AN ABSTRACT OF THE THESIS OF

Cortnie M. Krissman for the degree of Master of Science in Wildlife Science
presented on December 15, 2005.
Title: Range-wide Abundance and Fluctuating Asymmetry Patterns of Sagebrush-obligate Passerine Birds

Abstract approved:

W. Daniel Edge

North American sagebrush (*Artemisia* spp.) ecosystems are suffering from reductions in habitat extent and quality. Only about 50% of sagebrush remains from pre-settlement conditions, and much of the remaining habitat is fragmented or degraded by invasive species, fire suppression and overgrazing. Sagebrush-obligate species are experiencing population declines as a result of these ecosystem changes. To effectively conserve this ecosystem, it is essential to understand patterns of abundance and stress of the inhabitants at the landscape-level. Abundance of species across their geographic range is not uniform. Instead, abundance often decreases towards the periphery of the range where resources and habitat conditions become less suitable. In addition, stress in populations closer to the periphery of the range may be expressed in condition-dependent traits where suboptimal environmental conditions occur. Fluctuating asymmetry, random deviations from perfect symmetry in bilateral body parts, may reveal increased stress in these populations. I examined patterns of abundance and fluctuating asymmetry of Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphisipiza belli*), and Sage Thrasher (*Oreoscoptes montanus*), in the western United States, to determine how these responses vary with proximity to range periphery of sagebrush. Using negative binomial regression and Akaike's Information Criterion, I investigated associations between species abundance from North American Breeding Bird Survey count data and several local- and landscape-level variables derived from digital maps depicting the distribution of sagebrush throughout the United States. Abundance for these three sagebrush-obligate passerine birds was greatest in mid-elevation (1,200-2,300 m) areas and increased with sagebrush cover. I found little support for abundance declining as a function of proximity to range periphery. Using mixed model regression, I assessed the relationship between fluctuating asymmetry estimates in the tarsi of juveniles and the proximity of specimens to the periphery of sagebrush distribution. I predicted higher levels of fluctuating asymmetry in individuals nearer the range periphery. However, fluctuating asymmetry decreased with proximity to the range periphery for Sage Sparrow, and, although present Sage Thrasher, fluctuating asymmetry did not differ significantly across the geographic range for this species. Fluctuating asymmetry could not be estimated with confidence for Brewer's Sparrow. While this study revealed stress in these species, a more logistically complex

study to evaluate fluctuating asymmetry patterns across the landscape is necessary for determining areas of conservation priority. Loss of areas of high percent sagebrush cover due to habitat fragmentation and degradation will result in continued declines in abundance of sagebrush-obligate passerine birds. Knowing high abundances of sagebrush-obligate passerine birds occur in locations with high sagebrush cover at mid-elevations will aid land managers and conservation biologists in designing effective conservation strategies for these species.

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Range-wide Abundance and Fluctuating Asymmetry Patterns of Sagebrush-obligate Passerine Birds

by

Cortnie M Krissman

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented December 15, 2005
Commencement June 2006

Master of Science thesis of Cortnie M Krissman presented on December 15, 2005.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Cortnie M Krissman, Author

ACKNOWLEDGEMENTS

I feel extraordinarily fortunate to have had so many outstanding colleagues, supporters, and mentors on my journey through the completion of this research. My major advisor, Dan Edge, gave me continuous support and guidance, no-nonsense truths, and was always a delight to be around. Committee member, Laura Nagy, was a voice of positive reason, provided limitless guidance and advice, noticed the details, and was a wonderful mentor. Committee member, Cliff Pereira, provided me with abundant early morning statistical advice. I was blessed to have had such a wonderful support system for advice and encouragement. Much appreciation is due to Judy Li who served as Department Representative during my proposal review and to Steve Sharrow who served as Graduate Council Representative for my defense.

Funding from the Oregon State University, Department of Fisheries and Wildlife Department, Oregon Supplemental Laurels Scholarship, Henry Mastin Graduate Fund Award, and Pam and Paul Krissman made this research possible.

Carolyn Riemer and Suzanne Austin-Bythell made the field season more productive and memorable. John Sadowski and Fred Taylor of the Bureau of Land Management were critical support systems while we were in the field. The following museums allowed me access to their specimens and exposed me to an aspect of research I will fondly remember: National Museum

of Natural History, Smithsonian Institution; Museum of Vertebrate Zoology, University of California, Berkeley; Department of Fisheries and Wildlife, Oregon State University; Burke Museum, University of Washington; and Slater Museum of Natural History, University of Puget Sound. My appreciation goes to the efforts of thousands of North American Breeding Bird Survey volunteers and researchers, as well as Patrick Comer, Steve Knick and all the USGS researchers who provided fantastic digital habitat distribution data. Doug Robinson provided conceptual ideas during the beginning of this research, and Doug and Tara Robinson's early encouragements helped make my success here possible.

Graduate degrees, and for that matter any research, should not be attempted and likely cannot be successful without the support of fellow graduate students, many of whom, if you are as lucky as I, become life-long friends. Becky Flitcroft is an angel and GIS goddess and I am grateful to her for the many hours she spent working with me. Ian Rose helped me keep my sanity on many late-nights. I will always treasure the intriguing discussions of statistics Dan Rizzolo and I shared. Adrian Gall, and many, many others, stood by me during one of my hardest struggles. My endearing love to Lisa Sheffield, Aimee McIntyre, Randy Moore, Lisa Miller, Christina Romagosa, Sasha Lewis, Anne Mary Myers, and Lyndsay Frady; my life would be nothing without you. Finally, I would like to thank Mom, Dad, and Chole who selflessly gave me endless support and unconditional love.

CONTRIBUTIONS OF AUTHORS

Chapters two and three are formatted for submission to peer-reviewed journals. W. Daniel Edge contributed to the writing of each manuscript. Chapter 2, *Abundance Patterns of Sagebrush-obligate Passerine Birds in Western North America*, will be submitted to Landscape Ecology. Chapter 3, *Is Stress Related to Location of Development within Geographic Range of Sagebrush-Obligate Passerine Birds?*, will be submitted to Ecological Letters.

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In Loving Memory of Abbie Sorenson.

Range-wide Abundance and Fluctuating Asymmetry Patterns of Sagebrush-obligate Passerine Birds

CHAPTER 1

Introduction

Cortnie Krissman

The sagebrush (*Artemisia* spp.) ecosystem of North America is a unique area, spanning an estimated 480,000 to 669,000 km^2 (Connelly et al. 2004, Schroeder et al. 2004). This ecosystem supports over 350 species of plants and animals, and yet is relatively little studied (Connelly et al. 2004). Sagebrush ecosystems are suffering from anthropogenic alterations at alarming rates. Only approximately 50% of sagebrush remains from pre-settlement conditions (Welch 2005). In addition to the vast reduction in area of sagebrush distribution, introduction of exotic invasive plant species, habitat conversion and degradation have contributed to decline in sagebrush habitat quality (Connelly et al. 2004, Dobkin and Sauder 2004, Schroeder et al. 2004). These human-mediated actions have negative consequences for sagebrush-obligate species (Connelly et al. 2004).

Sagebrush-obligate species are experiencing declines in abundance as a result of declining extent and quality of sagebrush habitats (Bradford et al. 1998, Vander Haegen et al. 2000). Declining species reliant on this ecosystem included greater sage-grouse (*Centrocercus urophasianus*) and the federally endangered pygmy rabbit (*Brachylagus idahoensis*). Other sagebrush-obligate species, such as Brewer's Sparrow (*Spizella breweri*) and Sage Thrasher (*Oreoscoptes montanus*), also have experienced significant declines in abundance over the past four and a half decades (Sauer et al. 2005).

Brewer's Sparrow, Sage Sparrow (*Amphipiza belli*), and Sage Thrasher, are reliant on sagebrush ecosystems for breeding (Braun et al. 1976) and can serve as indicators of sagebrush habitat quality (Bradford et al. 1998, Knick et al. 2003). Because sagebrush-obligate birds are limited to breeding within sagebrush habitat (Braun et al. 1976), these species provided an opportunity to investigate how animals with similar and well-defined habitat requirements vary in abundance and fluctuating asymmetry with respect to the periphery of sagebrush distribution.

Range peripheries are often areas of suboptimal habitat conditions. Species are often less abundant nearer these peripheries than in areas more interior to the geographic range (Brown et al. 1995, Gaston 2003). The abundant center distribution hypothesis postulates that within a species' range, abundance tends to be highest at the center of the range, and declines towards the peripheries of the range (Hengeveld and Haeck 1982). It is unknown whether the abundance of these sagebrush-obligate passerine birds conforms to the abundant center distribution hypothesis.

Individuals in suboptimal conditions at range peripheries may also experience high levels of stress. Environmental stress is often revealed through condition-dependent traits and these traits may be useful indicators of stress occurring at the time and location of their development (Hill 1995). Developmental stability, the ability to withstand perturbations during development, is one such indicator of environmental stress. Random variation in bilateral symmetry is referred to as fluctuating asymmetry, and is one such measure of developmental stability.

Fluctuating asymmetry has previously been associated with environmental stress (see Lens et al. 1999; Eeva et al. 2000, 2003). If range peripheries are areas of suboptimal habitat conditions, individuals may experience increased stress and reveal higher levels of fluctuating asymmetry in these areas. Thus, asymmetry may increase as distance to periphery decreases and may indicate declining environmental conditions or habitat suitability towards the range periphery.

In Chapter 2, *Abundance Patterns of Sagebrush-obligate Passerine Birds in Western North America*, I model abundance of Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, with respect to local- and landscape-level variables including distance to range periphery. I hypothesized abundance of these passerine birds would decline with distance to sagebrush periphery.

In Chapter 3, *Is Stress Related to Location of Development within Geographic Range of Sagebrush-obligate Passerine Birds?*, I model fluctuating asymmetry with respect to range location for these three sagebrush-obligate passerine birds. I hypothesized fluctuating asymmetry for all species would increase as the distance to the sagebrush range periphery decreased.

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CHAPTER 2

Abundance Patterns of Sagebrush-obligate Passerine Birds in Western North America

Cortnie M. Krissman and W. Daniel Edge

ABSTRACT

North American sagebrush (*Artemisia* spp.) ecosystems are suffering from reductions in habitat extent and quality, resulting in a decline of sagebrush-obligate species. Understanding landscape-scale patterns of abundance of sagebrush-obligate species may help to design effective conservation strategies. We applied Akaike's Information Criterion to evaluate evidence for the abundant center distribution hypothesis, which postulates that species abundance decreases approaching the range periphery where habitat conditions may become less suitable. Using North American Breeding Bird Survey count data to estimate abundance and sagebrush distribution maps to measure multiple habitat variables, we found Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphipiza belli*), and Sage Thrasher (*Oreoscoptes montanus*) abundance to increase with percent sagebrush cover and elevation. *Post hoc* analyses, however, provided limited support for the abundant center hypothesis, after accounting for sagebrush cover and elevation. Loss of areas of high sagebrush cover due to habitat fragmentation and degradation likely will result in continued declines in abundance of sagebrush-obligate passerine birds. Conservation efforts should focus on protection of existing areas of high sagebrush cover as well as restoration of degraded habitat, preferably between 1,200 to 2,300 m elevations. Our results will aid land managers and restoration biologists in targeting optimal locations within the sagebrush landscape to conserve these species.

