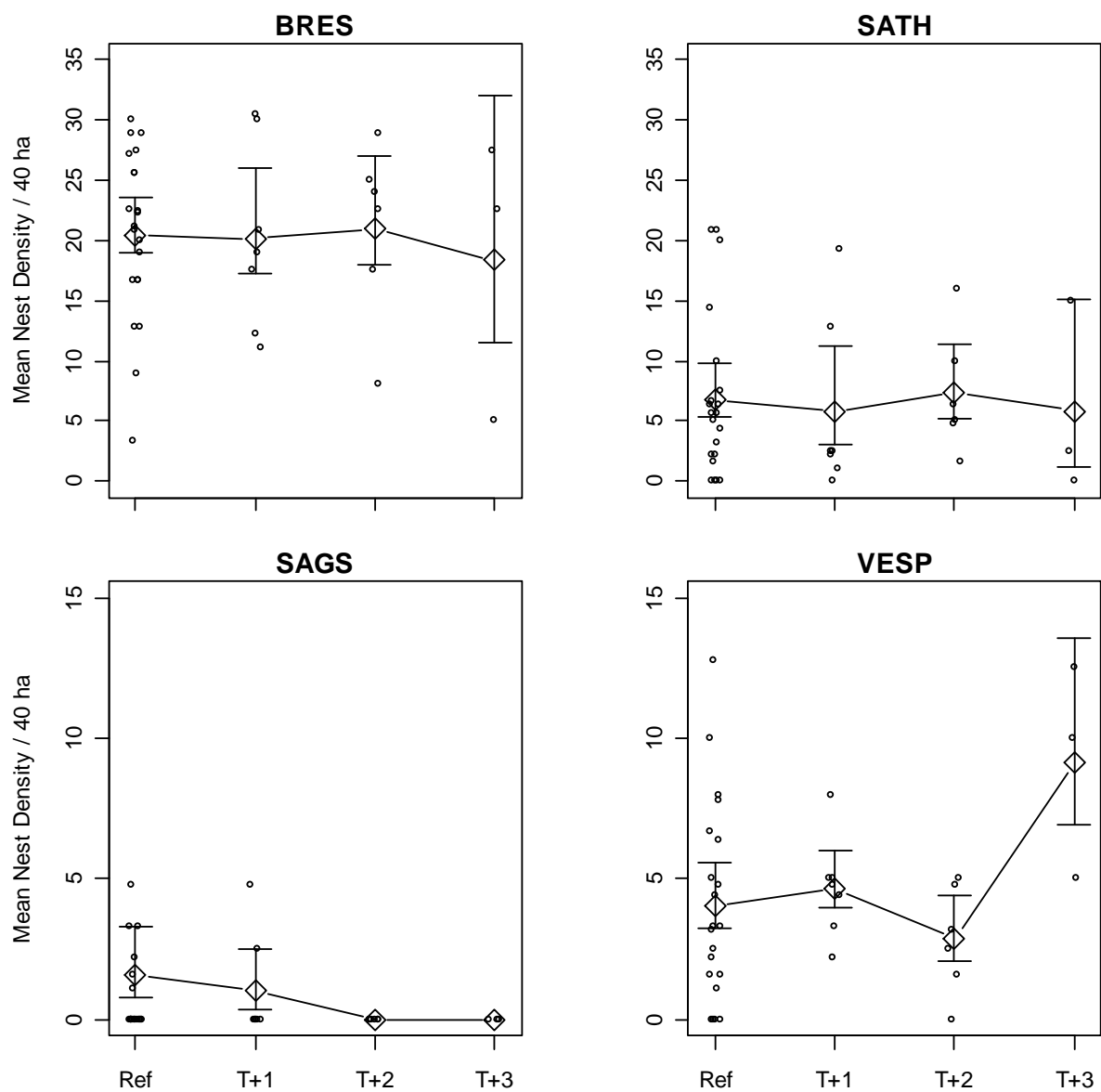
Figure 3.3. Plots of mean nest densities for each treatment age for each focal species.
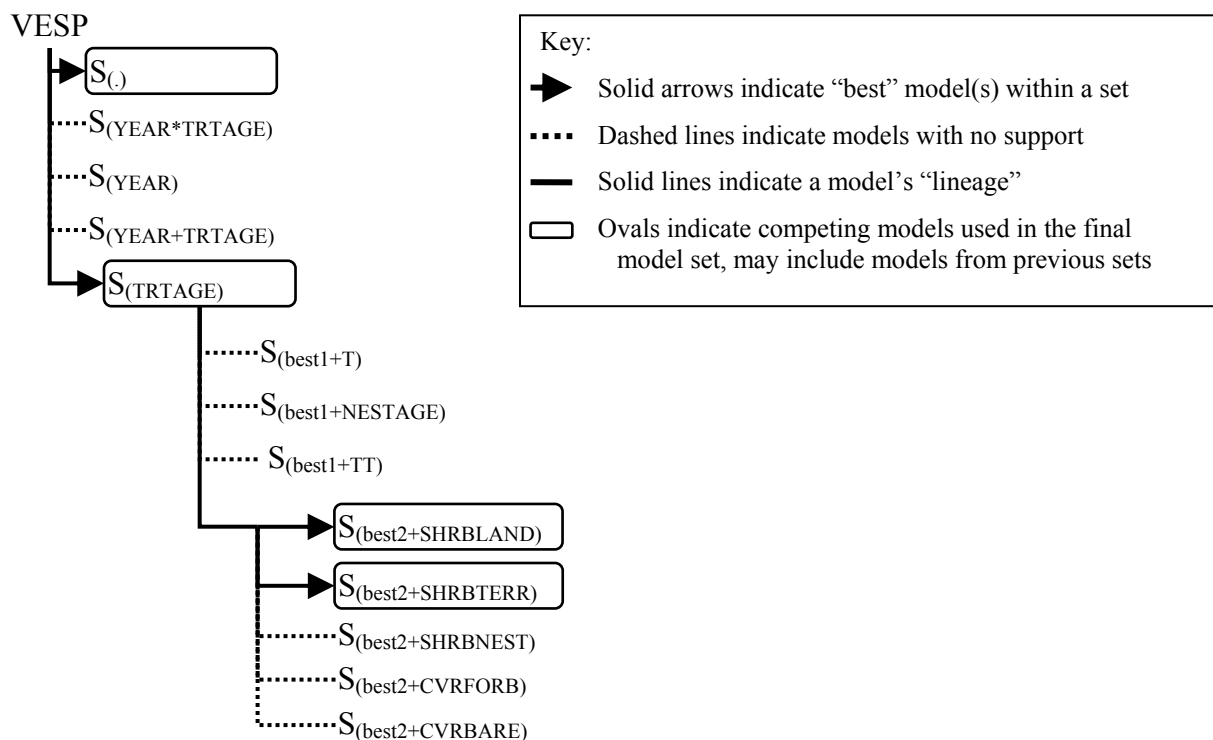
Figure 3.4. Visual model of vesper sparrow analysis flow. Notation follows Table 3.2. Both the S(.) or "dot" model and S($_{TRTAGE}$) model were equivalent models in set 1 and so were retained for set 2, where no improvement was made over set 1. The models in the final candidate set were S(.), S($_{TRTAGE}$), S($_{TRTAGE+SHRBLAND}$), and S($_{TRTAGE+SHRBTERR}$). Models in the final set were model averaged.

CHAPTER 4

LOCAL HABITAT CHARACTERISTICS AND NEST SUCCESS

OF SAGEBRUSH-STEPPE BIRDS

INTRODUCTION

Nest site selection is a process resulting from evolutionary pressures that maximize an individuals fitness. Each nest site selection is a presumed expression of this process, and represents the optimization of desirable attributes (e.g., food availability) balanced against undesirable attributes (e.g., presence of nest predators). This optimum is bounded by the locally available habitat, and the timing, scope, and quality of information available to the individual at the time of settling (Arlt and Part 2007, Valone 2007). As such, each nest site balances the needs of one nest against the individual's competing goals of total breeding season productivity and total lifetime productivity (Martin 1993, Martin et al. 2000). It likely never represents a maximized outcome for the individual nest. Yet nest success is an essential goal for each individual and successful nest locations should, on average, describe this optimized solution relative to the locally available choices. Researchers rely on the validity of this assumption to describe the range of nesting habitat, and what constitutes preferred nesting habitat attributes. These attributes may be related to the location itself at multiple scales, including those of the landscape, patch, and nest site. Many researchers have focused on characteristics of nest sites because of their relationship to nest success (Petersen and Best 1985a, Vander Haegen et al. 2000, Chalfoun and Martin 2007, Holmes 2007, Vander Haegen 2007).

