

Social-Ecological Research in the Sagebrush Ecosystem: Evaluating the Landscape Ecology
of Burrowing Animals and Implementing a Social-Ecological Impact Assessment

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctorate in Philosophy

with a

Major in Natural Resources

in the

College of Natural Resources

University of Idaho

by

Joseph D. Holbrook

Major Professors: Kerri Vierling and Janet Rachlow, Ph.D.

Committee Members: Steven Knick, Ph.D.; Steve Krone, Ph.D.; J.D. Wulforst, Ph.D.

Department Administrator: Lisette Waits, Ph.D.

December 2015

Authorization to Submit Dissertation

This dissertation of Joseph D. Holbrook, submitted for the degree of Doctorate of Philosophy with a Major in Natural Resources and titled “Social-Ecological Research in the Sagebrush Ecosystem: Evaluating the Landscape Ecology of Burrowing Animals and Implementing a Social-Ecological Impact Assessment,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Co-Major Professors: _____ Date: _____
 Kerri Vierling, Ph.D.

_____ Date: _____
 Janet Rachlow, Ph.D.

Committee Members: _____ Date: _____
 Steven Knick, Ph.D.

_____ Date: _____
 Steve Krone, Ph.D.

_____ Date: _____
 J.D. Wulfhorst, Ph.D.

Department Administrator: _____ Date: _____
 Lisette Waits, Ph.D.

Abstract

The goal of my research was to assist land management on public lands by advancing the understanding of how people interact with sagebrush landscapes, as well as assessing how ecological changes affect functionally important animals. I implemented a spatially extensive sampling design (see Chapter 1 for details) across Idaho and Oregon, USA, to evaluate how fire and biological invasions influence occupancy and abundance of harvester ants (*Pogonomyrmex* spp.), Piute ground squirrels (*Urocitellus mollis*), and American badgers (*Taxidea taxus*). Results suggest that occupancy of harvester ants was not influenced by biological invasions or fire, rather occupancy was positively driven by distribution of finer-textured soils and drier locals. Similarly, occupancy of ground squirrels was independent of fire and biological invasions, but positively associated with long-term precipitation, dispersal potential, and fine-textured soil. Density of harvester ants was positively affected by exotic annual and native perennial grasses, as well as fire. However, relative abundance of ground squirrels was positively associated with fine-textured soil, but negatively associated with cheatgrass (*Bromus tectorum*), fire frequency, human disturbance, and shrub cover. Badger occupancy was positively associated with ground squirrel occupancy and human disturbance (e.g., irrigated agriculture). These results suggest that the effect of fire and biological invasions are differentially influencing burrowing animals, with some winners (i.e., harvester ants) and losers (i.e., ground squirrels). Management actions targeted at restoring burrowing animals will need to be species- and parameter-specific (e.g., occupancy or abundance), and may or may not be associated with the large changes occurring in sagebrush systems.

Finally, I (and my research team) partnered with the U.S. Bureau of Land Management (BLM) and designed and implemented a social-ecological impact assessment

associated with a project targeting juniper (*Juniperus occidentalis*) tree removal for sage-grouse (*Centrocercus urophasianus*) conservation in Owyhee County, Idaho. Through questionnaires, deliberative workshops, and participatory GIS, we identified a range of values and place meanings for many stakeholders from different backgrounds. These results provided clear mitigation opportunities for the BLM to address social concerns surrounding a management project on public lands. Our social-ecological approach and process could be easily transferred to other proposed projects on public lands throughout the U.S.

Acknowledgments

The journey of my Ph.D. has allowed me to interact with many amazing people, and for that I am thankful. I am grateful to my advisors, Janet Rachlow and Kerri Vierling, for providing guidance, encouragement, criticism, and opportunity. I feel blessed to have had the opportunity to work with you both, and am honored to call you friends. Additionally, I thank my committee J.D. Wulfhorst, Steve Krone, and Steve Knick for valuable insight and support during my Ph.D. program. To my IGERT team (Ryan Niemeyer, Alex Suazo, Amanda Bentley Brymer), Rage in the Sage, thank you for being awesome! It has been a pleasure having you as colleagues, and a blessing to call you friends. A huge thanks to J.D. Wulfhorst who lead Rage in the Sage, and provided unwavering support and encouragement throughout our IGERT process. To the many students and faculty in the Fish and Wildlife Department and IGERT program, thank you for the support, encouragement, insightful discussions, afternoon beers, late-night parties, and most of all friendship. I look forward to crossing paths in the future.

The work presented in this dissertation would not have been possible without multiple collaborations, funding, or logistical support. First, I thank my Dad for being the absolute best field technician anyone could ask for. It was a true blessing getting to spend my days in the field with you, and I will forever look back with wonderful memories. I thank David Pilliod and Robert Arkle for being open to collaboration, and working with me on this research. The scope of my dissertation was exponentially increased with your partnership. Thanks to Michelle Wiest for your collaboration and advice on all things statistical. The National Science Foundation's IGERT program (Award 0903479) provided funding for all aspects of my work, and for that I am grateful. The Joint Fire Science Program (Project ID:

11-1-2-30) funded the collection of vegetation data in southern Idaho, without which my dissertation would not have been possible. Thanks to M. McGee, L. Okeson, J. Suhr Pierce, A. Talsma, and D. Miller for logistical support for our IGERT project. I also thank the Bureau of Land Management (Award L14AC00060) and the Idaho Governor's Office of Species Conservation (Award BOSEIA14) for financial and logistical support of our interdisciplinary project. Additionally, the Shikar Safari Club International Scholarship and the J. Michael and Sharon L. Scott Graduate Student Scholarship provided funding for tuition and fees and opportunities to present my research; thank you! Lastly, thank you to the University of Idaho for being my home for more than 8 years (for both my B.S. and Ph.D.), and providing opportunities that helped me achieve my career goals. Go Vandals!

Dedication

This work is a result of the enduring support and love of my father and mother, Dale and Chris. To you, my dissertation is dedicated.