INTRODUCTION

Species distributions are limited, and no species is distributed uniformly within its geographic range (Brown et al. 1995, Rodriguez 2002, Gaston 2003). Instead, species exhibit varying patterns of abundance because of differing ecological and evolutionary processes within the range. A thorough understanding of species distributions and abundance patterns at the scale of the geographic range is required for determining priority conservation areas, creating nature preserves, and conserving biodiversity (Brown et al. 1995, Orians and Soulé 2001, Sagarin and Gaines 2002). Species distribution patterns are also useful for determining how species are affected by exotic organisms, investigating community interactions and structure, establishing patterns of range expansion or decline, and monitoring population trends (Caughley 1994, Brown et al. 1995, Rodriguez 2002, Sagarin and Gaines 2002, Gaston 2003).

An important ecological relationship is between a species' abundance and the periphery of its geographic range. The geographic range periphery refers to the outermost limits of a species' distribution, as opposed to internal edges that may be caused by habitat fragmentation. The periphery of a species' distribution can be an area of unique population dynamics because populations in these areas may experience colonization events widening the range (Thomas et al. 2001). They may have lower abundances than, and be more isolated from, interior populations, resulting in reduced gene flow and higher levels of inbreeding (Caughley 1994, Gaston 2003). As global climate changes, species ranges may expand or contract (Thomas et al. 2001), and these range changes will likely begin near the range periphery. Understanding distribution patterns of abundance will aid in understanding these processes and provide critical information for conservation and management planning.

Patterns of abundance across a species' geographic range differ among species. Declining abundance of species from the interior toward the periphery of the geographic range is the most common distribution pattern (Brown et al. 1995, Gaston 2003). The abundant center distribution hypothesis postulates that within a species' range, abundance tends to be highest at the center of the range, and declines towards the peripheries of the range (Hengeveld and Haeck 1982). Typically, near the range periphery, habitats become patchier and organisms are less abundant than those in more interior areas (Lesica and Allendorf 1995, Brown et al. 1996, Stephens and Sutherland 1999, Sagarin and Gaines 2002, Gaston 2003). This decline in abundance towards the range periphery may be in response to declining habitat quality towards the periphery of the range. An exception to the abundant center distribution pattern, species may be most abundant near one side of the range while decreasing uniformly towards the opposite periphery (Gaston 2003).

The sagebrush (*Artemisia* spp.) ecosystem is a well-defined area in western North America, spanning nine states and into Canada that supports over 350 species of plants and animals. Several species, including Greater

Sage-grouse (*Centrocercus urophasianus*), Pygmy Rabbit (*Brachylagus idahoensis*), Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphipiza belli*), and Sage Thrasher (*Oreoscoptes montanus*), are considered sagebrush-obligate species because of their reliance on sagebrush habitats (Braun et al. 1976, Connelly et al. 2004). Because these species are limited to breeding within sagebrush habitat, they provide an opportunity to study how animals with similar and well-defined habitat requirements vary in abundance with respect to the range periphery of sagebrush. Knowledge of the overall abundance and distribution of sagebrush obligates is required for effective conservation (Knick et al. 2003).

We examined abundance patterns of Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, within the geographic range of sagebrush in the western United States. For the three species, we examined how abundance, estimated from North American Breeding Bird Survey (BBS) count data, varied with respect to the periphery of sagebrush distribution and other local- and landscape-level habitat characteristics. We applied Akaike's Information Criterion (AIC) to evaluate evidence for abundant center distribution hypothesis with respect to these passerine birds.

STUDY AREA AND METHODS

We chose Brewer's Sparrow, Sage Sparrow, and Sage Thrasher as focal species because they are acknowledged as sagebrush obligates (Braun et al. 1976) and thus, can serve as indicators of sagebrush habitat quality (Bradford et al. 1998, Knick et al. 2003). We obtained count data for these species from BBS (U. S. Geological Survey [USGS] Patuxent Wildlife Research Center 2004). These surveys span the geographic range of the sagebrush ecosystem, and are available for an extensive time span. Surveys, conducted annually during the month of June, consisted of 50, 3-minute point counts, spaced 0.8 km apart along a standardized 39.4-km route (Droege 1990). Surveys began half an hour before sunrise and finished no later than 10:00 hours. Surveyors, consisting of 165 trained volunteers, recorded avian abundance based on observations and vocalizations heard within a 0.4-km radius of each point count. Each individual was counted once. The 166 BBS routes analyzed here were selected based on their occurrence within sagebrush habitat represented in the Sagestitch map (Comer et al. 2002). We included point count data from 1990 to 1995 because it best corresponded to the sagebrush distribution data available; however, not all routes were surveyed over all years.

Limitations of BBS data include roadside bias of surveys, observer bias, and the use of multiple observers for individual routes over time (Sauer et al. 2005). The BBS route selection process strives for an independent, random sample of survey sites. Because of the nature of the surveys, there is potential bias to roadside habitat. However, we argue that this bias is not significant in sagebrush habitats because many of the routes are in low traffic areas that do not differ much from non-road areas. The best available data for avian abundance at the landscape scale are those from the BBS and are thus a valuable source of information.

Landscape and Habitat Variables

To determine the periphery of sagebrush distribution, we obtained a digital distribution map of sagebrush and associated vegetation from the USGS Interagency Sagebrush Working Group. This map (Fig 2.1) (Knick 2003) represented the percent cover of and combined spatial distribution of the following tall sagebrush species: Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), basin big sagebrush (*A. t. tridentata*), mountain big sagebrush (*A. t. vaseyana*), and silver sagebrush (*A. cana*). The low resolution (2.5 km) of this map enabled us to measure distances to a clearly defined periphery of tall sagebrush distribution. The geographic range periphery was defined as the outside boundary where sagebrush cover was 20 to 40% (Fig. 2.1) because it represented a periphery that is more consistent with the observed periphery of the sagebrush distribution when compared to the 0 to 20% boundary on the same map. The 0 to 20% boundary fell outside the range of sagebrush.

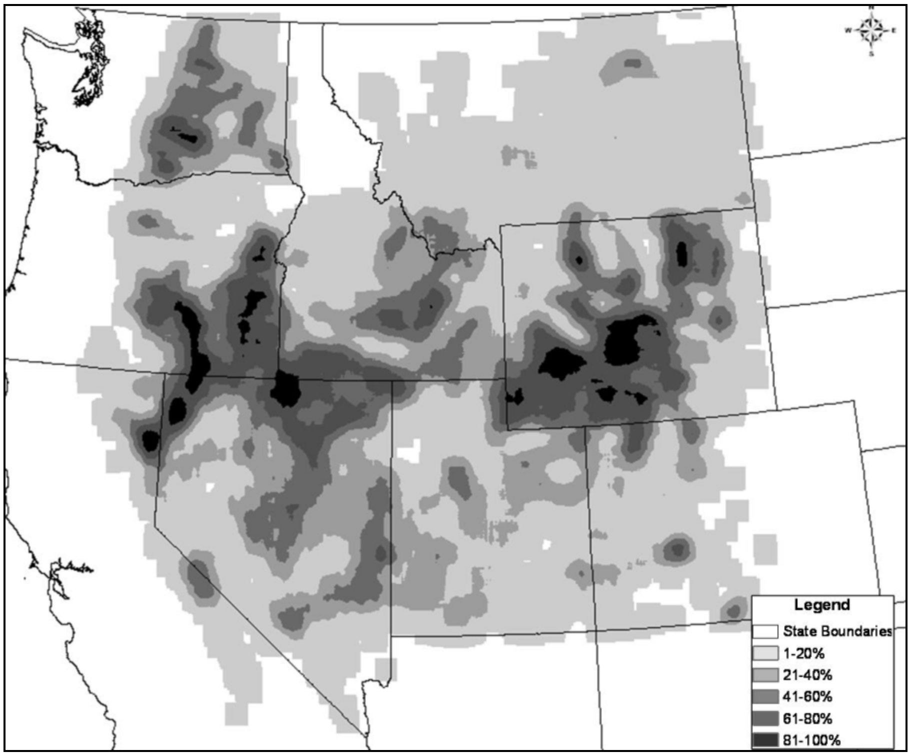

Figure 2.1. Map of sagebrush distribution in the western United States (Knick 2003). There are five categories of percent sagebrush cover, lighter representing lower percent cover and darker representing higher percent cover.

We performed analyses at two spatial scales (route and segment), which allowed us to determine the effect of scale upon avian abundance. The route-level analyses investigated abundance patterns at a coarser scale than the segment-level analyses. We divided each BBS route into five segments, each of which had an associated geographical midpoint (Figure 2.2). Because segments are derived from routes, segments from the same route are potentially autocorrelated. Annual variation and observer differences were not accounted for in our analyses.

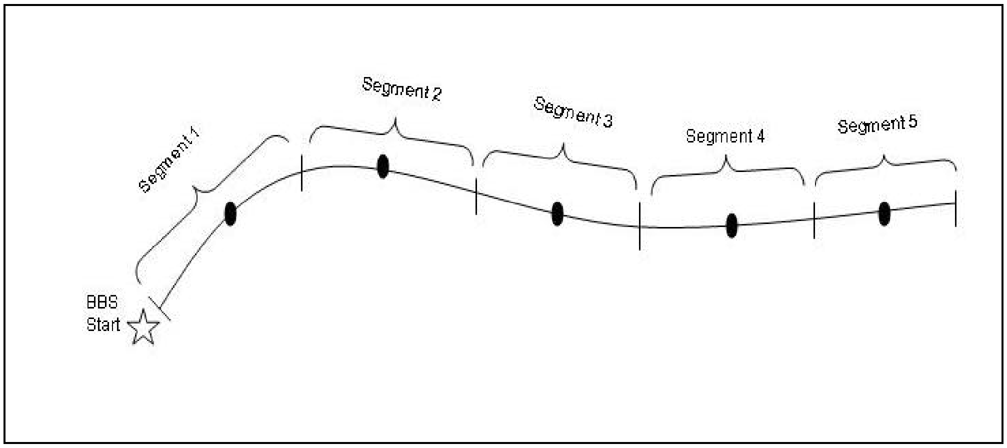

Figure 2.2 Breeding Bird Survey (BBS) routes were divided into segments. Each segment included ten BBS point counts. The segment midpoint is represented by an oval.

From this map we measured five habitat variables (distance to range periphery, percent sagebrush cover, distance to 100% sagebrush cover, fragmentation, and elevation) at the two spatial scales (Table 2.1). We measured the distance from the BBS route or segment midpoint to the geographic range periphery of sagebrush (Figure 2.3A) in ArcMAP (ArcGIS 9.0, Environmental Systems Research Institute 2004). We also measured the distance from the midpoint to the nearest location of 100% sagebrush cover (Figure 2.3B). We recorded the percent sagebrush cover at each BBS route or segment midpoint. Sagebrush fragmentation was quantified by USGS (2003) as the ratio of edge to sagebrush area, where lower values represented less sagebrush fragmentation. The resolution of the sagebrush fragmentation map was 500 m. We recorded sagebrush habitat fragmentation (FRAG) at each midpoint. Elevation (m) at the midpoints was obtained from USGS National Elevation Datasets (USGS 2002).

Table 2.1. Variables used in analysis of sagebrush-obligate passerine bird abundance with respect to habitat variables in the western United States, 1990-1995.