Prior work has not completely clarified if nest site selection itself is adaptive; that is, if nest success is mediated by the habitat characteristics of the nest site. While most theory on nest site selection (Cody 1985, Martin 1993, Pulliam 2000) suggests that the selection itself should be adaptive, empirical work has shown this is not always the case (e.g., Misenhelter and Rotenberry 2000, Arlt and Part 2007), with individuals sometimes selecting so-called "sink" habitat. It is also not clear that sites selected for nesting are structurally consistent, either across the species distribution, pre- and post-disturbance, or over time. While fragmentation of nesting habitat was not formally incorporated into early examinations of nesting habitat or nest success (e.g., Best 1972, Reynolds 1981, Castrale 1982, Petersen and Best 1985a, 1985b, 1991, Wiens and Rotenberry 1985, Winter and Best 1985, McAdoo et al. 1989, Rotenberry and Wiens 1989, Rodgers and Sexson 1990), research since has examined its role at multiple temporal and spatial scales (Wiens et al. 1986, Knick and Rotenberry 1995, 1997, 2000, Vander Haegen et al. 2002, Quinn 2004, Vander Haegen 2007).

Fragmentation in an initially contiguous habitat is thought to induce edge effects, such as increased predation, yet studies in many different habitats, including sagebrush-steppe, have been equivocal (Lidicker 1999, Laurance 2000, Misenhelter and Rotenberry 2000, Heske et al. 2001, Jones 2001, Chalfoun et al. 2002). Research and reviews have found mixed support for edge effects in sagebrush-steppe habitat (Paton 1994, Misenhelter and Rotenberry 2000, Chalfoun et al. 2002, Knick and Rotenberry 2002, Tewksbury et al. 2002, Vander Haegen et al. 2002, Kristan et al. 2003), though area sensitivities for individual species have been shown.

Important declines in sagebrush-steppe bird populations have been documented (Sauer et al. 2007), and the reintroduction of disturbance as a restoration tool has been cited as one means for recovering a mixture of shrub age classes and the accompanying interstitial grass and forbs. The application of disturbance as a restoration tool provides an opportunity to study the selection of nesting habitat under experimentally changed conditions. Our study area was well suited to such an exercise as the initial settings are large expanses of uniform, unbroken sagebrush steppe with relatively little recent artificial fragmentation. These areas provide a setting in which to describe the attributes of both the used and available habitat prior to and after the application of experimental disturbances. Together, they provide the means of assessing the consistency of nesting habitat selection and the strength of its correlation with nest success. In this context we sought to: (i) describe the selected nesting habitat of four focal species in sagebrush-steppe; (ii) test if selected nesting habitat is consistent between pre–and post treatment; and (iii) to determine which habitat characteristics, including distance to disturbance, are related to nest success. By pooling information from nests for a species over many locations in its distribution, at different times, and under different management regimes, it is possible to more completely describe the niche-breadth of a species nesting habitat (Knopf et al. 1990).

METHODS

Study area

Rich County, Utah, USA, is located at the intersection of the Wyoming Plateau, Great Basin, and Columbia Plateau ecoregions (Fig. 4.1). 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*). 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 (e.g., *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

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 leaves 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 (1250 m spacing) were randomly selected to establish 18 36-ha nest monitoring plots (600 m x 600m) within current or planned vegetation treatment areas in each of three large study allotments: Duck Creek (DC), Big Creek (BC), and Deseret Land and Livestock (DL) (Table 4.1, Fig. 4.1). Nest data from 12 nest plots monitored at least two consecutive years and covering each treatment age category were used for this work. Treatments occurred in portions (pastures) of the DC and DL areas, while the BC plots were used as reference. Each large study area contained 2-6 pastures, and treatments were implemented by pasture. Two pastures were treated between the 2003 and 2004 breeding seasons (no pre-treatment data, and three years post-treatment), one between the 2004 and 2005 breeding seasons (one year pre-treatment data, and two years post-treatment), and one between the 2005 and 2006 breeding seasons (two years pre-treatment data, and one year post-treatment). Reference sites were drawn from untreated sagebrush-steppe areas at least 1000 m away from the nearest experimental treatment.

Using the tessellation grid point as the southwest corner, nest plots were laid out using flagging every 50 m.

Each year, trained nest surveyors were randomly assigned one reference and one treated nest plot in which to locate and monitor nests of the four target species: Brewer's sparrow (BRES), sage sparrow (SAGS), sage thrasher (SATH), and vesper sparrow (VESP). Surveyors were precluded from having both plots in the same allotment, and returning surveyors did not monitor their plots from previous year to ensure observer error was randomized. Nest searching and monitoring were conducted only during appropriate weather conditions. Data were collected during the approximately 100-day breeding season (late April to early August), with sampling starting 0.5 h after dawn and ending at 12:00 h. To increase observer efficiency and minimize bias, each observer searched one-half of a nest plot on each visit, searching the other half on the subsequent visit. All known nests were monitored on every visit. Nests were located using a combination of systematic searches, behavioral cues, and physical evidence. Daily nest search maps derived from annotated GPS tracks were kept showing route(s) taken, nests found, and location of active and probable territories. Daily maps were also used to determine where additional search effort was needed to achieve uniform search effort.

When a nest was located, a flag or cairn was placed 10 m east of the nest with the nest ID number and species code. Nests were coded with a unique identifier. The nest UTM coordinates were recorded from a handheld GPS unit and a nest card filled out. Care was taken to minimize time spent at the nest to limit disturbance, and a variety of approaches and exits from the nest were used to minimize human scent around the nest.

Nests were not checked when being observed by suspected nest predators (e.g., corvids).

Nests were checked no more than every other day and no less often than every fourth

day, depending on the nest stage (building, laying, incubating, nestling, or fledgling)

(Martin and Geupel 1993). A nest found under construction was left alone for several

days to minimize disturbance and the likelihood of abandonment. Nests close to

transition events (hatching, fledging) were checked every other day to increase accuracy

of recorded hatching and fledging dates. Nest searches were completed before

monitoring of known nests each day because birds are most active from 0600 to 1000,

and observation of bird behavior is the key to locating nests.

Monitoring data for each nest included species, nest age, number and age of eggs

and nestlings, the number of brown-headed cowbird (*Molothrus ater*) eggs and nestlings,

and the nest's fate (where a nest that fledged any young was considered a success). Our

criteria for coding nest fate are given in Table A.1. in the Appendix. After nesting

activities concluded, vegetation data were collected. Vegetation data were collected each

year around the active nests as well as at randomly selected points; and in each case it

was noted if the sample was within the aerator footprint. Two methods were used to

estimate local cover variables. Estimates of forb, bare ground, and rock cover were

calculated using three 0.5 m^2 Daubenmire frames (placed at the point and 2 m from the

point in two randomly selected cardinal directions). For woody shrub cover, a point-

centered quadrat method was utilized (Etchberger and Krausman 1997). Of the 60

variables collected, 52 were measured or estimated in the field, 8 more collected via a

GIS and remote sensing data layers.

Statistical methods

Available habitat was defined through the analysis of vegetation data collected at random points within each grid; used habitat was defined by nest-centered vegetation plots. Stepwise logistic regression was used to describe the used vs. available nesting habitat, and then to estimate the relative importance of local vegetation characteristics on the nest success of four sagebrush-steppe associated species. Pre-analysis screening of predictive variables followed Hosmer and Lemeshow (2000), and included graphical analysis (R Development Team 2008), Spearman Rank Correlation (SAS Institute Inc. 2007), and *a priori* determination of important variables to retain based on the literature. Several variables were transformed to achieve normality to meet methodological assumptions, and to linearize relationships with each other. For each variable, the need for and type of transformation was determined by examination of density plots, variable bi-plots, and IV-DV biplots (R Development Team 2008). Seventeen independent variables (of the 60 possible) were retained for analyses with each species (Table 4.2). Model accuracy was assessed using 10-fold cross-validation. Accuracy metrics included percent correctly classified (PCC), sensitivity, specificity, the area-under-curve (AUC) plots, and Cohen's kappa (Fielding and Bell 1997).