Table of Contents

Authorization to Submit.....	ii
Abstract	iii
Acknowledgements	v
Dedication	vii
Table of Contents	viii
List of Tables.....	xi
List of Figures	xiii
Dissertation Introduction.....	1
Chapter 1: Sampling animal sign in heterogeneous environments: how much is enough?.....	2
Abstract	2
Introduction	3
Methods.....	5
Results and Discussion.....	8
Conclusion	11
References	12
Chapter 2: Occupancy and abundance of predator and prey: implications of the fire-cheatgrass cycle in sagebrush ecosystems	18
Abstract	18
Introduction	19
Methods.....	23
Results	34

Discussion	37
References	48
Chapter 3: Transition of vegetation states positively affects an aridland granivore in the Great Basin	69
Abstract	69
Introduction	70
Methods	73
Results	79
Discussion	81
Implications	86
References	88
Chapter 4: A social-ecological assessment for public land management: application of a conceptual and methodological framework	104
Abstract	104
Introduction	105
SEIA development	109
Methods	111
Results	114
Discussion	118
References	123
Dissertation Conclusion	136
Appendices	138

Appendix A: Sampling design for plants, American badgers, and Piute ground squirrels, and characteristic burrows for badger and ground squirrels (Chapter 2).....	138
Appendix B: Description of covariates used in American badger and Piute ground squirrel modeling (Chapter 2).....	140
Appendix C: Description of plant species found at the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA, and that were used in Piute ground squirrel models (Chapter 2).....	146
Appendix D: Questionnaire used to solicit responses from the social-ecological impact assessment (Chapter 4).....	148
Appendix E: Summary of all responses and example quotations from the social-ecological impact assessment (Chapter 4)	150
Appendix F: Institutional Review Board Approval from the University of Idaho for implementing the social-ecological assessment (Chapter 4)	159
Appendix G: License agreement to reprint manuscript from the Journal of Arid Environments (Chapter 1).....	160

List of Tables

<p>Table 2.1: Hypotheses and model selection results for models assessing occupancy (ψ) of Piute ground squirrels (<i>Urocitellus mollis</i>). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. BIC and AUC represent the Bayesian information criterion and the area under the curve of the receiver operating characteristic, respectively. The number of estimated parameters and model weights for each model are indicated by k and w_i.....</p>	59
<p>Table 2.2: Hypotheses and model selection results for models assessing occupancy (ψ) of American badgers (<i>Taxidea taxus</i>). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. AIC_c and AUC represent the Akaike's information criterion (adjusted for small sample size) and the area under the curve of the receiver operating characteristic, respectively. The number of estimated parameters and model weights for each model are indicated by k and w_i</p>	60
<p>Table 2.3: Hypotheses and model selection results for models assessing relative abundance (RA) of Piute ground squirrels (<i>Urocitellus mollis</i>). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. AIC_c represents Akaike's information criterion (adjusted for small sample size). The number of estimated parameters and model weights for each model are indicated by k and w_i, respectively. Spearman's rank correlation coefficients (ρ) between predicted and observed values are also displayed</p>	61
<p>Table 3.1: Covariate descriptions, correlations, and collection methods for the variables used in analyses of vegetation states and harvester ant (<i>Pogonomyrmex</i> spp.) occupancy and density</p>	97

Table 4.1: Perceived changes to social processes and ecological services, and the direction of subsequent impacts, concerning the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project in Owyhee County, USA128

List of Figures

- Figure 1.1:** Relative standard error (RSE) versus mean number of ground squirrel burrows per transect for 6 levels of *SD*. The number of transects represents the 4 sampling intensities (2–5 transects) we evaluated. Dashed line indicates our target threshold of $RSE \leq 0.30$. These data were collected at the Morley Nelson Birds of Prey National Conservation Area, Idaho, USA, during March 2013.....15
- Figure 1.2:** Relative standard error (RSE) versus mean number of harvester ant nests per transect for 6 levels of *SD*. The number of transects represents the 4 sampling intensities (2–5 transects) we evaluated. Dashed line indicates our target threshold of $RSE \leq 0.30$. These data were collected at the Morley Nelson Birds of Prey National Conservation Area, Idaho, USA, during March 2013.....16
- Figure 1.3:** Sampling duration versus mean number of ground squirrel burrows per transect. The number of transects represents the 4 sampling intensities (2–5 transects) we evaluated for $n = 20$ plots per sampling intensity. Dashed line indicates one hour of sampling. These data were collected at the Morley Nelson Birds of Prey National Conservation Area, Idaho, USA, during March 2013.....17
- Figure 2.1:** Hypothesized strength of effect across biotic and abiotic themes for occupancy of Piute ground squirrels (*Urocitellus mollis*) and American badgers (*Taxidea taxus*) and abundance of ground squirrels. Asterisks indicate an ecosystem stressor (i.e., biological invasions and fire) is embedded within the theme63
- Figure 2.2:** A) Location of Morley Nelson Snake River Birds of Prey National Conservation Area (i.e., study area) in southwestern Idaho, USA. B) Distribution of 1-ha plots ($n = 163$)

that were sampled for Piute ground squirrels (*Urocitellus mollis*) and American badgers (*Taxidea taxus*). C) Photograph of a badger on one of our 1-ha plots64

Figure 2.3: Standardized parameter estimates ($\pm 90\%$ credible intervals) describing the effect of explanatory variables (x-axis) on occupancy of Piute ground squirrels (*Urocitellus mollis*).

Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA.....65

Figure 2.4: Standardized parameter estimates ($\pm 90\%$ confidence intervals) describing the effect of explanatory variables (x-axis) on occupancy of American badgers (*Taxidea taxus*).

If a variable does not have a parameter estimate labeled top model it was not included. Data were collected on the Morley Nelson Snake River Birds of Prey National

Conservation Area in southern Idaho, USA.....66

Figure 2.5: Standardized parameter estimates ($\pm 90\%$ confidence intervals) describing the effect of explanatory variables (x-axis) on relative abundance of Piute ground squirrels

(*Urocitellus mollis*). If a variable does not have a parameter estimate labeled top model it was not included. Data were collected on the Morley Nelson Snake River Birds

of Prey National Conservation Area in southern Idaho, USA67

Figure 2.6: A) Cheatgrass (BRTE) and shrub cover ($\pm 90\%$ CI) as a function of treatment

history (x-axis) at the plot-level ($n = 52, 38,$ and 36 for identified burned, treated, and unburned plots, respectively). B) Relative abundance of Piute ground squirrels (*Urocitellus*

mollis; counts of recently active burrows, $\pm 90\%$ CI) as a function of treatment history. Data were collected on the Morley Nelson Snake River Birds of Prey