Variable	Variable label
Mean Brewer Sparrow count	MBRSP
Mean Sage Sparrow count	MSAGS
Mean Sage Thrasher count	MSATH
Distance (km) to periphery of sagebrush range from BBS route or segment midpoint	EDGE
Distance (km) to 100% sagebrush from BBS route or segment midpoint	DIST100
Percent sagebrush at BBS route or segment midpoint (20%, 40%, 60%, 80%, 100%)	PERCENT SAGE
Elevation (m) at BBS route or segment midpoint	ELEV
Quadratic elevation	$ELEV^2$
Habitat fragmentation [a] at BBS route or segment midpoint	FRAG

[a] Habitat fragmentation was quantified by USGS (2003) as the ratio of edge to sagebrush area.

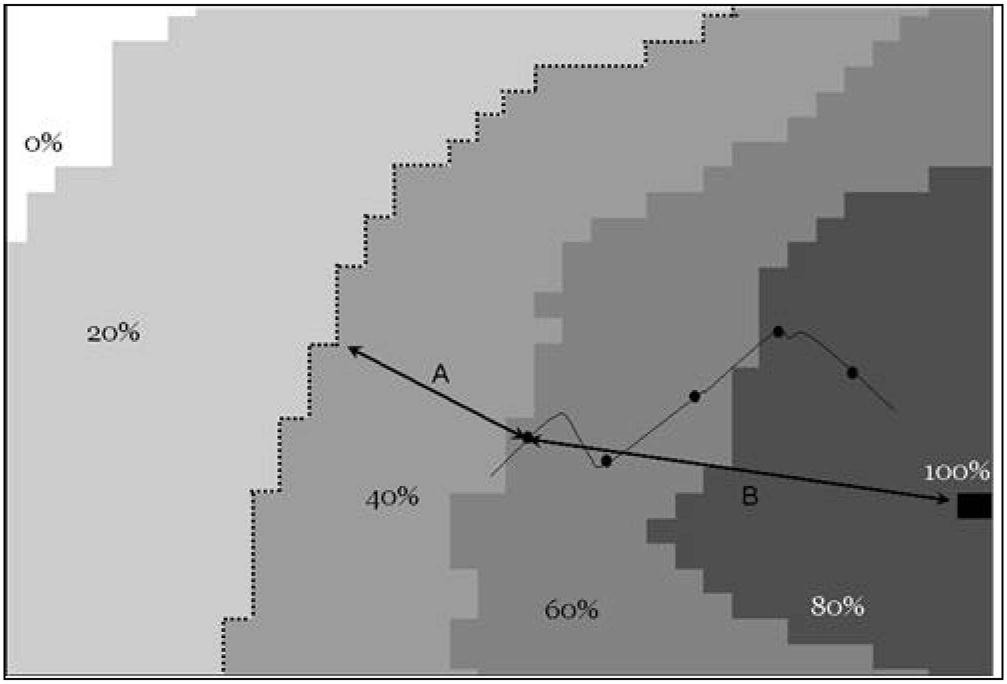

Figure 2.3. Example of measurement of the distance from a segment midpoint (dark ovals) to the boundary between 20% and 40% sagebrush cover (A) and to 100% sagebrush cover (B).

Statistical Analysis

We developed *a priori* models representing hypotheses regarding passerine bird abundance on the BBS routes within the distribution of sagebrush based on variables known or hypothesized to affect sagebrush-obligate passerine birds. We analyzed each species independently using the same model sets (Table 2.2). We included a null model that was limited to the intercept. None of the explanatory variables used in our analyses were highly correlated ($r^2 > 0.5$) with one another, reducing potential for multicollinearity in our analyses. Burnham and Anderson (2002) suggest fitting a fully parameterized model to assess the overall fit of the data. We fit a fully parameterized global model to assess goodness-of-fit based on Pearson's $?^2$/ df, where $P > 0.05$ indicates adequate fit. The global model fit for each species included the simple linear variables for the distance to the range periphery, the distance to the nearest boundary of 100% sagebrush cover, percent sagebrush cover, fragmentation, and elevation, a quadratic of elevation, and interactions between distance to range periphery and percent sagebrush cover, between distance to range periphery and fragmentation, and between distance to range periphery and linear elevation. The candidate model list was composed of 19 models that were simplified versions or combinations of the fully parameterized model. We conducted analyses using SAS 9.1 (Statistical Analysis System [SAS] Institute 2004).

Table 2.2. Negative binomial regression models for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher abundance in the western United States, 1990-1995.

Model [a]
Null
EDGE
PERCENT SAGE
FRAG
DIST100
ELEV
ELEV + ELEV^2
PERCENT SAGE + FRAG
PERCENT SAGE + EDGE
EDGE + FRAG
EDGE + ELEV
DIST100 + ELEV
PERCENT SAGE + ELEV
EDGE + (ELEV + ELEV^2)
DIST100 + (ELEV + ELEV^2)
PERCENT SAGE + (ELEV + ELEV^2)
EDGE + PERCENT SAGE + (EDGE * PERCENT SAGE)
EDGE + FRAG + (EDGE * FRAG)
EDGE + ELEV + (EDGE * ELEV)

[a] See Table 2.1 for variable descriptions.

Count data from BBS routes often contain multiple point counts and sometimes entire routes with no observations for a species. Data of this type approximate either Poisson or negative binomial distributions, but the negative binomial distribution often fits better when biological counts are considered (White and Bennetts 1996). For all analyses we used generalized linear models with a log link and negative binomial distribution to model average species counts (PROC GENMOD, SAS Institute 2004) because overdispersion was less when a negative binomial distribution was fit compared to a Poisson distribution (See Appendix A). To determine which distribution to use, we fit a fully parameterized global model for each species to both the Poisson and negative binomial distributions and examined overdispersion estimates and goodness-of-fit tests (Burnham and Anderson 2002:26). We then compared the values of Pearson's $?^2$/ df to determine which distribution produced lower overdispersion estimates. We also performed a likelihood ratio test based on the Poisson and negative binomial distributions when fit to each species' global model to determine which distribution produced less overdispersion. Finally, we compared graphs of residuals to determine which distribution best fit these data. A deviance goodness-of-fit test using Pearson's $?^2$ for the full model indicated that the negative binomial distribution was appropriate for these data ($?^2 \leq 1.019$, df = 820, $P > 0.05$) with the exception of Sage Sparrow and Sage Thrasher at the segment level ($?^2 \geq 1.268$, df = 820, $P < 0.001$).

We used Akaike's Information Criterion (AIC) to rank models for each species using a pre-defined model list (Burnham and Anderson 2002). The model with the smallest AIC value was selected as the best approximating model. We used ?AIC values to rank candidate models by their AIC distance from the best approximating model. Models were considered competing, and thus shared equal significance, when they were $\leq$2 ?AIC of the best approximating model. Models $\leq$4 ?AIC of the best approximating model were considered marginal (Burnham and Anderson 2002: 70). The relative variable importance provided additional evidence for individual variables in the model set, whether or not the variable of interest was included in the best approximating model (Burnham and Anderson 2002: 168). Relative variable importance was calculated by summing the weights of the models that include that variable; higher estimates indicated greater evidence for the importance of the variable. We present back-transformed (antilog) parameter estimates.

RESULTS

Segment level

The Brewer's Sparrow global model adequately fit the data (Appendix A). However, the global models for Sage Sparrow and Sage Thrasher did not adequately fit the data (Appendix A). Therefore, we present Sage Sparrow and Sage Thrasher segment-level analyses as exploratory.

At the segment level, results were similar for all three species. The best approximating model included the variables percent sagebrush and elevation as a quadratic (Table 2.3). No competing models were identified for any species. For each species, abundance was positively associated with increasing sagebrush cover and a downward quadratic of elevation (Tables 2.3 and 2.4). The downward quadratic elevation term indicates that abundance increased with increasing elevation until an optimum elevation is reached, at which point abundance decreases as elevation continues to increase. A 20% increase in sagebrush was associated with a multiplicative increase of 1.017 (95% CI: 1.012, 1.021), 1.030 (95% CI: 1.021, 1.039) and 1.034 (95% CI: 1.029, 1.040) in Brewer's Sparrow, Sage Sparrow, and Sage Thrasher abundance, respectively (Table 2.4). Elevation ranged between 138 and 3,380 m. Mean abundance for all species were highest between 1,200 and 2,300 m in elevation (Appendices C – E).

Table 2.3. AIC statistics for top five models of segment-level analysis of range-wide abundance patterns for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, 1990-1995. Models are ordered in terms of ? AIC.

Model [a]	AIC	?AIC
Brewer's Sparrow		
PERCENT SAGE + (ELEV + ELEV^2)	-11547.3	0.0
EDGE + (ELEV + ELEV^2)	-11542.4	4.9
DIST100 + (ELEV + ELEV^2)	-11511.4	35.9
ELEV + ELEV^2	-11498.8	48.5
EDGE + ELEV + (EDGE * ELEV)	-11490.8	56.5
Sage Sparrow		
PERCENT SAGE + (ELEV + ELEV2)	-2841.5	0.0
EDGE + (ELEV + ELEV2)	-2836.8	4.7
ELEV + ELEV2	-2800.3	41.2
DIST100 + (ELEV + ELEV2)	-2799.6	41.9
EDGE + PERCENT SAGE + (EDGE * PERCENT SAGE)	-2798.4	43.1
Sage Thrasher		
PERCENT SAGE + (ELEV + ELEV2)	-7652.9	0.0
EDGE + PERCENT SAGE + (EDGE * PERCENT SAGE)	-7617.2	35.8
EDGE + FRAG	-7605.7	47.2
EDGE + (ELEV + ELEV2)	-7605.2	47.7
PERCENT SAGE + ELEV	-7604.6	48.3

[a] See Table 2.1 for variable definitions.

The relative variable importance (Appendix B) for the variable for percent sagebrush cover was 0.92, 0.91, and 1.00 for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, respectively. The relative variable importance for the quadratic elevation variable was 1.00 for each species. The relative variable importance of the distance to the range periphery was 0.08, 0.09, and 0.00 for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, respectively.

Table 2.4. Regression coefficients for the best approximating models based on AIC for segment-level data for three sagebrush-obligate passerine birds in western United States, 1990-1995.

Variable [a]	Variable Estimate	95% CI
Brewer's sparrow		
INTERCEPT	0.078	0.040, 0.153
PERCENT SAGE	1.017	1.012, 1.021
ELEV	41.825	19.379, 90.270
ELEV^2	0.375	0.297, 0.473
Sage Sparrow		
INTERCEPT	0.000	0.000, 0.003
PERCENT SAGE	1.030	1.021, 1.039
ELEV	4.845×10^3	$484.928, 4.843 \times 10^4$
ELEV^2	0.079	0.039, 0.160
Sage Thrasher		
INTERCEPT	0.020	0.009, 0.044
PERCENT SAGE	1.034	1.029, 1.040
ELEV	47.842	19.648, 116.489
ELEV^2	0.346	0.261, 0458

[a] See Table 2.1 for variable definitions.

Route level

The global model adequately fit the data for each species (Appendix A). The best approximating model for each species was one in which abundance was positively associated with increasing sagebrush cover and a downward quadratic elevation term (Table 2.5). A 20% increase in percent sagebrush was associated with a multiplicative increase of 1.016 (95% CI: 1.006, 1.024), 1.034 (95% CI: 1.016, 1.051), and 1.033 (95% CI: 1.022, 1.044) in Brewer's Sparrow, Sage Sparrow, and Sage Thrasher abundance, respectively, after accounting for the quadratic elevation term (Table 2.6). Mean abundance for all species were highest between 1,200 and 2,300 m in elevation (Appendices F – H).