RESULTS

We located and monitored the nesting success of over 700 active nests of the four focal species on the 12 nest monitoring plots used in this analysis. Vegetation data was

collected on a subset of these nest sites (Table 4.3, n = 569). Almost 60% of all nests were Brewer's sparrow (Table 4.3). Vegetation at systematic random points (n = 602) on the 12 nest grids were also sampled. Over 20% (n = 101) fell within the treatment "footprint", defining our expectation of "available-treated" habitat. Over 501 random points fell in untreated areas and defined our expectation of "available-untreated" nesting habitat; 15% of these fell within 100 m of a treatment edge (i.e., LANDTRT – PTTRT = 74). Means and standard deviations of the 17 retained variables are presented in Table 4.2 for each species and for random points both in and out of treatment footprint. Note that negative distances to treatment edge (NEARDIST) indicate vegetation plots occurring within treated areas. Almost all nests were located in big sagebrush: 93% of Brewer's sparrow nests, 100% of sage sparrow nests, and 95% of sage thrasher nests. Over 45% of vesper sparrow ground nests were located under either big or low sagebrush.

Most (13 of 17) variables that defined nest sites for each species were significantly different ($\alpha = 0.05$) from the available habitat within treated areas, and several (10 of 17) were significantly different from available habitat within reference areas (Table 4.3).

Vegetation alteration

Vegetation cover variables were measured at the 12 unique nest monitoring grids at 1,171 points from 2004–2006; data from repeatedly sampled points (n = 569) was averaged. Cover variables were used to describe active nest sites for each of the four

focal species, and random points in both treated and reference nest monitoring plots

(Table 4.3). Treatment prescriptions ranged from 28–62% by management area (i.e.,

pasture), but the aerial extent of the treatment "footprint" as implemented ranged from

13–36% (mean 23%) of the pasture, and 23–40% (mean 29%) of the feasibly treatable

areas. This difference largely reflects the area of the reserved vegetation "islands."

Previous studies of the use of aeration equipment in this vegetation type (Summers 2005)

indicated woody shrub kill-rates, by individual plant, to be in the 50–75% range within

the treatment footprint. This was consistent with our observations, and translated to an

average reduction in mean shrub cover within the treatment footprint of 12% (Table 4.3).

Mean shrub cover averaged over 35% across all reference plots, reflecting the

relatively intact state of the vegetation. The mean difference in forb cover ranged from -1

to 9% (mean 0.6%) between reference and treated areas. Mean increase in total grass

cover was 8%; however, native grass cover did not increase in treatment areas.

Compared to the average of random sites, all four bird species used sites with less shrub

density, more dead shrub foliage, taller shrubs, less native grass cover, and more bare

ground cover. As expected, all three sagebrush-steppe associated species used sites with

more shrub cover, and less grass and forb cover than average (Table 4.3).

Used vs. available logistic model results are shown in Table 4.4; models relating

local habitat characteristics to nest success are shown in Table 4.5. Model coefficients

considered significant at an $\alpha = 0.05$ are shown in boldface for both tables. Used vs.

available logistic model fits were, respectively: BRES 29.2, SAGS 42.3, SATH 35.0, and

VESP =33.1. Model fits for the local habitat characteristics related to nest success were,

respectively: BRES 1.7, SAGS 100.0 (non-convergence), SATH 39.0, and VESP =21.2.

Figures 4.2 (a) and (b) show AUC plots for each model and species, and indicate good

overall model accuracy for the used vs. available models, and relatively poor model

performance for all but the SATH and VESP models of local habitat characteristics

related to nest success. Table 4.6 (model 1) gives several model fit statistics based on a

10-fold model cross-validation, including PCC, model specificity and sensitivity,

Cohen's kappa, and AUC. All models showed good PCC, moderate agreement (all kappa

values within the range of 0.41 to 0.60), and AUC values above 0.8.

Many variables were significantly related to the presence of a nest for each

species (Table 4.4). These support a conclusion that each bird had non-randomly

selected consistent nesting habitat characteristics. Variables significantly related to nest

success varied with species. Only the presence of a treatment within 100 m of the nest

(LANDTRT) was considered significantly related to the poorly fit BRES model of nest

success. Shrub density, shrub richness, and forb cover were all negatively related to nest

success in both SATH and VESP. Both species were also positively related to shrub

vigor (% dead foliage).

Results from the nest success model (Table 4.5, Fig. 4.2b) examining which local

habitat characteristics were correlated with nest success were mixed: model fit statistics

were 1.7, 100, 39.0, and 21.2 for BRES, SAGS, SATH, and VESP, respectively.

Brewer's sparrow and sage sparrow models showed poor PCC (<50%), no agreement

(negative kappa values, Table 4.5, model 2), and had low AUC values (<0.5). Sage

thrasher and vesper sparrow nest success models were better behaved: PCC scores were

>80%, showed moderate agreement (kappa within the range of 0.41 to 0.60), and had marginally acceptable AUC values (~0.60).

DISCUSSION

We sought to: (i) describe the selected nesting habitat of four focal species in sagebrush-steppe; (ii) determine if selected nesting habitat is consistent between reference and treatment areas; and (iii), determine which local (vegetation plot scale) habitat characteristics are related to nest success. Our experimental vegetation treatments were designed to mimic current practice, but treatment effects generally achieved fewer of the stated vegetation management goals than expected: native grass and forb cover components were increased by less than 1% (an increase of 15-20% was projected), shrub cover was reduced by 12% (shrub cover reductions of 50-75%% were expected).

Descriptions of nesting habitat characteristics were similar to previous research on each of the four species examined here, although percent shrub cover is at the upper extreme of reported values for all four species (e.g., Rotenberry et al. 1999). Similarly, used habitat differed between these species as expected. The three sagebrush-steppe associated species (Brewer's sparrow, sage sparrow, and sage thrasher) all nested in tall stands of mature sage comprised of fewer, larger shrubs and less grass and forb cover than did vesper sparrow. It is interesting to note that with the exception of percent shrub cover, vesper sparrows selected nesting habitat that was largely indistinguishable from the three sagebrush-steppe associated species in terms of shrub components: density, height, and vigor, implying this is a truly ecotonal species. All four species selected

consistent habitat (no significant differences) between treated and reference areas at fine grains (i.e., variables measured within the 2 m vegetation plot), with the only differences revealed at broader scaled measures (i.e., distance to edge).

The comparison of the reference and treated plot data tells us that the nesting habitat selected by each species is largely consistent over space and time, and remained so even when available habitat was changed considerably. This in turn implies a responsive movement occurred for each species. For example, with 20-40% (mean 28%) of the areal extent of their potential nesting habitat altered, shrubsteppe obligates selected nearby nest sites with the same attributes as before treatment and the same as found on reference plots. Because abundance did not change for at least two of these species, we believe there was a small-scale response to the treatment that involved packing of nests into remaining islands and peninsulas. Brewer's sparrow and sage thrashers maintained consistent nesting densities pre- and post-treatment, suggesting that the scale of packing movements were small because they occurred with the confines of the nest plot. If true, this observed small-scale packing movement also supports the idea that shrubsteppe habitat often is not saturated (Dunning 1986, Wiens and Rotenberry 1987, Wiens 1991, Greene and Stamps 2001), and that local movement can occur in response to disturbance.

The age of the treatment also provided insights into the scale of these movements for two species whose nest densities did change in response to treatment. Sage sparrows did not nest in any treatment plot older than 1 year, apparently moving beyond our plot boundaries. Prior to treatment, sage sparrow were not as uniformly distributed or as abundant as were the other focal species, but the observed relationship between nesting

and treatment was consistent in every site occupied and in all 3 years. These data lend indirect support for observations of sage sparrow sensitivity to patch sizes below 150-200 ha (Martin and Carlson 1998). Our single steppe-associated focal species, the vesper sparrow, reacted in accordance with our expectations by taking advantage of expanded nesting habitat and increasing their mean nest densities by colonizing the treatment areas. But they did not do so until the third year after treatment, reinforcing the idea that lengthy longitudinal studies are required to capture lagged responses to disturbances.

Logistic regression models of used vs. available nesting habitat were well fit and reasonably accurate overall, and largely supported the patterns seen in the descriptive statistics and those expected from prior work. The small scale movement implied for Brewer's sparrow and sage thrasher by the consistency of selected habitat in an inconsistent setting is seen in the significant negative relationship with point treatment and distance to disturbance variables for both birds.

Our third and final objective was to determine which local habitat characteristics were correlated with nest success. Our results here were equivocal. Sage sparrow models did not converge, likely due to small sample size. However, the Brewer's sparrow models were also very poorly fit despite the large sample size. The cause of this poor fit is unknown, but it appears there are no strong relationships between local habitat characteristics, as defined and measured here, and nest success in Brewer's sparrow in our study sites. This may indirectly support the idea that the processes affecting nest predation rates, the dominant cause of nest failure in our study, relate to habitat fragmentation at larger scales than do nesting habitat selection processes (Chalfoun et al.