National Conservation Area in southern Idaho, USA.....68

Figure 3.1: Triangles indicate the distribution of 1-ha plots ($n = 358$) that were sampled for harvester ants (<i>Pogonomyrmex</i> spp.) within southern Oregon and Idaho, USA, during 2008-2009 and 2013-2014.....	98
Figure 3.2: Percent cover of exotic annual grass (EAG), native perennial grass (NPG), and shrubs as a function of time since fire (x-axis). Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.....	99
Figure 3.3: A) Proportion of plots occupied, and B) density (colony/100 m ²) of harvester ant (<i>Pogonomyrmex</i> spp.) colonies as a function of time since fire (x-axis). Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.....	100
Figure 3.4: Percent cover of exotic annual grass (EAG), native perennial grass (NPG), and shrubs as a function of realized vegetation state (x-axis). Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.....	101
Figure 3.5: A) Proportion of plots occupied by harvester ants, and B) density (colony/100 m ²) of harvester ant (<i>Pogonomyrmex</i> spp.) colonies as a function realized vegetation state. Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.....	102
Figure 3.6: Standardized parameter estimates ($\pm 90\%$ CIs) from A) occupancy model and B) density model that described the effect of covariates (x-axis) on harvester ants (<i>Pogonomyrmex</i> spp.). Data were collected from throughout southern Oregon and Idaho, USA.....	103
Figure 4.1: Inset map shows the western USA with Owyhee County, Idaho, in dark grey. Map of Owyhee County shows the proposed project boundary and five landmarks for the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project.....	131

- Figure 4.2:** Flow diagram of the social-ecological impact assessment (SEIA) framework (modified from Slootweg et al. 2001). Human impacts are in solid lines and all other components are in dotted lines. All arrows represent pathways to human impacts.....132
- Figure 4.3:** Percent of the total range observed for responses for each question. Horizontal line is the average range observed across all questions133
- Figure 4.4:** Participant responses to seven questions (Supporting Information: Table S4, except question #8) concerning the current state of Owyhee County (i.e., baseline) and the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project alternatives: no action, full suite, and cut and scatter. Displayed scored as baseline-normalized by subtracting the participant baseline score from his/her alternative score134
- Figure 4.5:** Frequency of the polygons derived for all values combined (a), social values (b), economic values (c), and ecological values (d) in Owyhee County, Idaho, USA. The proposed project boundary for the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project is indicated by the dotted lines. Point 1 and 2 in panel (a) indicate the Owyhee and Bruneau-Jarbidge watersheds and associated wilderness areas135

Dissertation Introduction

Sagebrush ecosystems in western North America are among the most imperiled in the world, and they are socially and ecologically dynamic. Conservation and management of sagebrush landscapes is socially complicated because much of the sagebrush ecosystem occurs within lands that are management in a multiple-use framework by federal agencies, such as the U.S. Bureau of Land Management and U.S. Forest Service. Therefore, many stakeholders have a vested interest in management, which often results in conflicts about land management. Similarly, sagebrush habitats are increasingly declining because of the drastic expansion of exotic grasses (in low elevations) and conifers (in high elevations), changes in fire ecology, and anthropogenic development. Given the conservation concern associated with sagebrush ecosystems, coupled with their socially and ecologically dynamic nature, additional research is much needed. For example, despite the widespread landscape changes to sagebrush habitats, little is known concerning how those landscape changes directly and indirectly influence animals that provide important functions (e.g., burrowing animals), which has implications for the greater animal community. Second, with an increase in human conflict associated with land management projects aimed at habitat improvement, federal agencies are looking to develop creative approaches that incorporate social dimensions related to management actions. Collectively, advancing the understanding of how landscape changes influence functionally important species (Chapters 1, 2, and 3), as well as developing approaches to incorporate social dimensions of land management activities (Chapter 4), will improve the ability of managers to make decisions targeted at the animal community as well as mitigate aspects of projects that are likely to result in social conflict. Together, this will aid in effective conservation and decision making within sagebrush ecosystems.

Chapter 1: Sampling animal sign in heterogeneous environments: how much is enough?

Published in the Journal of Arid Environments

Holbrook, J., R. Arkle, J. Rachlow, K. Vierling, and D. Pilliod. 2015. Sampling animal sign in heterogeneous environments: how much is enough? *Journal of Arid Environments* 119:51-55.

Co-authors: Robert S. Arkle, Janet L. Rachlow, Kerri T. Vierling, and David S. Pilliod

Abstract

Animal ecologists often use animal sign as a surrogate for direct observation of organisms, especially when species are secretive or difficult to observe. Spatial heterogeneity in arid environments makes it challenging to consistently detect and precisely characterize animal sign, which can bias estimates of animal abundance or habitat use. Piute ground squirrels (*Urocitellus mollis*) and Owyhee harvester ants (*Pogonomyrmex salinus*) live in arid environments and are fossorial, which can make them difficult to observe directly. Their relative abundance can be assessed using sign (i.e., burrows and nests). We implemented an *over-sampling* framework (i.e., recorded an excessive amount of information) with two observers to 1) identify a sampling intensity that balanced precision with our resource constraints, and 2) assess classification and detection of squirrel burrows and ant nests across vegetation conditions. We sampled 20 1-ha plots for ground squirrel burrows and ant nests using six 4 m × 100 m belt transects. Analyses of precision and sampling effort indicated that three belt transects covering 1200 m² per ha provided sufficient precision, while minimizing effort. Regardless of vegetation conditions, counts by two observers were strongly correlated for ground squirrel burrows ($r = 0.99$, $P < 0.001$, $df = 18$; slope = 0.92) and harvester ant nests ($r = 0.99$, $P < 0.001$, $df = 18$; slope = 1.01) indicating observer consistency and perhaps

high detection probability. These findings illustrate an approach for evaluating sampling designs in many ecological contexts.

Introduction

Accurate estimates of a species' distribution and abundance across landscapes are fundamental to animal ecology (Wilson and Delahay, 2001; Morrison et al., 2006). However, obtaining reliable counts of secretive (e.g., nocturnal), cryptic, or fossorial animals can be difficult, particularly when sampling extensive landscapes. As a surrogate for direct observation, wildlife biologists often rely on animal sign such as tracks (e.g., Bonesi and Macdonald, 2004), scat (e.g., Hodges and Mills, 2008; Alves et al., 2013), or burrows (e.g., Lara-Romero et al., 2012). Detection and enumeration of this sign is then used to produce estimates of occupancy, true density or abundance, or relative abundance. In some cases, counts of animal sign may not correlate with occurrence or true abundance because of imperfect detection, mis-match of scales, animal behavior, or a disconnect between sign deposition and individuals (MacKenzie et al., 2002; Pollock et al., 2002; Bonesi and Macdonald, 2004). Ensuring sign surveys are applied appropriately is essential. For instance, if the research objective is to assess factors influencing relative abundance, it is important to evaluate detection of sign and ensure sampling is sufficiently precise to identify changes in these metrics (Engeman, 2005; Morrison et al., 2006). Understanding what influences the detection and precision of values derived from animal sign is especially important when temporal or spatial variation is high.