Table 2.5. AIC statistics of top five models for route-level analysis of range-wide abundance patterns for Brewer’s Sparrow, Sage Sparrow, and Sage Thrasher, 1990-1995. Models are ordered in terms of ?AIC.

Model [a]	AIC	?AIC
Brewer’s Sparrow		
PERCENT SAGE + (ELEV + ELEV^2)	-1977.3	0.0
EDGE + (ELEV + ELEV^2)	-1977.0	0.4
DIST100 + (ELEV + ELEV^2)	-1967.1	10.3
ELEV + ELEV^2	-1965.4	12.0
PERCENT SAGE + ELEV	-1955.3	22.1
Sage Sparrow		
PERCENT SAGE + (ELEV + ELEV2)	-379.7	0.0
EDGE + (ELEV + ELEV2)	-376.8	2.9
ELEV + ELEV2	-367.0	12.7
PERCENT SAGE + EDGE	-366.1	13.6
EDGE + FRAG + (EDGE * FRAG)	-366.0	13.7
Sage Thrasher		
PERCENT SAGE + (ELEV + ELEV2)	-1283.1	0.0
PERCENT SAGE + EDGE	-1272.3	10.8
EDGE + (ELEV + ELEV2)	-1272.1	11.0
PERCENT SAGE + FRAG	-1272.1	11.0
EDGE + FRAG + (EDGE * FRAG)	-1270.3	12.8

[a] See Table 2.1 for variable definitions.

Competing models, which included the variables for the distance to the range periphery and quadratic elevation, were identified for Brewer’s Sparrow and Sage Sparrow (? AIC = 0.4 and 2.9, respectively, Table 2.5). An increase in distance to range periphery of 1 km was associated with a multiplicative increase of 1.011 (95% CI: 1.005, 1.017) and 1.026 (95% CI: 1.010, 1.041) in Brewer’s Sparrow and Sage Sparrow abundance, respectively, after accounting for quadratic elevation (Table 2.6). No competing models were identified for Sage Thrasher.

Table 2.6. Regression coefficients for best approximating and competing models based on AIC for route-level abundance data for three sagebrush-obligate passerine birds in western United States, 1990-1995. ?AIC values are given for competing models.

Variable [a]	Variable Estimate	95% CI
Brewer's Sparrow		
INTERCEPT	0.041	0.010, 0.164
PERCENT SAGE	1.016	1.008, 1.024
ELEV	110.952	20.730, 593.775
ELEV^2	0.272	0.164, 0.454
Brewer's Sparrow Competing Model ?AIC = 0.4		
INTERCEPT	0.071	0.019, 0.269
EDGE	1.011	1.005, 1.017
ELEV	106.113	20.130, 559.364
ELEV^2	0.274	0.165, 0.453
Sage Sparrow		
INTERCEPT	0.000	0.000, 0.005
PERCENT SAGE	1.034	1.016, 1.051
ELEV	7.774 x 10^4	191.771, 3.152 x 10^7
ELEV^2	0.037	0.011, 0.258
Sage Sparrow Competing Model ?AIC = 2.9		
INTERCEPT	0.000	0.000, 0.016
EDGE	1.026	1.010, 1.041
ELEV	2.119 x 10^4	107.716, 4.168 x 10^6
ELEV^2	0.053	0.011, 0.258
Sage Thrasher		
INTERCEPT	0.008	0.001, 0.048
PERCENT SAGE	1.033	1.022, 1.044
ELEV	173.608	19.509, 1.545 x 10^3
ELEV^2	0.234	0.119, 0.458

[a] See Table 2.1 for variable definitions.

The relative variable importance of the distance to range periphery variable was 0.45, 0.19, and 0.00 for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, respectively (Appendix B). The relative variable importance for percent sagebrush cover was 0.55, 0.81, and 0.99 for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, respectively. The relative variable importance for quadratic elevation was 1.00 for Brewer's Sparrow and Sage Sparrow, and 0.99 for Sage Thrasher.

Post Hoc Analyses

After determining that the best approximating model in all cases was a model including percent sagebrush cover and a quadratic elevation term, we conducted post hoc analyses using a revised set of candidate models to evaluate evidence for the abundant center distribution hypothesis after accounting for percent sagebrush cover and quadratic elevation. The revised list included a model with the variables distance to range periphery, percent sagebrush and quadratic elevation. From the *a priori* candidate model list (Table 2.2), we removed models containing the variables for distance to 100% sagebrush, fragmentation, and elevation as a simple linear variable because there was no supporting evidence for these variables in previous analyses (Table 2.7). Inference to populations should not be made from *post hoc* results as these analyses are strictly exploratory. However, we suggest these *post hoc* analyses be performed with future datasets to provide evidence supporting or refuting our results.

Table 2.7. *Post hoc* negative binomial regression models for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher abundance in western United States. Abundance was averaged at segment and route level over 1990-1995.

Model [a]
Null
EDGE
PERCENT SAGE
ELEV + ELEV^2
PERCENT SAGE + EDGE
EDGE + (ELEV + ELEV^2)
PERCENT SAGE + (ELEV + ELEV^2)
EDGE + PERCENT SAGE + (EDGE * PERCENT SAGE)
EDGE + (ELEV + ELEV^2) + (EDGE * ELEV)
EDGE + (ELEV + ELEV^2) + PERCENT SAGE

[a] See Table 2.1 for variable definitions.

Post Hoc *Segment Level*

The best approximating *post hoc* model for each species indicated that abundance was positively associated with increasing percent sagebrush cover, increasing distance to range periphery, and included a downward quadratic elevation term (Table 2.8). An increase in distance to range periphery of 1 km was associated with a multiplicative increase of 1.007 (95% CI: 1.002, 1.011), 1.013 (95% CI: 1.004, 1.022), and 1.009 (95% CI: 1.004, 1.014) in Brewer's Sparrow, Sage Sparrow, and Sage Thrasher abundance, respectively, after accounting for increasing percent sagebrush and the quadratic elevation term (Table 2.9).

Table 2.8. AIC statistics of top five models for segment-level *post hoc* analysis of range-wide abundance patterns for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, 1990-1995. Models are ordered in terms of ?AIC.

Model [a]	AIC	?AIC
<u>Brewer's Sparrow</u>		
EDGE + (ELEV + ELEV^2) + PERCENT SAGE	-11554.2	0.0
PERCENT SAGE + (ELEV + ELEV^2)	-11547.3	6.9
EDGE + (ELEV + ELEV^2)	-11542.4	11.8
EDGE + (ELEV + ELEV^2) + (EDGE * ELEV)	-11540.8	13.4
ELEV + ELEV^2	-11498.8	55.4
<u>Sage Sparrow</u>		
EDGE + (ELEV + ELEV^2) + PERCENT SAGE	-2847.7	0.0
PERCENT SAGE + (ELEV + ELEV^2)	-2841.5	6.2
EDGE + (ELEV + ELEV^2)	-2836.8	10.9
EDGE + (ELEV + ELEV^2) + (EDGE * ELEV)	-2835.3	12.4
ELEV + ELEV^2	-2800.3	47.4
<u>Sage Thrasher</u>		
EDGE + (ELEV + ELEV^2) + PERCENT SAGE	-7664.8	0.0
PERCENT SAGE + (ELEV + ELEV^2)	-7652.9	11.9
EDGE + PERCENT SAGE + (EDGE * PERCENT SAGE)	-7617.2	47.7
PERCENT SAGE + EDGE	-7607.7	57.1
EDGE + (ELEV + ELEV^2)	-7605.2	59.6

[a] See Table 2.1 for variable definitions.

Table 2.9. Regression coefficients for best approximating *post hoc* models based on AIC for segment-level abundance data for three sagebrush-obligate passerine birds in western United States, 1990-1995.

Variable [a]	Variable Estimate	95% CI
Brewer’s Sparrow		
INTERCEPT	0.093	0.047, 0.183
EDGE	1.007	1.002, 1.011
PERCENT SAGE	1.011	1.005, 1.017
ELEV	36.093	16.675, 78.116
ELEV^2	0.393	0.312, 0.497
Sage Sparrow		
INTERCEPT	0.001	0.000, 0.004
EDGE	1.013	1.004, 1.022
PERCENT SAGE	1.021	1.010, 1.032
ELEV	2887 x 10^3	299.226, 2.785 x 10^4
ELEV^2	0.094	0.047, 0.190
Sage Thrasher		
INTERCEPT	0.025	0.011, 0.054
EDGE	1.009	1.004, 1.014
PERCENT SAGE	1.027	1.020, 1.034
ELEV	37.033	15.305, 89.604
ELEV^2	0.377	0.286, 0.498

[a] See Table 2.1 for variable definitions.

Post Hoc *Route Level*

The best approximating *post hoc* model for Brewer’s Sparrow and Sage Thrasher at the route level indicated that abundance was positively associated with higher percent sagebrush cover, increasing distance to range periphery and included a downward quadratic elevation term (Table 2.10). An increase in distance to periphery of 1 km was associated with a multiplicative increase of 1.006 (95% CI: 0.999, 1.014) and 1.008 (95% CI: 0.999, 1.018) in Brewer’s Sparrow and Sage Thrasher abundance, respectively, after accounting for increasing percent sagebrush cover and the quadratic elevation term (Table 2.11.)

Table 2.10. AIC statistics of top five models for route-level *post hoc* analysis of range-wide abundance patterns for Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, 1990-1995. Models are ordered in terms of ? AIC.

Model[a]	AIC	?AIC
<u>Brewer's Sparrow</u>		
EDGE + (ELEV + ELEV^2) + PERCENT SAGE	-1978.2	0.0
PERCENT SAGE + (ELEV + ELEV^2)	-1977.3	0.9
EDGE + (ELEV + ELEV^2)	-1977.0	1.3
EDGE + (ELEV + ELEV^2) + (EDGE * ELEV)	-1975.0	3.2
ELEV + ELEV^2	-1965.4	12.8
<u>Sage Sparrow</u>		
PERCENT SAGE + (ELEV + ELEV^2)	-379.7	0.0
EDGE + (ELEV + ELEV^2) + PERCENT SAGE	-379.5	0.2
EDGE + (ELEV + ELEV^2)	-376.8	2.9
EDGE + (ELEV + ELEV^2) + (EDGE * ELEV)	-375.1	4.6
ELEV + ELEV^2	-367.0	12.7
<u>Sage Thrasher</u>		
EDGE + (ELEV + ELEV^2) + PERCENT SAGE	-1284.5	0.0
PERCENT SAGE + (ELEV + ELEV^2)	-1283.1	1.4
EDGE + (ELEV + ELEV^2)	-1272.1	12.4
EDGE + (ELEV + ELEV^2) + (EDGE * ELEV)	-1270.5	14.0
EDGE + PERCENT SAGE + (EDGE * PERCENT SAGE)	-1267.6	17.0

[a] See Table 2.1 for variable definitions.