2002), or that settlement is essentially random once suitable nesting habitat is selected at large scales.

Correlations from sage thrasher and vesper sparrow models were consistent with each other but contrary to our expectations and the literature as we expected them to diverge. Increasing percentage of dead foliage was positively correlated to nest success for both species, and shrub density, shrub richness, and forb cover were all negatively correlated with their nest success. The negative correlation with increasing forb cover warrants brief note, as increasing the forb component was one of the goals of the restoration project. All three of the significant shrub related factors (shrub vigor, shrub density, shrub richness) describe a negative relationship with the shrub structure of altered areas: treatment reduced shrub density, released many other shrub species (e.g., rubber rabbitbrush, *Ericameria nauseosa*) thereby increasing shrub cover richness, and killed mature / senescent sagebrush individuals with higher proportions of dead foliage. However, the lack of significance for both distance-to-treatment measures (point treated and landscape treated) contrasts with these factors, implying an effect exists but that it is either not spatially structured or not related to treatment itself. These results also lack strong correlations with grass cover, shrub height, and bare ground cover, all of which are factors identified in the literature as important to nest success for these species. As our methods of data collection and analysis were largely in keeping with prior practice, these results imply broader scale controls on nest success. It may be that habitat selection for these species is a consistent and hence predictable process, but that nest success is largely

controlled by processes largely insensitive to local habitat characteristics in our study system.

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Table 4.1. Number and area (ha) of nest monitoring plots in each treatment age

category[1]. Eighteen unique nest plots were studied overall: 10 were sampled every

year, four others were sample in two consecutive years, and two were each only

sampled in 2004 and 2006. Twelve plots were used for this study. Plot size was

reduced each year for logistical reasons; as a result all analyses are first standardized

on area searched, then on number of plots per survey year. All but two of the plots

monitored in 2004 were monitored in every subsequent year, and all plots in 2006 but

one were monitored in both prior nesting seasons. Note that: 1) experimental

treatments had not aged into the T+2 and T+3 age categories until 2005 and 2006

respectively, 2) the reference category includes pre-treatment data, and 3) all plots in

all years are treated as independent replicates.

YEAR	Reference	T+1	T+2	T+3	Total
2004	9 (324)	3 (108)	—	—	12 (360)
2005	12 (432)	2 (72)	4 (144)	—	18 (648)
2006	4 (64)	2 (32)	2 (32)	3 (48)	11 (176)

[1] T+ (1:3) columns indicate the number of breeding seasons since mechanical

treatment of vegetation, i.e., if a vegetation treatment occurred prior to the 2005 breeding

season but after the 2004 breeding season, then nest monitoring data collected in the 2005

breeding season were considered to be T+1 samples (e.g., the first breeding season post-

treatment).

Table 4.2. Local vegetation characteristic variables and descriptions.

Variable	Name	Description
SUCCFAIL	Succeed or Fail	Did nest successfully fledge young? Y/N
PTTRT	Point treated	Does point fall into treatment? Y/N
LANDTRT	Land treated	Has landscape been treated? Y/N
ELEV	Elevation	In meters
SLOPE	Slope	Measured in degrees
ASPECT	Linearized aspect	$(((\cos (aspect - 30))) / 180 * \pi) + 1) / 2$
NEARDIST	Distance to nearest edge	Measured in m to nearest artificial edge
SHRBDENS	Shrub density	Shrub density (point-quarter, stems/m^2)
SHRBRICH	Shrub richness	Mean woody shrub species per plot
MEANVIGR	Mean vigor	Mean % dead foliage in standing shrubs
MAXWIEN	Mean max. shrub height	Mean of Wiens pole maximums, in dm
CVRSHRB	Cover of shrubs >10 cm	Mean of shrub cover
CVRGRAS	Cover of grasses	Daubenmire mean grass cover
CVRGRSNT	Cover of native grasses	Daubenmire mean native grass cover
CVRFORB	Cover of forbs	Daubenmire mean forb cover
CVRLITT	Cover of litter	Daubenmire mean flitter cover
CVRBARE	Cover bare	Daubenmire mean bare ground cover
NSHRBHEI	Nest shrub height	Nest shrub height, in cm

Table 4.3. Descriptive statistics for retained variables. Sample sizes and means (SD) are given, see Table 4.2 for variable descriptions

	Treated	Reference	BRES	SAGS	SATH	VESP
n	101	501	340	28	122	79
PTTRT	101	0	39	3	14	30
LANDTRT	101	74	142	5	48	41
ELEV	2034 (44)	2053.31 (69.67)	2040 (58.03)	2021 (40.2)	2029 (39.53)	2042 (54.32)
SLOPE	3.0 (5.33)	4.5 (5.69)	5.0 (4.44)	4.0 (3.72)	4.0 (3.6)	4.0 (6.58)
ASPECT	0.513 (0.38)	0.6095 (0.35)	0.646 (0.34)	0.461 (0.38)	0.591 (0.35)	0.562 (0.35)
NEARDIST	-27 (654.96)	1178 (4158.98)	494 (839.45)	741 (647.15)	421 (732.09)	324 (672.65)
SHRBDENS	0.46 (0.46)	0.52 (4.5)	0.24 (0.24)	0.13 (0.07)	0.30 (0.22)	0.35 (0.42)
SHRBRICH	2.2 (0.60)	3.2 (2.23)	2.9 (2.02)	2.7 (1.05)	2.6 (1.65)	2.7 (1.76)
SHRBVIGR	10.9 (11.33)	10.9 (14.51)	12.5 (13.02)	15.9 (13.12)	18.1 (15.31)	17.8 (19.6)
MAXWIEN	4.5 (2.51)	4.5 (2.45)	5.1 (2.56)	5.3 (2.4)	5.1 (2.54)	5.1 (2.56)
CVRSHRB	23.0 (16.24)	35.6 (20.8)	38.9 (20.52)	41.7 (20.03)	39 (18.11)	23.7 (15.17)
CVRGRAS	29.0 (16.74)	21.0 (14.0)	23.1 (15)	15.7 (12.74)	25.3 (16.65)	27.5 (16.98)
CVRGRSNT	7.7 (11.77)	9.1 (9.44)	4.4 (6.57)	5.8 (13.17)	3.2 (4.38)	6.2 (11.61)
CVRFORB	13.7 (11.33)	13.1 (12.8)	11.6 (11.95)	7.2 (6.76)	13.1 (14.88)	12.1 (10.02)
CVRLITT	7.2 (6.45)	8.2 (11.35)	7 (11.12)	7.5 (8.8)	6.1 (8.18)	5.5 (4.34)
CVRBARE	16.3 (14.32)	16.4 (14.89)	25.4 (20.58)	27.3 (22.55)	28 (20.68)	31.9 (23.05)
NSHRBHEI	___	___	31.5 (13.11)	25.3 (6.5)	27.2 (14.23)	4.1 (10.79)

Table 4.4. Local nesting habitat: used vs. available logistic model results. Variables considered significant ($\alpha = 0.05$) are in boldface.