Many terrestrial environments, including arid lands, exhibit spatial heterogeneity reflecting variation in soil, topography, climate, and plant competition for limited resources (e.g., Hunter and Price, 1992). Animal distribution, habitat use, and abundance are often

associated with this variability because of resource needs such as food, water, and shelter (Morrison et al., 2006). Sampling animal populations in variable environments can be challenging, often resulting in a trade-off between precision of parameter estimates and sampling effort (Wilson and Delahay, 2001; Hodges and Mills, 2008). Effort can be defined by number of sampling units or sub-samples, time used for each sample, or financial cost. Evaluating the precision versus effort trade-off is important to identify a protocol that maximizes detection and statistical precision, yet balances financial and logistical constraints. Few studies evaluate the performance of sampling protocols (Morrison et al., 2006), which is surprising considering the influence of sampling design on statistical analyses and research objectives.

We sought to implement an approach that could be used by others to evaluate relative abundance or habitat use of animals using sign surveys. We include relative abundance and habitat use together because counts per unit area can be interpreted as both, depending on the relationship between sign and individuals. Our objectives were to assess 1) how precision of abundance estimates varied as a function of sign abundance and variation, and sub-sampling intensity, 2) how sampling effort varied with abundance of sign, and 3) if and how sign classification and detectability changed across vegetation conditions and sign abundances. We implemented an *over-sampling* design (i.e., recording an excessive amount of data relative to logistical constraints) with two observers in the sagebrush-steppe, a heterogeneous and arid landscape. We surveyed for recently active burrows of Piute ground squirrels (*Urocitellus mollis*; hereafter ground squirrels) and nests of Owyhee harvester ants (*Pogonomyrmex salinus*; hereafter harvester ants). Ground squirrels and harvester ants are ecologically important because of their role as ecosystem engineers (Laundré, 1993; MacMahon et al.,

2000), prey (Marti et al., 1993), and seed consumers (Van Horne et al., 1998; Anderson and MacMahon, 2001). Our over-sampling approach allowed us to identify a precise and efficient sampling protocol characterizing ground squirrel and harvester ant relative abundance. This framework could be applied by other investigators assessing sampling designs in spatially heterogeneous environments.

Methods

The Morley Nelson Birds of Prey National Conservation Area (BOP) is a 1,962 km² region within southwestern Idaho (Latitude: 43.283, Longitude: 116.200), and captures a gradient of ground squirrel and harvester ant densities. The Snake River canyon in the BOP provides nesting habitat for one of the most abundant and diverse assemblages of raptors world-wide (Olendorff and Kochert, 1977), which primarily forage on small mammals including ground squirrels (Marti et al., 1993). The BOP is an arid (110–350 mm annual precipitation) sagebrush-steppe environment that is managed under a multiple-use framework by the Bureau of Land Management. The BOP landscape has been increasingly fragmented over the last 100 years or so, primarily due to exotic grass invasion, human use, military training, livestock grazing, and increased fire frequency (Yensen et al., 1992). These factors have contributed to a gradient of non-native plant invasion and successional stages within vegetation communities, including big sagebrush (*Artemisia tridentata*), native perennial grasslands, and exotic annual grasslands (i.e., primarily cheatgrass, *Bromus tectorum*).

We collected data within 100 m × 100 m (1 ha) plots ($n = 20$). Each plot was selected based on a stratified random design within areas that were historically sagebrush. To capture a gradient of successional and non-native plant invasion stages, three strata were delineated using the best available GIS data: 1) areas that were previously burned and seeded (aerial or

drill seeded with native and non-native rangeland perennial plant species), 2) areas that were burned and not seeded, and 3) unburned areas (i.e., fires absent for at least 50 years). We randomly selected sampling plots in each stratum to capture a representative distribution of burrowing animal relative abundance.

Two observers visited the sampling plots in late March 2013, and surveyed for recently active ground squirrel burrows and harvester ant nests. The end of March coincides with the emergence of all ages of ground squirrels (i.e., high squirrel activity), and substantial ant activity within our study area. At each 1-ha plot, both observers independently counted burrows or ant nests within six $100\text{ m} \times 4\text{ m}$ belt transects spaced $\geq 16\text{ m}$ apart in a north-south orientation (i.e., 6 sub-samples per plot). To ensure survey consistency, we extended a 100 m tape that we used as our transect center, used a 2 m long PVC pipe to determine if burrows or nests were within belts, and recorded counts in 50 m increments. Additionally, we surveyed half of the belt (i.e., 2 m wide) at any one time to increase detection probabilities. We classified ground squirrel burrows as recent if the entrance was approximately 6–12 cm wide (Laundré, 1989), $>5\text{ cm}$ deep, and had $\geq 2\text{--}3\text{ mm}$ of fine soil at the burrow entrance. We classified harvester ant nests as active if we observed individuals in or on the nest. If we observed no ants on a nest, we disturbed the surface to observe if individuals responded.

Data Analysis

We first examined how the precision of plot-level estimates of burrow and nest counts changes as a function of the number of transects surveyed within each plot. To capture the maximum heterogeneity between transects, we selected sub-samples (i.e., 2–5 transects) from the six $4\text{ m (wide)} \times 100\text{ m (long)}$ belt transects in each plot that maximized the spatial distance between transects (i.e., $\geq 16\text{ m}$ apart). For each sub-sample, we calculated the mean

number of burrows or nests and associated *SD*. We plotted the means and *SD*s for all sub-samples across plots to identify the range that encompassed most of the means and *SD*s we observed. For ground squirrels, the range of means and *SD*s was 1.00–15.00 and 1.00–7.00, respectively. The median number of burrows per transect and *SD* across plots and sampling intensities was 8.33 ± 3.48 . For harvester ants, means ranged between 0.10–3.00, and *SD*s were 0.10–1.25. The median number of nests per transect and *SD* (excluding means of zero) across plots and sampling intensities was 0.50 ± 0.58 .