Two competing models were identified for Brewer's Sparrow, each within two ? AIC units of the best model: one with distance to the range periphery and quadratic elevation and one with percent sagebrush cover and quadratic elevation (?AIC = 0.9 and 1.3, respectively, Table 2.10). An increase in distance to range periphery of 1 km was associated with a multiplicative increase of 1.011 (95% CI: 1.005, 1.017) in Brewer's Sparrow abundance, after accounting for the quadratic elevation term (Table 2.11). In addition, Brewer's Sparrow abundance was associated with higher percent sagebrush cover and a downward quadratic elevation term (Table 2.10). One competing model for Sage Thrasher was identified and included the terms for percent sagebrush cover and quadratic elevation (?AIC = 1.4, Table 2.10). An increase in percent sagebrush cover was associated with increasing Sage Thrasher abundance, after accounting for curvilinear elevation.

The best approximating *post hoc* model for Sage Sparrow at the route level indicated that abundance was positively associated with higher percentage of sagebrush cover and a quadratic elevation term (Tables 2.10). An increase in percent sagebrush of one unit (20%) was associated with a multiplicative increase of 1.034 (95% CI: 1.016, 1.051) in Sage Sparrow abundance, after accounting for the quadratic elevation term (Table 2.11). One competing model, with the variables distance to range periphery, percent sagebrush cover, and a quadratic elevation term, was identified (? AIC = 0.2, Table 2.10). An increase in distance to range periphery of 1 km was associated with an increase of 1.011 (95% CI: 0.994, 1.028) in Sage Sparrow abundance, after accounting for increasing percent sagebrush and the quadratic elevation term (Table 2.11).

Table 2.11. Regression coefficients for best approximating and competing *post hoc* models based on AIC for route-level abundance data for three sagebrush-obligate passerine birds in the western United States, 1990-1995. ?AIC values are given for competing models.

Variable [a]	Variable Estimate	95% CI
Brewer's Sparrow		
INTERCEPT	0.052	0.013, 0.204
EDGE	1.006	0.999, 1.014
PERCENT SAGE	1.010	0.999, 1.021
ELEV	93.382	17.772, 490.635
ELEV^2	0.288	0.174, 0.477
Brewer's Sparrow Competing Model ?AIC = 0.9		
INTERCEPT	0.071	0.019, 0.269
EDGE	1.011	1.005, 1.017
ELEV	106.113	20.130, 559.364
ELEV^2	0.274	0.165, 0.453
Brewer's Sparrow Competing Model ?AIC = 1.3		
INTERCEPT	0.041	0.010, 0.164
PERCENT SAGE	1.016	1.008, 1.024
ELEV	110.952	20.730, 593.775
ELEV^2	0.272	0.164, 0.454
Sage Sparrow		
INTERCEPT	0.000	0.000, 0.005
PERCENT SAGE	1.034	1.016, 1.051
ELEV	7.775 x 10^4	191.771, 3.152 x 10^7
ELEV^2	0.037	0.006,0.217
Sage Sparrow Competing Model ?AIC = 0.2		
INTERCEPT	0.000	0.000, 0.007
EDGE	1.011	0.994, 1.028
PERCENT SAGE	1.025	1.004, 1.047
ELEV	3.484 x 10^4	110.335, 1.100 x 10^7
ELEV^2	0.047	0.009, 0.259
Sage Thrasher		
INTERCEPT	0.010	0.002, 0.057
EDGE	1.008	0.999, 1.018
PERCENT SAGE	1.026	1.013, 1.039
ELEV	144.995	17.068, 1.231 x 10^3
ELEV^2	0.248	0.128, 0.480
Sage Thrasher Competing Model ?AIC = 1.4		
INTERCEPT	0.008	0.001, 0.048
PERCENT SAGE	1.033	1.022, 1.044
ELEV	173.608	19.509, 1.545 x 10^3
ELEV^2	0.234	0.119, 0.458

[a] See Table 2.1 for variable definitions.

DISCUSSION

Sagebrush ecosystems are suffering from anthropogenic alterations at alarming rates (Knick et al. 2003, Connelly et al. 2004). Loss and fragmentation of sagebrush habitat has led to the listing of Brewer's Sparrow, Sage Sparrow, and Sage Thrasher as species of concern in many western states by Partners in Flight Western Working Group (Knick and Rotenberry 2002, Rotenberry 1998). Brewer's Sparrow and Sage Thrasher have experienced significant declines in abundance over the past four and a half decades (Sauer et al. 2005). Conversion of sagebrush for "range improvement" has lead to the decrease in the abundance of Sage Sparrow and Sage Thrasher and fluctuations in Brewer Sparrow density (Wiens and Rotenberry 1985). Knick et al. (2003) suggest the three focal species in our study may be important indicators of sagebrush habitat quality. Our results indicate that sagebrush-obligate passerine bird abundance is influenced by sagebrush cover, regardless of the distance to range periphery, lending additional support to this claim. Anthropogenic alterations to the sagebrush landscape, such as altered fire regimes and conversion for agriculture, have had negative consequences for sagebrush-obligate species (Connelly et al. 2004). Activities that further reduce sagebrush cover will likely reduce the abundance of these species.

The abundant center distribution postulates that species' abundance decreases from the interior to the periphery of the geographic range. However, our analyses failed to show overwhelming support this hypothesis for Brewer's

Sparrow, Sage Sparrow, and Sage Thrasher. For each species and at both spatial scales, there was no support for a simple linear model with the distance to periphery (EDGE) variable. Based on the competing models Brewer's Sparrow and Sage Sparrow abundance increased with distance to the periphery at the route level. However, due to the poor fit of the global model to the data for these two species, inferences are questionable for these relationships. Thus, these relationships provide only limited support of the hypothesis that abundance decreases towards range periphery. There were no competing models for Sage Thrasher; abundance was associated solely with percent sagebrush cover and elevation (quadratic) at both spatial scales. Our *post hoc* analyses, however, revealed support for the abundant center distribution hypothesis. For each species, abundance increased as a function of distance to range periphery after accounting for both elevation and percent sagebrush. Because these analyses were *post hoc*, they should be viewed as exploratory. Future analyses should also evaluate detailed evidence for the abundant center distribution hypothesis for this group of species.

Percent sagebrush cover and elevation (as a quadratic term) were always fundamental variables for these species at both spatial scales. Higher abundance for all species was associated with higher percent sagebrush cover and a downward elevation quadratic at each spatial scale. Our models highlighted the importance of sagebrush cover. Specifically, abundance of sagebrush-obligate passerine birds increased as percent sagebrush cover increased. These species are reliant on sagebrush for nest habitat, food resources, and protection from predators. Because our analyses showed theses species are more abundant in areas with higher cover of sagebrush regardless of position within geographic range, conservation efforts should focus on protection of remaining areas of high percent sagebrush and increasing the amount of sagebrush cover in degraded habitats, as supported by other research (Wiens and Rotenberry 1981, Paige and Ritter 1999, Dobkin and Sauder 2004).

Abundance of all species was associated with quadratic elevation; all species were most abundant between 1,200 and 2,300 m. The importance of elevation in our analyses may be explained in several ways. First, these passerine birds are frequently associated with big sagebrush subspecies (*A. tridentata*) and tend to use low sagebrush species (*A. arbuscula* and *A. nova*), which occur at higher elevations, to a lesser extent (Martin and Carlson 1998, Paige and Ritter 1999, West 1983, Wiens and Rotenberry 1981). Higher elevations also experience a greater level of juniper (*Juniperus* spp.) and pinyon pine (*Pinus edulis*) encroachment, another factor that negatively influences sagebrush and sagebrush obligates (Connelly et al. 2004). Lower elevations experience harsher climatic conditions (lower precipitation and higher temperatures) and encroachment of invasive exotic species, particularly cheatgrass (*Bromus tectorum*, Connelly et al. 2004), making mid-elevations ideal for these species. Thus mid-elevations (1,200 – 2,300 m) contain sites where these three species are most abundant and are areas where conservation efforts might be most effectively focused.

Limitations in our study introduce uncertainties to our results and conclusions. Although most models fit adequately, the segment-level models for Sage Sparrow and Sage Thrasher fit poorly. The finer resolution models for Sage Sparrow and Sage Thrasher should be viewed as exploratory analyses and warrant further investigation.

Our study highlights important conservation implications for sagebrush ecosystems and provides insights into the broader study of conservation biology. Sagebrush habitat in the western United States spans an estimated area of 480,000 to 669,000 km^2 (Connelly et al. 2004, Schroeder et al. 2004), approximately half the area prior to European expansion in the 1800's. In addition to the vast reduction in area of sagebrush distribution, the spread of invasive exotic plant species, habitat conversion for agriculture and urbanization, disruption of natural fire regimes and overgrazing have contributed to the destruction of sagebrush habitat (Connelly et al. 2004, Schroeder et al. 2004). By conserving and restoring sagebrush habitats, we can protect not only the focal species of this study, Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, but also other significant sagebrush-obligate species such as Greater Sage-grouse and Pygmy Rabbit.

ACKNOWLEDGEMENTS

Laura Nagy and Cliff Pereira provided advice on data analysis and commented on the manuscript. Doug Robinson provided conceptual ideas during the beginning of this research. Partial funding was provided by Oregon Supplemental Laurels Scholarship, Henry Mastin Graduate Fund Award, and Oregon State University, Department of Fisheries and Wildlife. We thank Patrick Comer, Steve Knick, and the many BBS volunteers and USGS researchers who helped make this research possible.

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Chapter 3

Is Stress Related to Location of Development within Geographic Range of Sagebrush-obligate Passerine Birds?

Cortnie M. Krissman and W. Daniel Edge

ABSTRACT

Effective conservation strategies require knowledge of where species may be stressed within their geographic range. Individuals in suboptimal habitats, such as those occurring near range peripheries, may be more stressed than individuals in more suitable habitats. Fluctuating asymmetry, small deviations in bilateral symmetry, is thought to result from an organism's inability to buffer environmental stresses during development. We investigated patterns of fluctuating asymmetry in Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphispizia belli*), and Sage Thrasher (*Oreoscoptes montanus*) across the geographic distribution of sagebrush (*Artemisia* spp.). We hypothesized that individuals closer to the periphery of the geographic range of sagebrush would have higher levels of fluctuating asymmetry than individuals further from the periphery. In contrast to our hypotheses, fluctuating asymmetry, estimated from mixed model regression with restricted maximum likelihood parameters, decreased with increasing proximity to the range periphery for Sage Sparrow; did not differ across the range for Sage Thrasher; and could not be estimated with confidence for Brewer's Sparrow. For Sage Sparrow, habitats near the range periphery may be optimal for development. Sage Thrasher may be more resilient to environmental stressors during development compared to the other sagebrush obligates investigated here. We encourage further studies using stratified sampling designs.

INTRODUCTION

When environmental conditions influence distributional patterns, individuals at various locations within a species' range may show physical signs of stress via condition-dependent traits. The ability to withstand developmental mishaps as a result of harsh environmental conditions is referred to as developmental stability (Palmer and Strobeck 1986, Møller and Swaddle 1997). Although genotype codes for symmetrical development of bilateral traits, fluctuating asymmetry, small, random deviations from perfect bilateral symmetry, occurs as a result of reduced developmental stability (Van Valen 1962, Palmer and Strobeck 2003). Fluctuating asymmetry in condition-dependent traits may reveal areas of increased environmental stress for certain species.