	BRES		SAGS		SATH		VESP	
	Est (SD)	z (Pr(>|z|))	Est (SD)	z (Pr(>|z|))	Est (SD)	z (Pr(>|z|))	Est (SD)	z (Pr(>|z|))
Intercept	-0.58 (0.96)	-0.61 (0.54)	**27.35 (9.91)**	**2.76 (0.01)**	**-4.65 (0.88)**	**-5.32 (0.00)**	**-1.99 (1.01)**	**-1.96 (0.05)**
PTTRT(Y)	**-0.97 (0.30)**	**-3.25 (0.00)**	---	---	**-1.01 (0.41)**	**-2.47 (0.01)**	---	---
LANDTRT(Y)	**0.73 (0.25)**	**2.90 (0.00)**	---	---	---	---	---	---
ELEV	---	---	**-0.01 (0.01)**	**-2.45 (0.01)**	---	---	---	---
SLOPE	**0.47 (0.12)**	**3.99 (0.00)**	---	---	---	---	---	---
ASPECT	0.39 (0.26)	1.51 (0.13)	---	---	---	---	---	---
NEARDIST	**-0.00 (0.00)**	**-2.65 (0.01)**	---	---	**-0.00 (0.00)**	**-5.04 (0.00)**	**-0.00 (0.00)**	**-2.96 (0.00)**
SHRBDENS	**-2.78 (0.55)**	**-5.08 (0.00)**	**-7.15 (1.99)**	**-3.60 (0.00)**	-1.04 (0.71)	-1.47 (0.14)	**-3.63 (0.94)**	**-3.85 (0.00)**
SHRBRICH	-1.25 (0.69)	-1.82 (0.07)	-3.33 (2.25)	-1.48 (0.14)	---	---	---	---
SHRBVIGR	---	---	0.18 (0.13)	1.46 (0.15)	**0.17 (0.07)**	**2.58 (0.01)**	**0.20 (0.07)**	**2.83 (0.01)**
MAXWIEN	**0.11 (0.04)**	**3.26 (0.00)**	**0.20 (0.09)**	**2.10 (0.04)**	**0.13 (0.05)**	**2.51 (0.01)**	0.09 (0.06)	1.53 (0.13)
CVRSHRB	0.70 (0.38)	1.85 (0.07)	**2.97 (1.12)**	**2.66 (0.01)**	**1.65 (0.59)**	**2.80 (0.01)**	**-2.37 (0.76)**	**-3.13 (0.00)**
CVRGRASS	**0.18 (0.06)**	**2.95 (0.00)**	---	---	**0.23 (0.09)**	**2.64 (0.01)**	**0.35 (0.10)**	**3.43 (0.00)**
CVRGRSNT	**-0.91 (0.09)**	**-10.39 (0.00)**	**-0.76 (0.25)**	**-3.08 (0.00)**	**-1.09 (0.13)**	**-8.24 (0.00)**	**-0.76 (0.15)**	**-5.21 (0.00)**
CVRFORB	**-0.50 (0.07)**	**-7.59 (0.00)**	**-1.34 (0.25)**	**-5.35 (0.00)**	**-0.69 (0.10)**	**-6.60 (0.00)**	**-0.76 (0.12)**	**-6.15 (0.00)**
CVRLITT	**0.44 (0.07)**	**6.28 (0.00)**	0.32 (0.20)	1.59 (0.11)	**0.41 (0.10)**	**4.02 (0.00)**	**0.28 (0.12)**	**2.33 (0.02)**

Table 4.5. Local nesting habitat: nest success logistic model results. Variables considered significant ($\alpha = 0.05$) are in boldface.

	BRES		SAGS		SATH		VESP	
	Est (SD)	z (Pr(>|z|))	Est (SD)	z (Pr(>|z|))	Est (SD)	z (Pr(>|z|))	Est (SD)	z (Pr(>|z|))
Intercept	0.34 (0.35)	0.99 (0.32)	-2441 (473806)	-0.01 (1.00)	**8.73 (3.47)**	**2.52 (0.01)**	**8.73 (3.47)**	**2.52 (0.01)**
PTTRT(Y)	---	---	---	---	---	---	---	---
LANDTRT(Y)	**0.45 (0.23)**	**1.99 (0.05)**	---	---	---	---	---	---
ELEV	---	---	---	---	---	---	---	---
SLOPE	---	---	---	---	---	---	---	---
ASPECT	---	---	693 (136166)	0.01 (1.00)	---	---	---	---
NEARDIST	---	---	1.052 (204)	0.01 (1.00)	---	---	---	---
SHRBDENS	---	---	2843 (551199)	0.01 (1.00)	**-4.39 (1.81)**	**-2.42 (0.02)**	**-4.39 (1.81)**	**-2.43 (0.02)**
SHRBRICH	---	---	---	---	**-5.77 (2.21)**	**-2.61 (0.01)**	**-5.77 (2.21)**	**-2.61 (0.01)**
SHRBVIGR	---	---	235 (46028)	0.01 (1.00)	**0.28 (0.11)**	**2.43 (0.02)**	**0.28 (0.11)**	**2.43 (0.02)**
MAXWIEN	-0.06 (0.04)	-1.46 (0.15)	-282 (54778)	-0.01 (1.00)	---	---	---	---
CVRSHRB	---	---	---	---	---	---	---	---
CVRGRASS	---	---	---	---	---	---	---	---
CVRGRSNT	---	---	---	---	---	---	---	---
CVRFORB	---	---	---	---	**-0.34 (0.13)**	**-2.56 (0.01)**	**-0.34 (0.13)**	**-2.56 (0.01)**
CVRLITT	---	---	---	---	---	---	---	---

Table 4.6. Accuracy metrics for logistic models.

	Model[1]	PCC	Specificity	Sensitivity	Kappa	AUC
BRES	1	339	469.03	0	0	-4.601 (5.35)
BRES	2	1	1.07	338	467.96	0.025 (0.13)
SAGS	1	1	0.11	337	467.85	0.003 (0.00)
SAGS	2	1	0.04	336	467.85	-0.003 (0.03)
SATH	1	1	2.28	335	465.52	0.000 (0.00)
SATH	2	1	0.03	334	465.49	0.184 (0.35)
VESP	1	1	0.42	333	465.07	0.007 (0.01)
VESP	2	1	1.55	332	463.52	-0.070 (0.05)