We then built a matrix for each sampling intensity across plots with means as rows and *SD*s as columns, and populated the matrix with calculations of relative standard error ($RSE = SE/\text{mean}$). We used RSE rather than relative *SD*, or coefficient of variation, because *SD* describes the variation within a sample, whereas *SE* indicates the reliability of estimated means; that is, *SE* describes the variation within the sampling distribution. To examine patterns of the RSEs, we plotted RSE as a function of burrow or nest abundances, *SD* of abundances, and sampling intensity. We were interested in identifying a sampling intensity that reached a $RSE \leq 30\%$ (e.g., McCune and Grace, 2002) near the overall (i.e., across plots and sub-samples) median number of burrows or nests per transect and median *SD*. We chose this criterion because, on average, we wanted our precision to be at least 30% of our average abundances.

Second, we assessed how sampling duration (i.e., person-hours) changed as a function of plot-level abundance of ground squirrel burrows and sampling intensity to determine the level of sampling that maximized time efficiency. We calculated sub-sample duration by multiplying a fraction to the total time spent sampling (i.e., six $4 \text{ m} \times 100 \text{ m}$ transects on each plot). For example, the duration of sampling for three transects was estimated by multiplying

the total duration by 0.50 because three transects was half of six. We used only ground squirrel burrow data because their burrows were more numerous than ant nests, and were the primary determinant of time spent sampling.

Finally, we evaluated classification and detection error of sign by correlating plot-level counts of ground squirrel burrows and harvester ant nests between observers. A strong and positive relationship with a linear slope and correlation coefficient (r) of approximately one would be expected if detection probabilities were high and classification of burrows and nests were consistent between observers (assuming no shared biases). However, both slope and r values would be expected to decline as detection probabilities decreased and sign classification errors occurred due to increased variation. We evaluated these predictions using correlation analyses in the program R (R Core Team, 2013).

Results and Discussion

Precision and Effort

The pattern of precision across the range of means, SD s, and sampling intensities differed between ground squirrels and harvester ants. The RSE for ground squirrels was below 30% at a mean of 8 burrows per transect and a $SD = 4$ for sampling intensities ≥ 3 transects (Figure 1.1). RSE continued to decrease as burrow abundance increased, and fell below 20% at the maximum recorded burrow abundance. In contrast, the pattern of RSE for harvester ants was less influenced by sampling intensity (Figure 1.2). RSE for harvester ants never fell below 30% for any sampling intensity at a mean of 0.50 nests per transect and a $SD = 0.58$. However, at a mean of 2–3 nests per transect, RSE was near or below 30% across all SD s at sampling intensities of ≥ 3 transects. Additional harvester ant data were available from a broader sample of 82 1-ha plots collected in 2013, and the mean number of nests per

transect was 1.90 (unpublished data). Assuming these data were a better approximation of harvester ant abundances, sampling intensities ≥ 3 transects would result in a RSE below 30%.

We identified that sampling duration depended on burrow abundance in addition to sub-sampling intensity within plots. At a sub-sampling intensity of < 3 transects, our belt-transect method generally required less than one hour per plot (Figure 1.3). However, sampling intensities > 3 transects increased the duration of sampling up to two hours. Interestingly, intermediate to low burrow abundance (e.g., 3–8 burrows per transect) required the greatest duration per burrow counted. This was likely due to vegetation characteristics on plots associated with burrow abundances in that particular range. For example, the mean shrub cover for burrow abundances between 3–8 was 12.7%, versus 2.8% for the remaining burrow abundances.

Analyses of precision and effort indicated that a three transect sampling protocol would best satisfy the trade-off between statistical precision and effort. First, three transects provided relatively high precision given the overall abundances and *SDs*. As ground squirrel burrow abundance increased above the median, precision remained high with RSE ranging from 30% to $< 20\%$. Consequently, as ecological signal increased (i.e., increasing population size), our ability to detect differences among plots also increased; analogous patterns have been documented in similar studies (Hodges and Mills, 2008; Alves et al., 2013). Second, at a mean of ≥ 2 ant nests per transect the RSE was near or below 30% across *SDs* at a sampling intensity of ≥ 3 transects. Higher precision was more desirable at lower abundances, however, it was apparent that additional sampling effort would not substantially increase precision (Figure 1.2). Finally, a three transect protocol was relatively efficient in terms of time spent sampling at each plot (i.e., approximately 1 hour). Sampling > 3 transects would decrease time

efficiency, assuming an eight hour workday, travel time to study area and between plots, and relatively large sample sizes (e.g., >100–150 plots). Indeed, a three transect design appeared to strike an efficient balance between statistical and logistical constraints, and would best capture relative abundance for ground squirrels and harvester ants in our ecological context.

Classification and Detection

Our correlation analyses indicated consistent patterns between observers for counts of ground squirrel burrows and harvester ant nests across a gradient of vegetation characteristics. Cover estimates were 0.0–30.1% for shrubs, 0.1–38.3% for perennial grasses, and 0.0–94.4% for cheatgrass, which was the dominant exotic annual grass. We observed a strong positive correlation between observers for ground squirrel burrow counts ($r = 0.99$, $P < 0.001$, $df = 18$; slope = 0.92, $SE = 0.03$). Similarly, counts of harvester ant nests were strongly associated between observers ($r = 0.99$, $P < 0.001$, $df = 18$; slope = 1.01, $SE = 0.02$).

These results suggest that observers were consistent in classifying ground squirrel burrows and harvester ant nests, and detection probabilities were likely high (assuming no consistent biases among observers). We believe that consistency among observers was achieved because 1) burrows and nests were generally in conspicuous locations (i.e., in open areas), 2) we surveyed only 2 m of the 4 m belt transect at any one time, and 3) tall vegetation structure (i.e., shrubs, which could act as barriers to observer vision) was generally sparse. Furthermore, prior to sampling both observers spent 3–4 days calibrating classification decisions for ground squirrel burrows where squirrels were actively observed entering and exiting entrances, which contributed to among observer consistency. Collectively, our results indicate that the belt-transect survey protocol, and burrow and nest classification, was effective at detecting and quantifying burrows and nests across gradients of vegetation cover.

Additionally, because variation between observers was minimal it appears that a double observer approach is not needed, which has large implications for cost savings.