Abundance across a species range often declines towards the range periphery and this pattern is commonly attributed to declining habitat suitability closer to those peripheries (Brown et al. 1996). Thus, range peripheries are often assumed to be areas of biological or environmental stress (Brown et al. 1996). Previous studies have shown that fluctuating asymmetry increases in areas of stress. For example, in areas close to a pollution-producing copper smelter, fluctuating asymmetry increased in the tarsi of Pied Flycatchers (*Ficedula hypoleuca*) and primaries of Great Tits (*Parus major*) (Eeva et al. 2000). Increased fluctuating asymmetry was associated with habitat fragmentation and deterioration in tarsi of six avian species in Kenyan rainforests (Lens et al. 2002a). Fluctuating asymmetry could be a useful bioindicator with which to monitor stress in ecologically marginal habitats as well as range peripheries (Lens et al. 1999). If the periphery of the range is indeed more environmentally stressful than the interior, fluctuating asymmetry should be greater nearer the range periphery compared to the interior of the range.

We examined range-wide patterns of fluctuating asymmetry in the tarsi of juveniles of three sagebrush-obligate passerine birds. Because the distributions of these species are limited to sagebrush (*Artemisia* spp.) habitat, we were able to compare how the asymmetry of these species varies as a function of distance to their shared range periphery. We measured the tarsi of juvenile birds and applied a mixed regression model with restricted maximum likelihood parameters to test for measurement error and directional asymmetry and to estimate fluctuating asymmetry across the geographic range. We hypothesized individuals nearer the geographic range periphery would have higher levels of fluctuating asymmetry than birds further from the range periphery.

METHODS

Species, Specimens, and Measurements

We evaluated three species of sagebrush-obligate passerine birds: Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphipiza belli*), and Sage Thrasher (*Oreoscoptes montanus*). These species are accepted as sagebrush obligates due to their reliance on sagebrush ecosystems for breeding (Braun et al. 1976), and can serve as indicators of sagebrush habitat quality (Bradford et al. 1998, Knick et al. 2003). We measured museum specimens because obtaining a large sample size from locations throughout the range was logistically unfeasible. We evaluated specimens maintained in the following museums: National Museum of Natural History, Smithsonian Institution (Washington, D.C.); Museum of Vertebrate Zoology, University of California, Berkeley (Berkeley, California); Department of Fisheries and Wildlife, Oregon State University (Corvallis, Oregon); Burke Museum, University of Washington, (Seattle, Washington); and Slater Museum of Natural History, University of Puget Sound (Tacoma, Washington).

To ensure the correct relationship between location and fluctuating asymmetry, we limited our analysis to juveniles because juveniles are typically captured at the site of development. Individuals were aged according to (Pyle 1997). To ensure the specimens were captured near their hatching locations, we limited the collection dates to individuals captured between 1 March and 15 August. Museum specimens spanned a wide range of years: Brewer's

Sparrow, 1909-1997; Sage Sparrow, 1894-1997; and Sage Thrasher, 1899-1992. Tarsi were measured twice each in a variable pattern (left-right-left-right or right-left-right-left) using electronic slide calipers precise to 0.1 mm; the instrument was reset to zero after each measurement following the methods of Lens et al. (1999). Measurements were made by one observer (CMK) to reduce variability. To reduce observer bias, the measurements were not visualized until the measurement was complete.

Range Periphery Measurements

To determine the periphery of sagebrush distribution, we obtained a digital distribution map of sagebrush and associated vegetation from the United States Geologic Survey (USGS) Interagency Sagebrush Working Group. This map (Fig 3.1) (Knick 2003) represented the percent cover of the combined spatial distribution of the following tall sagebrush species: Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), basin big sagebrush (*A. t. tridentata*), mountain big sagebrush (*A. t. vaseyana*), and silver sagebrush (*A. cana*). The low resolution (2.5 km) of this map enabled us to measure distances to a clearly defined periphery of tall sagebrush. The geographic range periphery is defined as the outside boundary where sagebrush cover was 20% to 40% (Fig. 3.1). We used this boundary because it represented a periphery that is more consistent with the observed periphery of the sagebrush distribution when compared to the 0% to 20% boundary on the same map. The 0% to 20% boundary fell outside the range of sagebrush distribution.

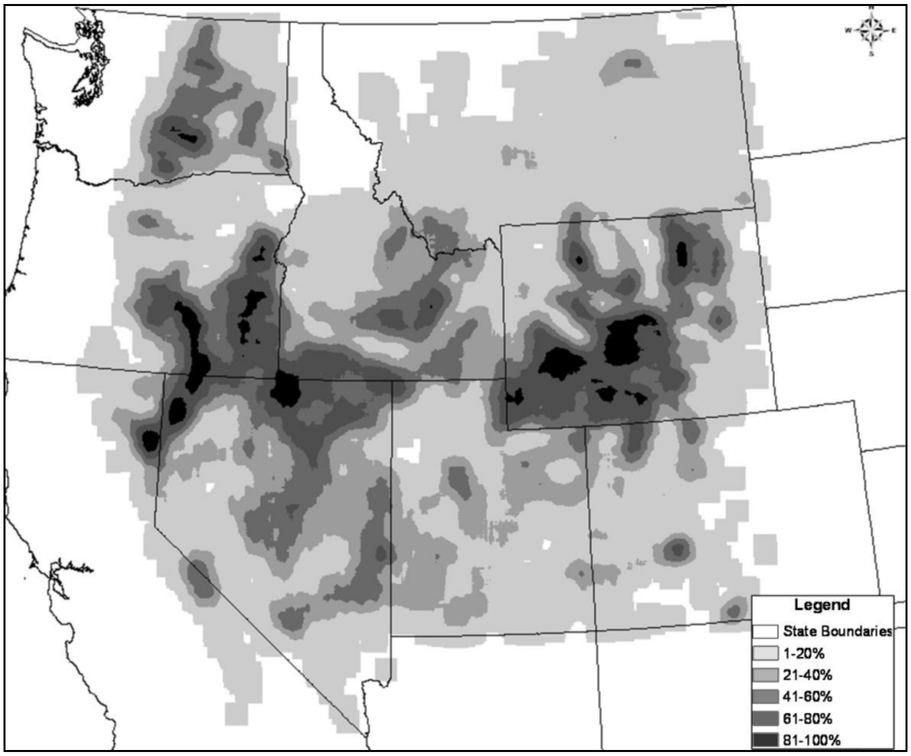

Figure 3.1. Distribution of sagebrush (*Artemisia* spp.) in the western United States (Knick 2003). There are five categories of percent sagebrush cover, lower percent cover represented by lighter shades and higher percent cover represented by darker shades.

Using this map we measured the distance (km) from the collection site of the specimen to the geographic range periphery of sagebrush in ArcMAP (ArcGIS 9.0, Environmental Systems Research Institute 2004). For each species, distance categories were created to estimate variances for these groups. These categories were created to include an equal, or near equal, sample size within each category for each species (Table 3.1); thus, distance categories differed for each species.

Statistical Analysis

The distribution of signed (R – L) and unsigned |R - L| asymmetry was inspected graphically for antisymmetry, which is characterized by a bimodal distribution and thus the absence or near absence of symmetrical individuals (Rowe et al. 1997). Without visual inspection for antisymmetry, results indicative of fluctuating asymmetry may be due to true fluctuating asymmetry or could be attributed to overlooked antisymmetry. Our data did not reflect strong antisymmetry for any species.

Fluctuating asymmetry was estimated and analyzed using a mixed regression model with restricted maximum likelihood parameters (van Dongen et al. 1999). The independent variable was tarsus length; fixed effects in the model included intercept, side (R or L), and distance category; and random effects were intercept, side, and error. Restricted maximum likelihood (Lens et al. 2002b) allows for the distinction of measurement error from fluctuating asymmetry which is necessary because fluctuating asymmetry is typically small and may be confounded by large values of measurement error (Lens et al. 2002b, Palmer and Strobeck 2003). Measurement error was distinguished from fluctuating asymmetry with a likelihood ratio test (LR) comparing models with and without the random ‘side’ effect. Because the null is on the boundary of the parameter space, the asymptotic null distribution is a 50:50 mixture of $?^{2}_{(0)}$ and $?^{2}_{(1)}$, so that the $?^{2}_{(1)}$ *p* value was divided by 2 to give the significance level of the test (see Van Dongen et al. 1999: 95 for details). Directional asymmetry, in which there is a population-level bias towards one side of a bilateral trait (Møller and Swaddle 1997), was tested for using an F-test with Satterthwaite's degrees of freedom adjustment (Palmer and Strobeck 1986). To determine if fluctuating asymmetry differed between three distance categories, we calculated a likelihood ratio test with significance level from a $?^2_{(2)}$ distribution. Measurement error did not differ between distance categories for any species (Van Dongen et al. 1999) so, for each species, pooled estimates of measurement error were used.

RESULTS

Measurement error could not be distinguished from fluctuating asymmetry for Brewer's Sparrow; so fluctuating asymmetry could not be detected reliably for this species (LR = 1.8, df = 1, p = 0.18). Measurement error was significantly different than fluctuating asymmetry in Sage Sparrow (LR = 4.8, df = 1, $p = 0.03$) and Sage Thrasher (LR = 30.2, df = 1, $p < 0.0001$), and thus, we were able to estimate fluctuating asymmetry for these species. The pooled estimates of fluctuating asymmetry were 0.020 mm and 0.098 mm for Sage Sparrow and Sage Thrasher, respectively. There was suggestive, but inconclusive evidence of directional asymmetry in Brewer's Sparrow ($F_{1, 40}$ = 2.8, $p = 0.102$), while directional asymmetry was not detected in Sage Sparrow ($F_{1, 40}$ = 0.86, $p = 0.360$). There was substantial evidence of directional asymmetry in Sage Thrasher ($F_{1, 27}$ = 8.99, $p = 0.006$).

There was evidence that fluctuating asymmetry differed significantly between distance categories for Sage Sparrow (LR = 12.7, df = 2, p = 0.002), but not for Sage Thrasher (LR = 4.6, df = 2, p = 0.1). Fluctuating asymmetry was greatest in the distances farthest from the range periphery for Sage Sparrow (Table 3.1).

Table 3.1. Measurement error (mm) for Brewer’s Sparrow, Sage Sparrow and Sage Thrasher, and fluctuating asymmetry estimates (mm) of tarsi, and associated ? ^{2} test for Sage Sparrow and Sage Thrasher from mixed model analyses.

	Measurement error (SE)	Fluctuating asymmetry (SE)
Brewers Sparrow		
	0.276 (0.043)	
Sage Sparrow		
	0.100 (0.016)	
Distance category 1 (0 – 7.0 km) *n* = 14		0.021 (0.018)
Distance category 2 (7.1 – 27.0 km) *n* = 14		-0.007* (0.008)
Distance category 3 (27.1 – 66.0 km) *n* = 13		0.046 (0.028)
Sage Thrasher		
	0.083 (0.016)	
Distance category 1 (0 – 7.0 km) *n* = 13		0.109 (0.054)
Distance category 2 (7.1 – 31.0 km) *n* = 6		0.041 (0.036)
Distance category 3 (31.1 – 68.0 km) *n* = 9		0.119 (0.070)

* No evidence of fluctuating asymmetry in this category. (With no boundary constraint, fluctuating asymmetry estimate would be negative.)

DISCUSSION

Fluctuating asymmetry in Brewer's Sparrow tarsi could not be estimated reliably due to large measurement error. Measurement error may have been problematic for Brewer's Sparrow because the smaller tarsi of this species ($\bar{x}$ = 17.1 ± 0.7 mm) were more challenging to measure precisely compared to the larger tarsi of Sage Sparrow ($\bar{x}$ = 20.9 ± 0.7 mm) and Sage Thrasher ($\bar{x}$ = 30.5 ± 1.1 mm).