[1]Logistic model 1 = used vs. available nesting habitat; logistic model 2 = local habitat characteristics related to nest success.
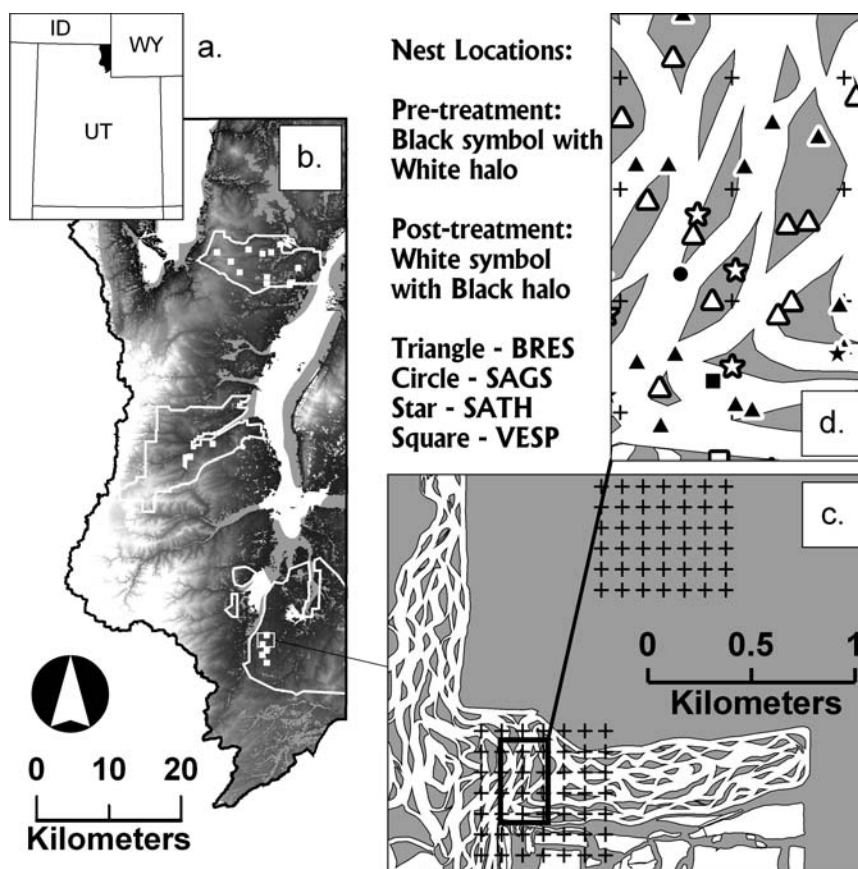
Figure 4.1. Maps of nest grids and nests. Inset map a shows relative the position and size of Rich Co. in North America, inset map b shows the extent of sagebrush-steppe (shaded areas), pasture boundaries, and nest monitoring grid locations (n = 18, white squares) in Rich County, inset map c. shows a close-up of two 36 ha nest monitoring plots (grids of black crosses, 100m spacing) and mosaic treatment design (in white), and inset map d shows nest locations for Brewer's sparrow (triangles), sage sparrow (circles), sage thrasher (stars), and vesper sparrow (squares). Pre-treatment nest locations are black symbols haloed in white, post-treatment nest locations are white symbols haloed in black.
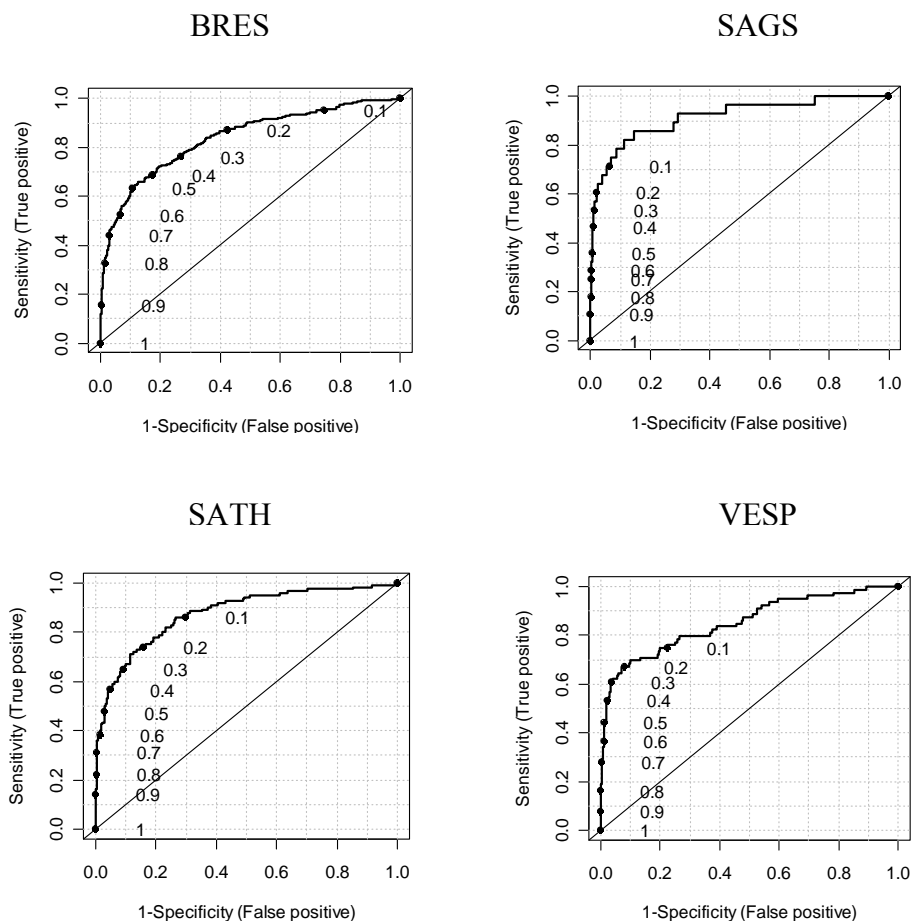
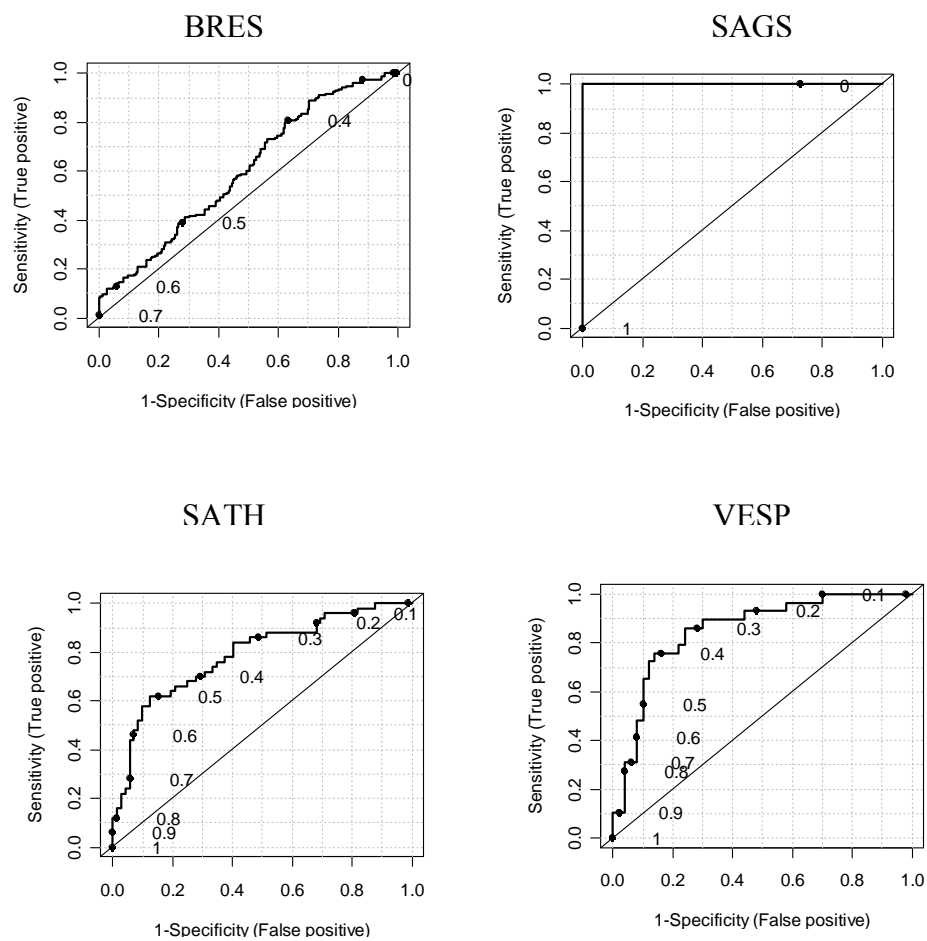Figure 4.2a. Area under curve (AUC) plots for used vs. available logistic models.

Figure 4.2b. Area under curve (AUC) plot for nest success logistic models.

CHAPTER 5

THE EFFECT ON NON-TARGET SPECIES OF HABITAT RESTORATION

IN THE SAGEBRUSH-STEPPE

INTRODUCTION

Past and future treatment context

Restoration treatments (*sensu* Olson and Whitson 2002) are planned throughout the Great Basin, with the loosely stated goal of improving sage-steppe ecosystem health by manually restoring endemically scaled disturbance regimes. Roughly 400,000 ha (~1 million acres) of shrubsteppe vegetation is slated for restoration treatments by 2009 in Utah alone. This resurgence of management activity is in part a reaction to observed large-scale and long-term declines in both shrubsteppe wildlife and rangeland-based lifestyles, and partly in recognition that the last 30 years of neglect cannot be considered benign.

Given the changed circumstances since the last major implementation of shrubsteppe vegetation treatments in the 1970s, both ecologically and politically, fire (prescribed or wild) is likely to result in extensive type conversions to undesirable annual exotic grasses and forbs (at least at low elevations - Crawford et al. 2004). Given the generally negative public reaction to the chemical treatments of the past, mechanical disturbance is likely to be the primary technique employed by management agencies. These are not, however, the historic disc-and-seed mechanical treatments designed for forage, but are intended to promote the recovery of shrubsteppe habitat in time. The

mosaic layout and moderate treatment proportions prescribed in the restoration treatments studied here are being promoted as both beneficial to the health of the ecosystem and the health of rangelands-dependent local economies. While the expected benefits are believed to accrue at multiple scales, not all species are expected to benefit equally, and not all species are expected to benefit at all scales.

In terms of anthropogenic disturbance, mechanical treatments are not well studied in the pre-scale field experiment paradigm (Castrale 1982, Kerley and Anderson 1995). While the newer forms of intentionally benign mechanical treatments are less well studied in terms of shrubsteppe bird responses when compared to fire and chemical treatments, expected responses to mechanical treatments may have parallels in previous studies of prescribed- and wild-fire, and chemical spraying. The modern mechanical approach is considered a more discrete, more targeted and tailored approach, and most of all is less likely to cause a type conversion to exotic annual grasses and forbs. They also create edges that are less abrupt, in terms of the structural changes over distance, and create a less severe contrast-edge type.

What is likely to be the effect of these planned large-scale treatments? There are three main lines of evidence to consider. Reliable data from the large-scale "shrub eradication" treatments of the 1950-70's for non-game species is either non-existent or equivocal, but more recent lines of evidence (e.g., Knick and Rotenberry 1995, 2000, 2002, Dobkin and Sauder 2004) and arguments (e.g., Knick et al. 2003, Crawford et al. 2004) suggest links between observed long-term population declines in sagebrush-steppe bird species and the large-scale type conversion projects of the past. These links are

correlational at best, and relate most to habitat loss, fragmentation, and secondary

processes, such as the loss of habitat quality through invasive plant species. But many of

these same authors caution that we cannot rule out the concurrent and likely synergistic

changes in migratory and over-wintering habitats, many of which have been equally

widely altered and reduced (e.g., Bock 1984, Bock and Bock 1999).