Conclusion

Assessing the statistical and logistical performance of sampling protocols is essential in ecological research and monitoring to ensure research objectives are achieved and results are defensible. However, because of time and budget limitations, survey designs are often implemented without proper statistical evaluation and field testing. Survey designs are frequently chosen because of previous use, convenience, or convention (Morrison et al., 2006). Our framework allowed us to assess the trade-off between sampling precision and survey effort for sign surveys of ground squirrels and harvester ants across a sagebrush-steppe landscape. Furthermore, we were able to demonstrate that detection and classification of animal sign was consistent between observers, and was unaffected by the gradient of vegetation conditions. If we had documented higher discrepancies between observer counts, it would have been useful to model the influence of environmental covariates on count differences. These analyses might be required in other ecological contexts, and would inform the modification of sampling schemes. By implementing our over-sampling approach, other researchers and managers could maximize the efficacy of their survey design, especially during pilot studies. Disturbances such as fire and invasive species will continue to alter landscapes, and there is an urgent need to quantify these changes. Evaluating the accuracy and efficacy of sampling protocols to characterize spatial and temporal variation is a means to satisfy that need.

References

- Alves, J., A. A., da Silva, A. Soares, and C. Fonseca. 2013. Pellet group count methods to estimate red deer densities: precision, potential accuracy and efficiency. *Mammalian Biology* 78:134–141.
- Anderson, C. J., and J. A. MacMahon. 2001. Granivores, exclosures, and seed banks: harvester ants and rodents in sagebrush-steppe. *Journal of Arid Environments* 49:343–355.
- Bonesi, L., and D. W. Macdonald. 2004. Evaluation of sign surveys as a way to estimate the relative abundance of American mink (*Mustela vison*). *Journal of Zoology (London)* 262:65–72.
- Engeman, R. M. 2005. Indexing principles and widely applicable paradigm for indexing animal populations. *Wildlife Research* 32:203–210.
- Hodges, K. E., and L. S. Mills. Designing fecal pellet surveys for snowshoe hares. *Forest Ecology and Management* 256:1918–1926.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Lara-Romero, C., E. Virgós, G. Escribano-Avila, J. G. Mangas, I. Barja, and X. Pardavila. 2012. Habitat selection by European badgers in Mediterranean semi-arid ecosystems. *Journal of Arid Environments* 76:43–48.
- Laundré, J. W. 1989. Horizontal and vertical diameter of burrows of five small mammal species in southeastern Idaho. *Great Basin Naturalist* 49:646–649.

- Laundré, J. W. 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. *Oecologia* 94:43–48.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* 31:265–291.
- Marti, C., K. Steenhof, M. Kochert, and J. Marks. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. *Oikos* 67:6–18.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. *Wildlife-habitat relationships*. Island Press, Washington, D.C., USA.
- Olendorff, R. R., and M. N. Kochert. 1977. Land management for the conservation of birds of prey. Pages 294-307 *in* R. D. Chancellor, editor. *World Conference on Birds of Prey: report of proceedings, Vienna 1975*. International Council for Bird Preservation, London, UK.
- Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105–119.

- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 20 March 2014.
- Van Horne, B., R. L. Schooley, and P. B. Sharpe. 1998. Influence of habitat, sex, age, and drought on the diet of Townsend's ground squirrels. *Journal of Mammalogy* 79:521–537.
- Wilson, G. J., and R. J. Delahay. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research* 28:151–164.
- Yensen, E., D. L. Quinney, K. Johnson, K. Timmerman, and K. Steenhof. 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. *American Midland Naturalist* 128:299–312.

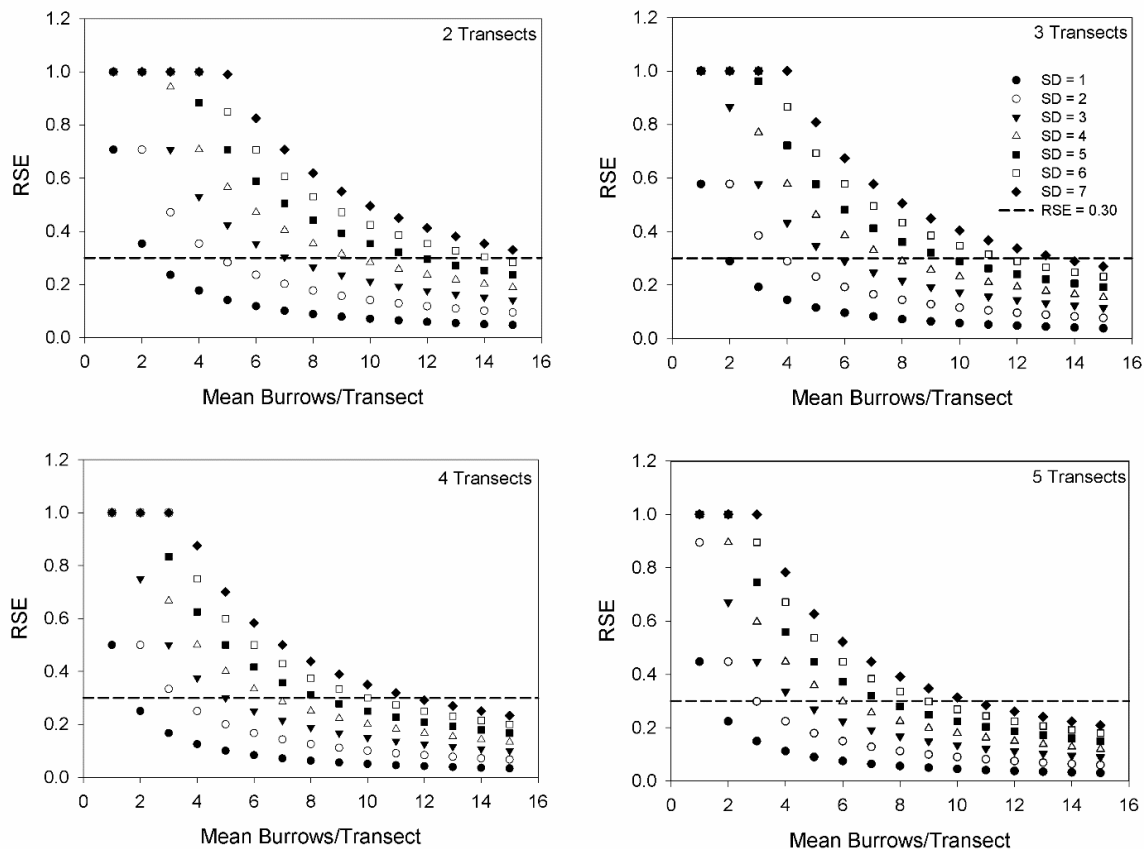


Figure 1.1. Relative standard error (RSE) versus mean number of ground squirrel burrows per transect for 6 levels of *SD*. RSE values > 1 were set to one for graphing purposes and because we were only interested in RSE values in this range. The number of transects represents the 4 sampling intensities (2–5 transects) we evaluated. Dashed line indicates our target threshold of $RSE \leq 0.30$. These data were collected at the Morley Nelson Birds of Prey National Conservation Area, Idaho, USA, during March 2013.