We documented fluctuating asymmetry in Sage Sparrow and Sage Thrasher, but there was no evidence of higher fluctuating asymmetry nearer the range periphery. Contrary to our hypothesis that fluctuating asymmetry would be greatest nearer the range periphery, Sage Sparrow fluctuating asymmetry was higher further from the range periphery. Assuming fluctuating asymmetry is an adequate correlate of developmental stress due to environmental conditions (Leary and Allendorf 1989, Lens et al. 2002a), these results would indicate individuals nearer the range periphery experience less stress than those farthest from the range periphery. Differences in fluctuating asymmetry across the geographic range were not detectable for Sage Thrasher. This species, compared to other sagebrush obligate passerine birds, could be more resilient to environmental stressors during development.

The directional asymmetry we observed in Sage Thrasher is more likely due to observer handedness, or the differing skill levels of the hands (Helm and Albrecht 2000), than true directional asymmetry. Directional asymmetry at the population level in a highly functional bilateral trait, such as avian tarsi, is unlikely. Although Helm and Albrecht (2000) did not find directional asymmetry in tarsi, they did find handedness accounted for directional asymmetry in stonechat (*Saxicola torquata*) wing chords.

Although fluctuating asymmetry was detected in two species, the patterns we observed with respect to the distance from the range periphery may be confounded by the fact that the interior of the geographic range was not adequately represented by our data; specimens were not available for distances >68 km from the range periphery. On an ecosystem scale, areas between 150 - 300 km from the range periphery might be considered interior habitats. We could not account for temporal variability because the specimen collection dates were widespread (1894 to 1997). Substantial habitat change occurred within the sagebrush ecosystem over the range of collection dates representing our samples (West 1996). Further studies should be designed with these limitations in mind; the patterns revealed by such studies may provide important conservation implications.

Fluctuating asymmetry is relatively inexpensive, easy to use, and can be applied across many taxa; therefore, it is an attractive potential conservation tool (Leary and Allendorf 1989, Lens et al. 2002a). From the viewpoint of the potential for conservation applications of this method, we were encouraged to be able to detect fluctuating asymmetry in Sage Sparrow and Sage Thrasher. More defined patterns may be revealed from a stratified sampling design in which juveniles within a restricted time period and at multiple locations throughout the range could be measured for fluctuating asymmetry and then related to the current distribution of sagebrush. Knowing where a species is stressed within its range could be useful for determining where conservation efforts should be focused.

ACKNOWLEDGEMENTS

Laura Nagy and Cliff Pereira provided advice on data analysis and comments on the original manuscript. Doug Robinson contributed to the original ideas of this research. Partial funding was provided by Oregon Supplemental Laurals Scholarship, Henry Mastin Graduate Fund Award, and Oregon State University, Department of Fisheries and Wildlife. We thank Pat Comer, Steve Knick, and many USGS researchers for providing digital distribution data. We thank the following museums and their staff: National Museum of Natural History, Smithsonian Institution; Museum of Vertebrate Zoology, University of California, Berkeley; Department of Fisheries and Wildlife, Oregon State University; Burke Museum, University of Washington; and Slater Museum of Natural History, University of Puget Sound.

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Chapter 4

Conclusions

Cortnie M. Krissman

The sagebrush (A*rtemesia* spp.) ecosystem of the western United States is one where the needs of many unique species collide with human interests. Little of this habitat remains pristine, due to in large part to anthropogenic impacts that have occurred since European expansion in the 1800's. Agricultural conversion, livestock grazing, and urbanization have led, in part, to the decreased extent and fragmentation of this landscape. Fire regimes have been altered allowing conifer expansion. In other locations within the sagebrush ecosystem, invasive species are spread by increasing disturbance and out-compete native shrubs and forbs, greatly altering the habitat. Sagebrush-obligate species are declining, likely as a result of these changes. Thus, it is necessary to understand how anthropogenic alterations may impact these species. Here, we examined patterns of abundance and an indicator of stress of Brewer's Sparrow, Sage Sparrow, and Sage Thrasher, three sagebrush-obligate passerine birds, across the geographic range of sagebrush.

In Chapter 2, we examined the influence of local- and landscape-level variables upon sagebrush obligate abundance. We found little evidence Brewer's Sparrow, Sage Sparrow, and Sage Thrasher abundances were influenced by proximity to range periphery, as suggested by the abundant center distribution hypothesis (Hengeveld and Haeck 1982). Instead, elevation and percent sagebrush were the most influential variables related to abundance. At each spatial scale, high abundances of these species occurred in areas of high percent sagebrush and at mid- elevations, not at the interior of the sagebrush range, as postulated by the abundant center distribution hypothesis. However, our *post hoc* analyses that modeled elevation and percent sagebrush with distance to the range periphery indicated each of these three variables may play important roles in influencing abundance of these passerine birds. Because the *post hoc* analyses were exploratory, we suggest further research addressing these results. Activities that further reduce sagebrush cover will likely reduce the abundance of these species. Our results suggest that Brewer's Sparrow, Sage Sparrow, and Sage Thrasher are highest in abundance in areas at mid-elevations (1,200m – 2,300 m) with high sagebrush cover; thus, locations meeting these requirements should be targeted for conservation or restoration.

In Chapter 3, we examined how fluctuating asymmetry of sagebrush-obligate species varied with distance to the range periphery of sagebrush. Significant differences in magnitude of fluctuating asymmetry between distances categories existed for Sage Sparrow, but did not increase towards the range periphery, as predicted. Instead, Sage Sparrow fluctuating asymmetry was greatest farthest from the range periphery. Sage Thrasher fluctuating asymmetry did not vary significantly between distance categories. We were unable to estimate fluctuating asymmetry with confidence for Brewer's Sparrow due to large measurement error. We detected directional asymmetry in Sage Thrasher, which we attributed to observer handedness. Assuming fluctuating asymmetry is an adequate correlate of developmental stress due to environmental conditions (Leary and Allendorf 1989, Lens et al. 2002a), these results indicate Sage Sparrow nearer the range periphery experience less stress than those farthest from the range periphery. These areas should be investigated for their conservation potential for this species.

A thorough understanding of species distributions and abundances is required to effectively apply conservation methods such as creating nature preserves, and, overall, to conserve biodiversity (Brown et al. 1995, Sagarin and Gaines 2002). Conversion of sagebrush for "range improvement" has led to the decrease in the abundance of Sage Sparrows and Sage Thrashers and fluctuations in Brewer Sparrow densities (Wiens and Rotenberry 1985). Loss and fragmentation of sagebrush habitat has lead to concerns surrounding the conservation of these three obligates (Rotenberry 1998); these species are listed by Partners in Flight Western Working Group as species of concern in many western states (Knick and Rotenberry 2002). Brewer's Sparrow and Sage Thrasher have declined significantly in abundance over the past four and a half decades (Sauer et al. 2005). Although Sage Sparrows and Sage Thrashers are sagebrush obligates, it has been suggested they do not occupy all available habitat (Knick and Rotenberry 1995).

Overall abundance and distribution of these sagebrush obligates is necessary information for their conservation (Knick et al. 2003). Our results suggest Brewer's Sparrow, Sage Sparrow, and Sage Thrasher depend on high sagebrush cover at elevations between 1,200 m and 2,300m. Abundance patterns across species' ranges must be thoroughly investigated; this information has many uses aiding conservation of biodiversity, as it yields clearer understanding of differing ecological and evolutionary process at various locations within the range, from core to the periphery.

Sagebrush forms a unique habitat where human needs collide with those of the species specially adapted to living in this seemingly harsh landscape. Sagebrush habitat has been altered for livestock and agriculture since the European expansion westward and is thus disappearing (Braun et al. 1976). Conversion of sagebrush shrubland to agricultural fields leads not only to landscape-level habitat fragmentation and habitat loss for sagebrush obligates, but also allows for exotics to invade native shrublands (Rotenberry 1998). Invasive plants, particularly cheatgrass (*Bromus tectorum*), provide abundant fuels for fires, thus altering the disturbance regime of this ecosystem, while also suppressing the regeneration of native shrubs (Rotenberry 1998). Suppression of natural fire regimes, on the other hand, allows for juniper woodland invasion into sagebrush habitat (Miller and Rose 1999). Thus, humans may cause the redistribution of species' ranges, decline of habitat quality within a range, as well as alter abundances within species ranges. By conserving or restoring mid-elevation areas with high sagebrush cover, land managers can aid in the conservation of Brewer's Sparrow, Sage Sparrow, and Sage Thrasher.

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APPENDICES

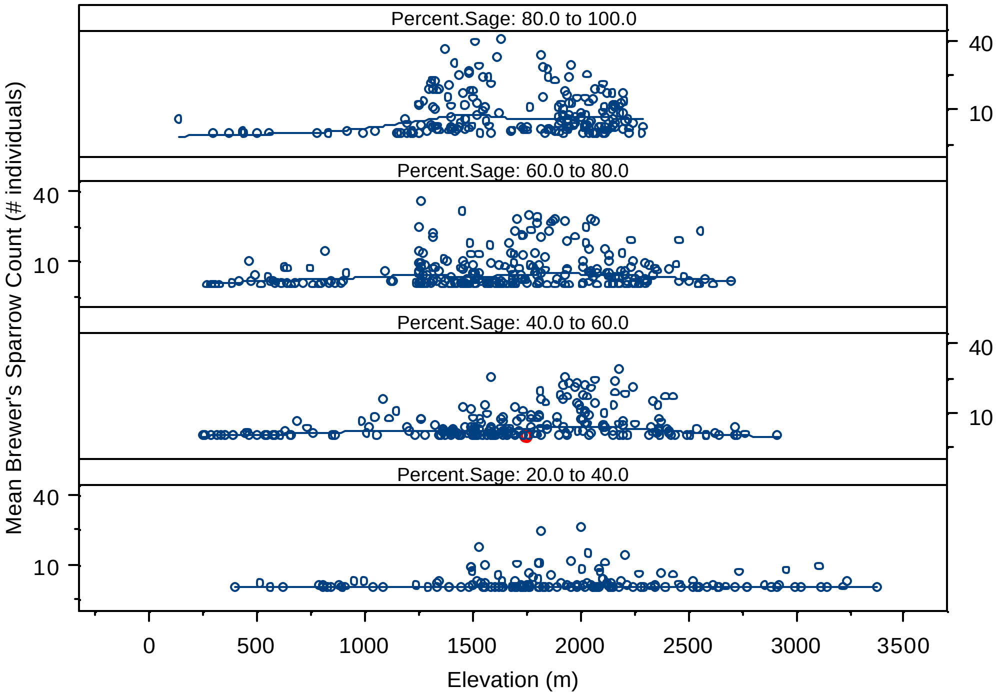
Appendix A. Pearson's ?^{2}/df values for global models fit to Poisson and negative binomial distributions for segment- and route-level analysis of range-wide abundance patterns of Brewer's Sparrow, Sage Sparrow and Sage Thrasher, 1990-1995. Values closer to 1 are considered best with regards to dispersion. *P*-values for ?^{2} distributions indicate adequate fit when greater than 0.05.