Early experimental studies in shrubsteppe systems (Howe et al. 1996) ground our

current understanding of species-habitat associations. Importantly, these were also a

fertile bed for the conceptualizations of scale and non-linearity in ecological systems that

now pervade ecological thought. Despite this attention, however, no casual links

between fragmentation and the loss of habitat suitability have been defined, nor have

mechanisms been conclusively established. Ironically, the conceptual importance of

scale also calls into question some of the generalizability of the results from these

typically small extent and fine grained studies when applied to large extent mechanical

treatments. Because habitat selection is a scale-dependent process (e.g., Chalfoun and

Martin 2007), it is difficult to separate effects from the scale (extent, grain) at which the

treatments were applied, and the scale at which they were studied. Analogously,

typically short-duration studies of treatment effects and habitat relationships are both

subject to landscape history (Knick and Rotenberry 2000), and ecological history (Wiens

and Rotenberry 1985, Van Horne et al. 1997, Misenhelter and Rotenberry 2000, Remes

and Martin 2002, Shochat et al. 2005). Further, the majority of avian studies done on

treatments are based on treatments intended to be type conversions (i.e., the treatment

goal was "sagebrush control"), occurred in related habitats (e.g., grassland or pinyon-

juniper), used non-mechanical forms of disturbance (e.g., fire, chemical) or used mechanical forms guaranteed to convert the habitat (e.g., disc-and-seed). They were also most often natural experiments (*sensu* Diamond 1986) and hence were difficult to randomize or replicate at meaningful ecological time-or spatial scales.

Evidence from recent large-scale studies and simulations (Vander Haegen et al. 2000, Knick and Rotenberry 2002, Wisdom et al. 2002a, 2002b, 2005, Vander Haegen 2007) suggest that interactions among scales influences habitat selection, that temporal effects such as weather on demographics may be large and unpredictable (see Perritt and Best 1989, Rotenberry and Wiens 1991, Van Horne et al. 1997, Mahony et al. 2006, Preston and Rotenberry 2006), and that these may mask detection of ecological relationships (i.e., lagged responses to habitat and predation risk - Bolger et al. 1997, Arlt and Part 2007).

In order to answer the question whether species-specific responses to large scale mechanical treatments consistent across time, space, and sagebrush-steppe bird species, we studied habitat occupancy, relative abundance, habitat preferences and associations at multiple scales, and nest success of four bird species across replicated mechanical treatments in Rich County over 3 years. These four focal species are common, widespread, and are considered essential members of the sagebrush-steppe avifauna. Three of these, the Brewer's sparrow, the sage sparrow, and the sage thrasher, are considered sagebrush-steppe obligate birds (Braun et al. 1976, Knick et al. 2003), and are in regional population declines severe enough to warrant inclusion on several state species of concern lists (Gorrell et al. 2005). Work by Vander Hagen et al. (2000) and

Vander Hagen et al. (2007) also indicates that local breeding densities all four of these focal species are sensitive to the proportion of the landscape that had been converted to non-shrubsteppe habitats. In addition, all four species are sensitive to fragmentation of landscape-level habitat, albeit at different levels. Each species also has documented differences in nesting habitat preferences (Martin and Carlson 1998, Reynolds et al. 1999, Rotenberry et al. 1999, Jones and Cornely 2002).

My treatments were mix of case-control and BACI design elements, and set in a large-scale field experiment setting. Treatment prescriptions were intentionally light but large, and designed to mimic current management prescriptions being applied in the sagebrush-steppe. Intensity was typically a one-pass (Lawson aerator) intended to achieve a 50-75% reduction in shrub cover without losing the native understory grass and forb components. It was applied to approximately 20% of the areas having mature (mean >30%) shrub cover, and laid out in a mosaic pattern that left islands and peninsulas of intact habitat throughout. Treatment proportions, as actually implemented, ranged from 3.9% to 26.2% (49 to 265 ha) overall, and treatment proportions of actually "treatable" area (e.g., areas without steep slopes, rock outcrops, or poor soils with little shrub cover) ranged from 4.2% to 22.6%.

Research summary

Our broad research goal was to investigate sagebrush-steppe passerine bird habitat associations at multiple temporal and spatial scales. The sagebrush-steppe system can be thought as the integration of ecological and anthropogenic effects and processes

operating at different, overlapping scales. We investigated several of these effects through variables directly and indirectly postulated to be linked to sagebrush-steppe avifauna. Examples of direct measures included the areal extent of potential nesting habitat, and the linear distance to artificial edges. Indirect measures include the nest plot's size (36 ha), an extent that implicitly scales much of this work by bounding our observed patterns seen in habitat preference and habitat quality. Spatial measures also incorporated the effects of area at different ecological scales (nest site, territory, and landscape) in an attempt to include ecologically meaningful extents in the analyses. Temporal measures included seasonal and annual effects, and were designed to detect lagged responses should they occur. We argue that time-based studies are necessary in order to describe the effects of restoration treatments on nesting success, on habitat preference and quality, overall bird abundance, and on habitat occupancy.

The objective in Chapter 2 was to examine the local-to-landscape scale effects of mechanical restoration treatments on local extirpation and abundances of nine passerine birds: 3 sagebrush steppe-obligates, 3 shrub-associated, and 3 steppe-associated. In general, the occupancy models indicated that the study species were relatively insensitive to change in habitat quality. Similarly, the abundance models showed only broad declines in overall pooled species numbers, and while the group identified as sagebrush-steppe obligates declined, so did most others. Functionally, the species that declined most, and most consistently over time, were those strongly associated with shrubs in general (i.e., green-tailed towhee, gray flycatcher).

The objective in Chapter 3 was to examine the effect of changing the availability of nesting habitat on both the attractiveness and quality of an area at multiple spatial extents. The results confirmed the need for long-term study effects due to lagged responses in expressed preference and changes to habitat quality. Time since treatment affected nest success in 2 of the 4 species (Brewer's sparrow and vesper sparrow), yet the changes in habitat quality did not forecast changes in habitat preference as expected. For example, sage sparrow nest success was indistinguishable between pre- and first year post-treatment, but all nesting efforts ceased beyond the second year. This suggests a change in habitat preference for this species. For the other three species, non-adaptive mismatches seemingly occurred as habitat preference indicated a potential for treatments to create benign appearing "sink" habitat for species that remained. Further evidence indicating the umbrella species concept is misapplied at this scale came from the inconsistent responses to treatment within the shrubsteppe-obligate category. While each species' response was consistent between plots and over time, responses to treatment varied in scale, timing, and direction among the study species.

Patterns of nest density and nest site descriptions demonstrated population-level movement in response to treatments, with both Brewer's sparrow and sage thrasher maintaining similar pre- and post-treatment nest densities and nest site characteristics. This suggests that these species simply moved nest sites to remaining habitat areas, and was supported by the mapped locations of nest sites pre- and post-treatment (e.g., Fig. 3.1). Unfortunately, the larger scale responsive movement observed in both the sage

sparrow and the vesper sparrow, out of and into the nest plot respectively, does not inform the saturation question.

The objective in Chapter 4 was to describe nesting habitat characteristics for the four focal species, test if the selected nesting habitat is consistent between pre– and post-treatment and between treated and reference areas, and to determine which habitat characteristics, including distance to disturbance, are related to nest success. Descriptions of nesting habitat characteristics support previous work in terms of structural characteristics, with the exception that the measures of shrub cover reported here are at the upper end of ranges reportedly used for all four species. Nesting habitat characteristics were also largely consistent between pre-and post treatment, between years, and between reference and treatment sites, further supporting the responsive movement documented in Chapter 3. Habitat selection was consistent even when the available habitat was not, implying that these species are in fact choosing these sites and not merely settling in proportion to availability. However, selected nesting habitat was not strongly tied to nest success at local (nest) scale. Further, nest success in three of the four focal species was negatively related to qualities of the landscape that the treatment was designed to enhance (e.g., grass cover, forb cover, reduced shrub cover).

Focal species-specific results

Brewer's Sparrow.—Similar to other recent work (Mahony et al. 2006, Chalfoun and Martin 2007, Vander Haegen 2007), Brewer's sparrows experienced relatively low overall nest success: 42% mean success rate in untreated areas. Most nest loss (>80%)

was due to nest predation, although losses due to weather were ephemerally important in some years (e.g., 2004) and in some periods (e.g., early spring of 2006). The general pattern of our data does not support the concept of habitat occupancy as a consistent predictor of local habitat quality for Brewer's sparrow, at least within a four year post-treatment window. The large extent (>1200 m) presence/absence model from Chapter 2 showed no differences in habitat occupancy with treatment age, but after an initial increase over the pooled reference sites, the mean number of nests, eggs, and fledglings per ha all declined with treatment age. Overall, Brewer's sparrow breeding habitat quality, but not it attractiveness, appears to be negatively impacted by the treatments, although the specific mechanism is not clear.