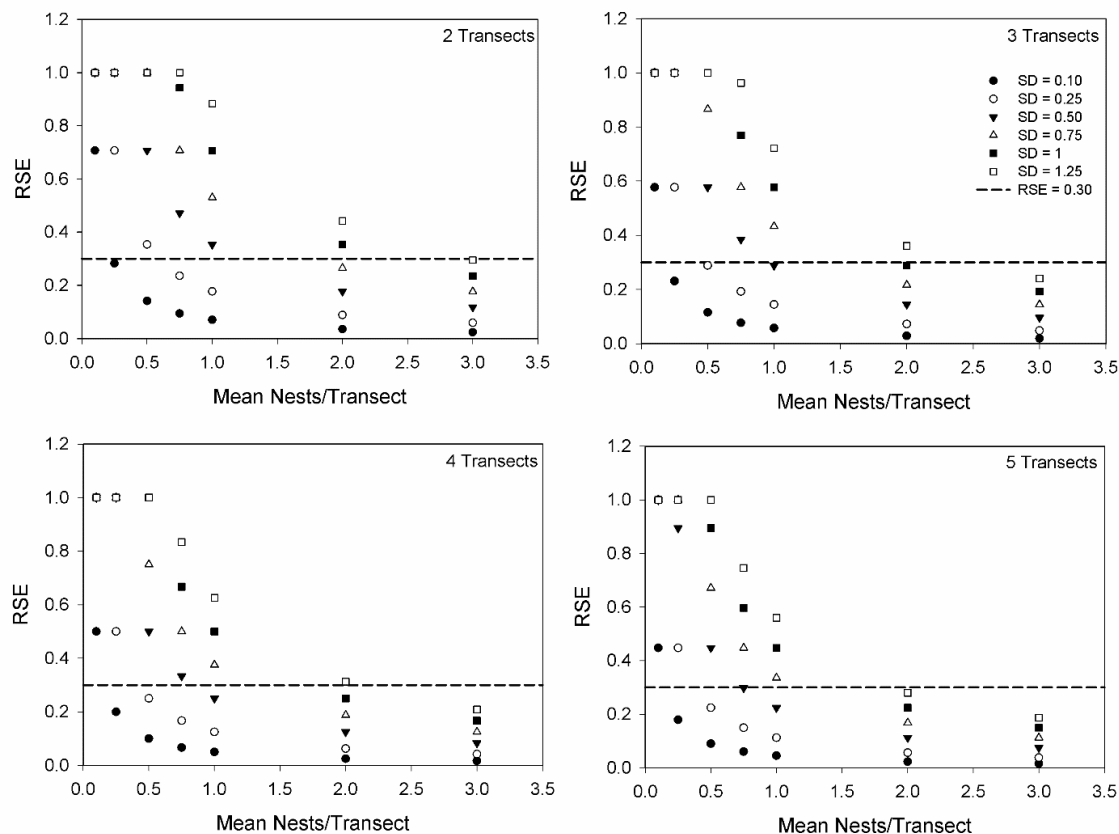


Figure 1.2. Relative standard error (RSE) versus mean number of harvester ant nests per transect for 6 levels of *SD*. RSE values > 1 were set to one for graphing purposes and because we were only interested in RSE values in this range. The number of transects represents the 4 sampling intensities (2–5 transects) we evaluated. Dashed line indicates our target threshold of $RSE \leq 0.30$. These data were collected at the Morley Nelson Birds of Prey National Conservation Area, Idaho, USA, during March 2013.

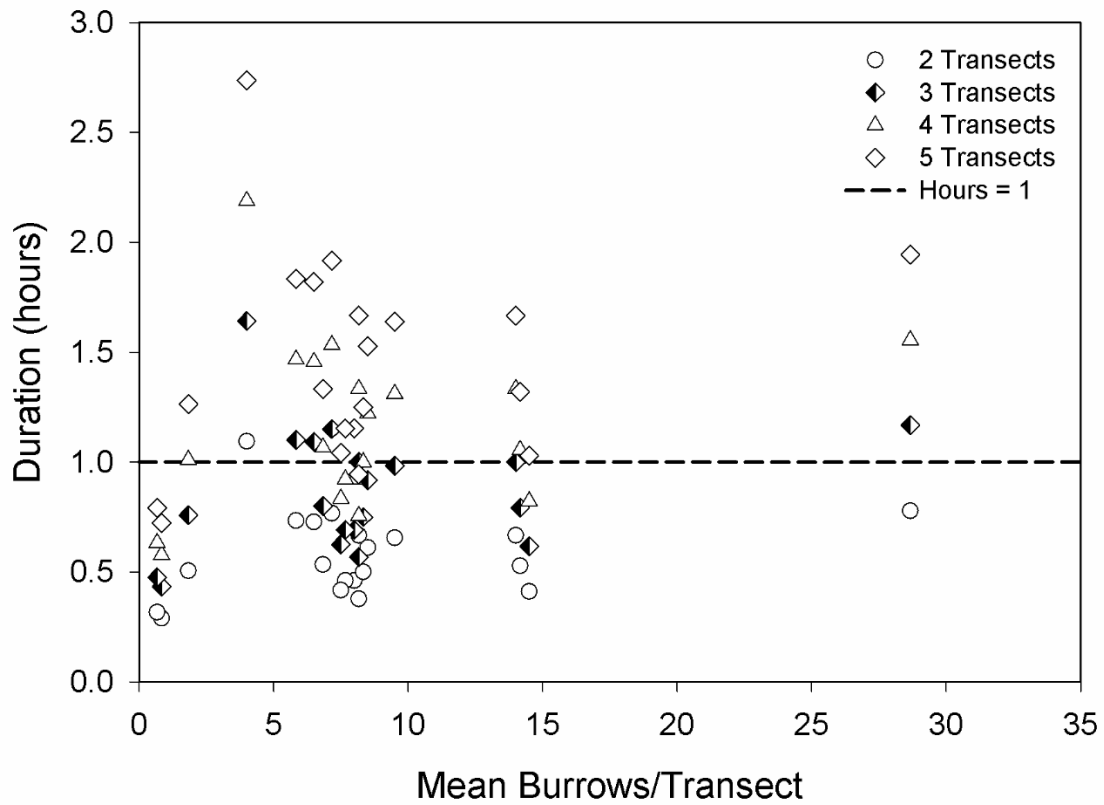


Figure 1.3. Sampling duration versus mean number of ground squirrel burrows per transect. The number of transects represents the 4 sampling intensities (2–5 transects) we evaluated for $n = 20$ plots per sampling intensity. Dashed line indicates one hour of sampling. These data were collected at the Morley Nelson Birds of Prey National Conservation Area, Idaho, USA, during March 2013.