Species	Poisson distribution Pearson's ?^{2}/ df	Negative binomial distribution Pearson's ?^{2}/ df
Segment-level		
Brewer's Sparrow	8.125, df = 820 ($p < 0.001$)	0.980, df = 820, ($p = 0.652$)
Sage Sparrow	10.170, df = 820 ($p < 0.001$)	1.473, df = 820, ($p < 0.001$)
Sage Thrasher	7.966, df = 820 ($p < 0.001$)	1.268, df = 820, ($p < 0.001$)
Route-level		
Brewer's Sparrow	5.232, df = 155, ($p < 0.001$)	1.000, df = 155, ($p = 0.487$)
Sage Sparrow	4.905, df = 155, ($p < 0.001$)	0.872, df = 155, ($p = 0.874$)
Sage Thrasher	4.652, df = 155, ($p < 0.001$)	1.019, df = 155, ($p = 0.419$)

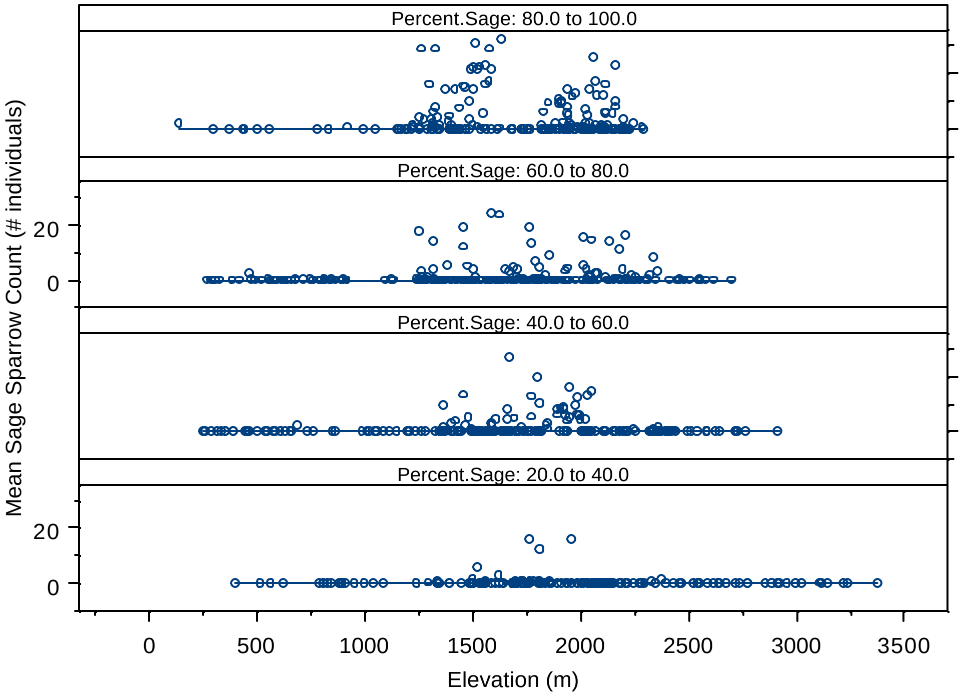
Appendix B. AIC relative variable importance for segment- and route-level analyses of range-wide abundance patterns of Brewer's Sparrow, Sage Sparrow and Sage Thrasher, 1990-1995.

	Brewer's Sparrow	Sage Sparrow	Sage Thrasher
Segment-level			
Elevation (Quadratic)	1.00	1.00	1.00
Percent Sagebrush Cover	0.92	0.91	1.00
Distance to Range Periphery	0.08	0.09	0.00
Route-level			
Elevation (Quadratic)	1.00	1.00	0.99
Percent Sagebrush Cover	0.55	0.81	0.99
Distance to Range Periphery	0.45	0.19	0.00

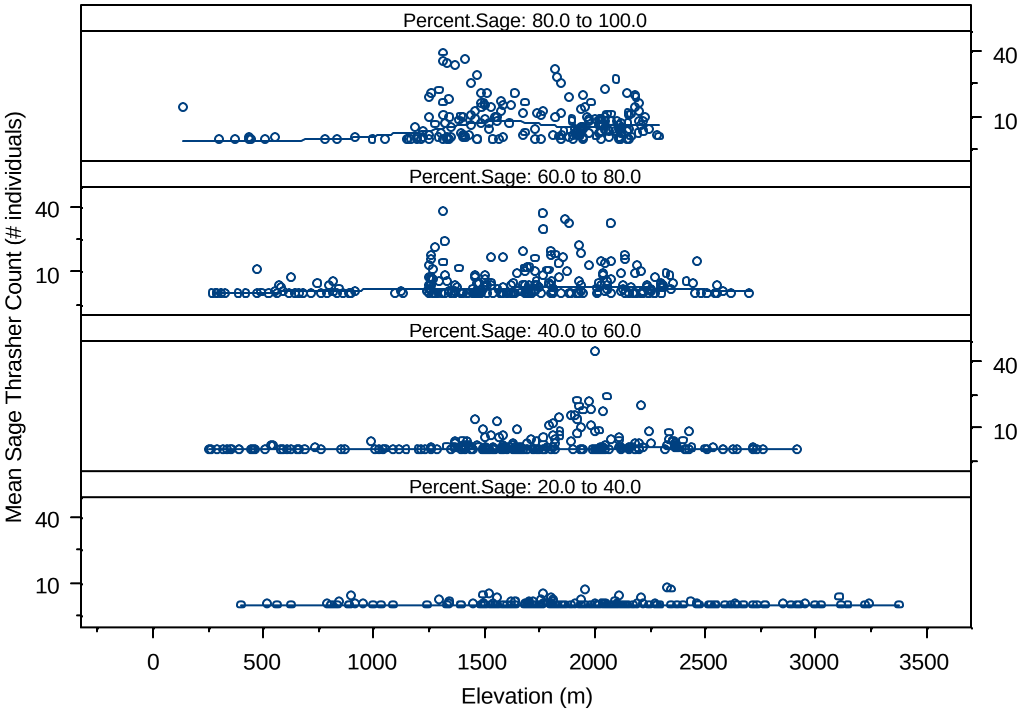
Appendix C. Trellis graph based on negative binomial regression model with percent sagebrush and quadratic elevation term of mean Brewer's Sparrow count for segment-level analysis, 1990-1995.



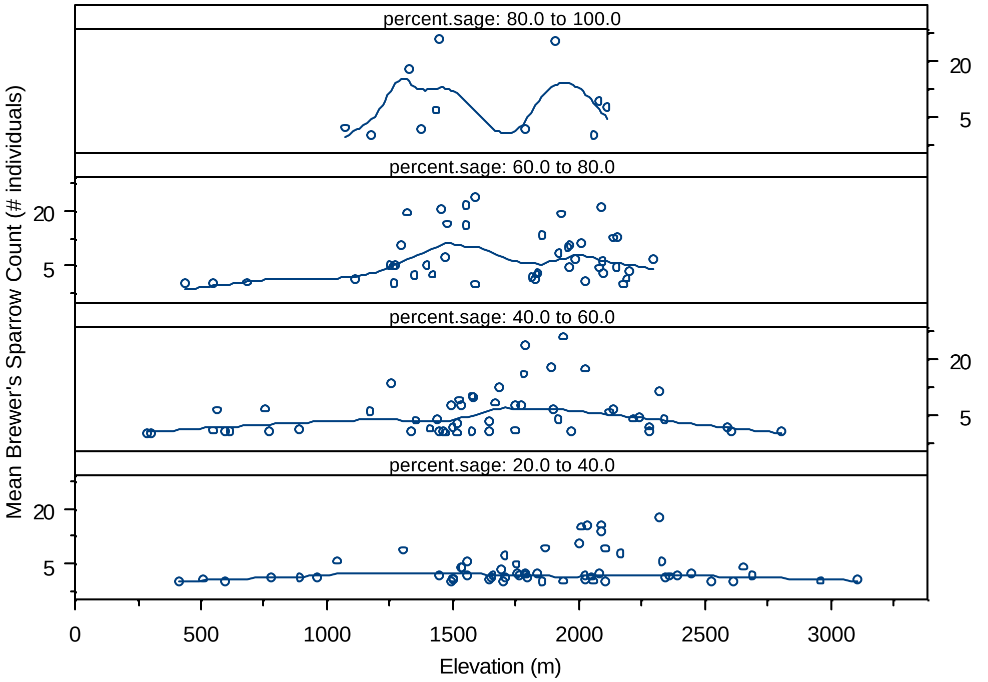
Appendix D. Trellis graph based of negative binomial regression model with percent sagebrush and quadratic elevation term of mean Sage Sparrow count for segment-level analysis, 1990-1995.



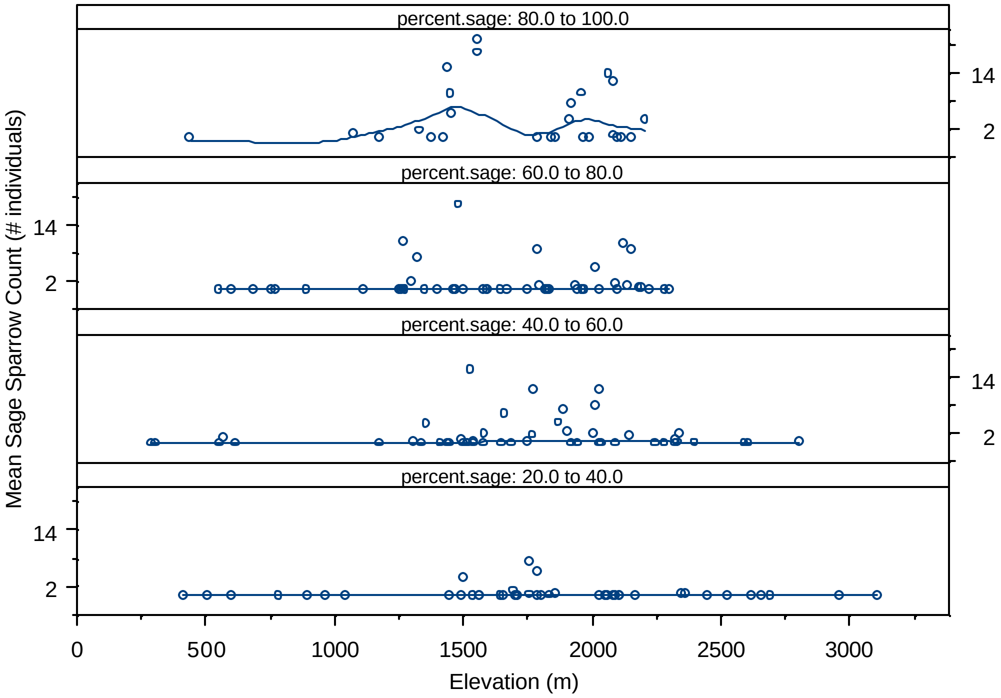
Appendix E. Trellis graph based on negative binomial regression model with percent sagebrush and quadratic elevation term of mean Sage Thrasher count for segment-level analysis, 1990-1995.



Appendix F. Trellis graph based on negative binomial regression model with percent sagebrush and quadratic elevation term of mean Brewer's Sparrow count for route-level analysis, 1990-1995.



Appendix G. Trellis graph based on negative binomial regression model with percent sagebrush and quadratic elevation term of mean Sage Sparrow count for route-level analysis, 1990-1995.



Appendix H. Trellis graph based on negative binomial regression model with percent sagebrush and quadratic elevation term of mean Sage Thrasher count for route-level analysis, 1990-1995.