Sage Sparrow. —Models of habitat occupancy indicated no treatment and treatment age effects on sage sparrows, and the sparrow nested in the vicinity of all treated plots where they had been previously observed. Models of abundance indicated a slow and steady decline in overall numbers, a pattern in overall abundance counter to the lagged response seen by Wiens et al. (1986). Despite treatments that directly impacted <20% (and as low as 5%) of all available, similar-appearing habitat, nesting sage sparrow nests were not found in treated areas after the first breeding season post-treatment. While the observed abandonment of fragmented areas supports existing studies (Rotenberry and Wiens 1980, Knick and Rotenberry 1995, Knick 1999, Vander Haegen et al. 2000, Vander Haegen 2007), both the severity and uniformity of the observed reaction here sets a new, lower, limit on the extent and intensity of tolerable disturbance for this species. The duration and consistency of these effects remains to be seen.

Sage Thrasher. —Sage thrasher responses to our treatments were considerably smaller in magnitude than predicted. The daily nest survival rates varied more as a consequence of annual variation in weather and climate than they did because of treatment and treatment age. Nor were there any observed differences in number of nests, clutch size, or numbers of fledglings in relation to treatment age. It appears that the treatments, as implemented, had little or no effect on sage thrasher nest survival rate, nest density, clutch size, or number of fledglings. Interestingly, most previous work has found strong correlations between Brewer's sparrow and sage thrasher habitat selection and response to fragmentation. Our results do not show similar responses to treatments, although we did limit our analysis to a fine-grained spatial perspective over a large extent.

Vesper Sparrow. —The last focal species, the vesper sparrow, is also the most general in its reported habitat selectivity. Considered a shrub specialist in the grasslands (Fletcher and Koford 2002, Lueders et al. 2006), a grassland specialist in contiguous shrubsteppe (Wiens and Rotenberry 1980), and a generalist in fragmented shrubsteppe landscapes (Vander Haegen et al. 2000, Vander Haegen 2007), the vesper sparrow was an excellent candidate for a species we expected to react immediately and positively to the treatments. While results generally conformed to expectations in terms of pattern, post-treatment gains in abundance were not maintained as treatments aged, and nest density did not increase until the third breeding season post-treatment. Nest density, daily nest survival rate, clutch size, and mean number of fledglings all increased initially with treatment over reference sites, though none of these parameters except nest density were

maintained beyond the second breeding season post-treatment, and nest success rates were ultimately lower in the preferred, treated, habitat.

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APPENDIX

Appendix

    Criteria used to determine nest fate. See Table A.1 for specifics. Some criteria were

sufficient (e.g., adults feeding dependent fledglings, dead nestlings), others were used in

a preponderance of evidence fashion (e.g., nest edge flattening or nesting material

disturbance can support either fledging or predation events depending upon the degree of

severity). If no definitive evidence was found (on follow-up visit) and if collateral

evidence was either conflicting or absent, then nests were coded as "fate – unknown" and

were not include in the analysis of DSR due to the potential for bias (Weidinger 2007) (n

= 417, or 19.3% of all nests located in the study). This value includes nests of all species

(not just focal four) across all years, and includes nests which were never determined to

be active or were not definitively from the survey year. Suspected "old" nests and nests

not clearly active were monitored for activity as several were either reused or later

became active after a hiatus.

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    estimates. Journal Of Ornithology **148**:207-213.

Table A.1. Criteria used to determine nest fate.

Fate	Evidence used to establish fate
Successful	Young observed leaving nest; adults attending/feeding appropriately aged young in territory; adults/young calling in vicinity, fecal droppings outside nest; flattened but otherwise undisturbed nest material.
Failed - Predated	Nest destroyed; eggs or immature nestlings destroyed or missing; nest lining torn out; contents missing prior to earliest fledging possible date
Failed - Abandoned	Eggs/nestlings intact but dead
Failed - Other	Preponderance of evidence leans toward failure and evidence of successful fledging absent on two visits; evidence of definitive non-predation event (e.g. livestock trampling)

CURRICULUM VITAE

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EDUCATION:

B.A. in Biology and Environmental Studies, Colby College, Waterville, Maine. (1/87)

GPA:3.2 (4.0=A) Dean's List. M.S. Zoology and Physiology, University of

Wyoming, Laramie, Wyoming. (12/97) GPA:3.98 Minor: Statistics, Emphasis in

Avian Ecology. Ph.D. in Ecology, Utah State University, Logan, Utah. (expected

7/08) GPA: 3.76 Emphasis in Wildlife Ecology. Dissertation research collected in

Rich County, Utah, 4/04 – 8/06.

EXPERIENCE:

UTAH PARTNERS IN FLIGHT COORDINATOR, Utah Division of Wildlife

Resources, Non-game Avian Program, Salt Lake City, Utah (11/07 – present).

Research: Directing statewide bird conservation efforts, coordinating state, federal,

and private partners research programs and management policy and actions; consult

with cooperators on bird research with emphasis on sampling theory, study design,

and data analysis. Supervise three long-term and large-scale research programs

with 3 permanent staff and 27 seasonal staff.

Management: write grants and manage program budgets; hire train and supervise

field team leaders with to manage field crews throughout the state.

AVIAN ECOLOGIST, Utah Division of Wildlife Resources, Non-game Avian

Program, Salt Lake City, Utah (1/98 – 11/07)

Research: conducted, analyzed, and supervised statewide habitat-based field studies
to monitor bird population abundance and trend in a variety of Utah habitats;
designed, built, and manipulated large relational databases for use in analyses (e.g.,
trend studies on 15 years of statewide riparian bird population monitoring data and
habitat-association analyses on same plus 4 iterations of statewide vegetation plot
data); conducted Non-game Avian Program analyses including: calculating local
and regional measures of diversity, estimating density using distance sampling
(program DISTANCE) and information-theoretic techniques, deriving population
trends using regression and GLM/GAM methods, modeling multivariate bird-
habitat associations and spatial analyses using non-parametric and non-linear
methods; compiled QA/QC, and analyze statewide bird datasets for peer-reviewed
publication and internal reports.

Management: Hired, trained, and supervised field crews of up 15 people; provided
crews (UDWR in-house and regional offices, USFS, BLM, NPS field crews) with
training in field skills (including bird ID by sight and sound), survey techniques
(including point count, point transect, line transect, spot mapping, constant-effort
mist netting, and tape-playback), and statistical methods training; nstructed a
workshop in translating distance sampling theoretical principles into practical field
studies at a national professional meeting; consulted on sampling design and
analysis issues with cooperators.

WILDLIFE TECHNICIAN, UDWR Non-game Avian Program, Salt Lake City, Utah
(5/97 – 11/97)

Research: Assisted with the design and establishment of riparian bird surveys, using both point count (ID by sight and sound) and constant-effort mist netting (MAPS) methodologies to track avian species populations, distributions, and habitat association; conducted point count and point transect surveys, collected vegetation and GPS location data; entered & plotted data, and assisted in data compilation for reports; completed an in-depth analysis of local scale bird-habitat associations on restored and reference sections of the Provo and Jordan Rivers (for the Utah Reclamation and Mitigation Commission) as a special project.

RESEARCH ASSISTANT, University of Wyoming, Laramie, Wyoming (4/95-5/97)

Designed, conducted, & analyzed a two-year field study of riparian avian-habitat associations in an urban-to-rural gradient of matrix development in the Salt Lake Valley, UT; Data collection methods included: a modified point transect approach (unlimited with distance estimations, ID by sight and sound, mapping), vegetation plots, and aerial photo interpretation. Statistical analyses included: regression (weighted, multiple, logistic, and Poisson), bootstrapping, multivariate methods (cluster, discriminant, PCA), and non-parametric techniques; consulted with USFWS and the UT Reclamation and Mitigation Commission on riparian habitat restoration for desirable native bird species.

BIOLOGICAL TECHNICIAN, University of Wyoming, Laramie, Wyoming (1/95-4/95)

Assisted a radio-telemetry study of Northern Goshawk migration and winter range in Wyoming and Colorado; fit birds with transmitters and tracked daily movements in the backcountry from 12-element tower antennas.

WILDLIFE TECHNICIAN, USFS, Ashley NF, Manila, Utah (5/91-1/95).

Designed, conducted, and analyzed year-round inventory and monitoring surveys for Threatened, Endangered, and Management Indicator Species in the Uinta Mountains, with an emphasis on avian species. Data collection methods included: fixed radius point counts (bird ID by sight and sound), vocalization tape play-backs, small mammal trapping, and snow track/trail analysis. Hired, trained, and supervised field crews of up to six, collaborated on various GIS projects (including developing a spatially explicit nesting-habitat model for Northern Goshawks in the Uinta Mountains).

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