***Chapter 2: Occupancy and abundance of predator and prey: implications of
the fire-cheatgrass cycle in sagebrush ecosystems***

Submitted to Ecosphere

Co-authors: Robert S. Arkle, Janet L. Rachlow, Kerri T. Vierling, David S. Pilliod, and
Michelle M. Wiest

Abstract

Sagebrush (*Artemisia tridentata*) ecosystems are declining due to biological invasions and changes in fire regimes. Understanding how ecosystem changes influence functionally important animals such as ecosystem engineers is essential to conserve ecological functions. American badgers (*Taxidea taxus*) are an apex predator and ecosystem engineer in that they move and redistribute large amounts of soil within sagebrush ecosystems. Piute ground squirrels (*Urocitellus mollis*) are also an ecosystem engineer as well as an essential prey resource for many predators, including badgers. Our research objective was to evaluate the relative importance of biological invasions and fire, abiotic factors, and biotic factors on badgers and ground squirrels. We sampled 163 1-ha plots during April-June across a gradient of burn histories within a 1,962 km² study area in southern Idaho, USA. At each plot, we characterized occupancy of ground squirrels and badgers and relative abundance of ground squirrels. Additionally, we characterized soil texture, climate, connectivity and dispersal potential, fire frequency, grazing, and cover of many plant species including a highly invasive exotic annual grass (cheatgrass; *Bromus tectorum*). We used an integrated approach to evaluate competing hypotheses concerning factors influencing occupancy and abundance. Results suggested that occupancy of ground squirrels was positively associated with long-term precipitation, dispersal potential, and fine-grained soil. Abundance of ground squirrels

was positively associated with fine-grained soil, but negatively associated with cheatgrass, fire frequency, human disturbance, and shrub cover. Badger occupancy was positively associated with ground squirrel occupancy and human disturbance (e.g., agriculture), which indicated affinity to prey. Our results provide insight into the relative influence of abiotic and biotic factors on predator and prey, and highlight how effects change across different population parameters. Our research suggests that widespread environmental change within sagebrush ecosystems, especially the fire-cheatgrass cycle (i.e., invasion of cheatgrass and increased fire frequency) and human land disturbances, are directly and indirectly influencing ground squirrels and badgers. However, we also found evidence that efforts to mitigate these stressors, for example establishing bunchgrasses post-fire, may provide targeted conservation strategies that promote these species and thus preserve the burrowing and trophic functions they provide.

Introduction

Drylands worldwide are experiencing unprecedented changes from shifts in climate, increases in land use, and biological invasions (e.g., Bestelmeyer et al. 2015, Cook et al. 2015), which has implications for animal populations and the ecological processes they mediate. For example, sagebrush ecosystems in western North America have been reduced to half of their historical range and are highly imperiled (Noss et al. 1995, Knick et al. 2003, Schroeder et al. 2004) because of stressors such as human settlement, conifer encroachment, wildfire, and biological invasions (Davies et al. 2011, Knick et al. 2011). A diversity of ecological processes are being lost as a consequence of such changes within dryland ecosystems. For instance, burrowing mammals provide essential ecological functions through trophic pathways and modifying physical attributes of ecosystems, yet many of these

mammals are in steep decline due to stressors aforementioned (Davidson et al. 2012).

Evaluating how ecosystem stressors within drylands influence the distribution and abundance of burrowing animals will contribute to development of effective management and conservation plans targeted at preserving ecosystem function (Davidson et al. 2012).

Burrowing mammals mediate ecological processes within sagebrush (*Artemisia tridentata*) ecosystems by modifying habitat (e.g., provide burrows) and filling important trophic roles. American badgers (*Taxidea taxus*; hereafter badger) and Piute ground squirrels (*Urocitellus mollis*; hereafter ground squirrel) are both ecosystem engineers in that they modify soil properties through digging activities and provide subterranean habitat for other species (*sensu* Jones et al. 1994, 1997, 2010). Badgers excavate digs for resting and denning that are characterized by mounded soil at the entrance of the excavation. Badger digs influence landscape heterogeneity directly and through changes in water infiltration processes, and soil chemistry and pH (Eldridge 2009, Eldridge and Whitford 2009). Badger digs occur at densities up to 790 mounds/ha (Eldridge 2004), providing abundant nesting habitat for species such as burrowing owls (*Athene cunicularia*; King and Belthoff 2001). Ground squirrels are obligate burrowers that influence soil characteristics as well as patterns of water distribution and recharge (Laundré 1993). Badger and ground squirrel activities directly and indirectly provide habitat to numerous non-burrowing organisms, like other mammals, reptiles, and amphibians (mechanisms in Kinlaw 1999, Davidson et al. 2012, Kinlaw and Grasmueck 2012). Moreover, badgers are apex predators in grasslands and shrublands, influencing ecosystems through changes in prey density and behavior (e.g., Estes et al. 2011). Ground squirrels are a common prey item for many species, including raptors, snakes, and mammalian carnivores (Messick and Hornocker 1981, Marti et al. 1993). Indeed, badgers and

ground squirrels provide essential trophic and non-trophic functions within sagebrush ecosystems, and therefore understanding how ecosystem stressors influence their populations is important for long-term conservation.

Understanding the relative effects of ecosystem stressors on animals across landscapes is difficult without a framework that evaluates both broad and local parameters such as distribution and abundance. Species distributions often are evaluated using broad-scale abiotic gradients such as temperature, precipitation, or soil characteristics (e.g., Thuiller et al. 2004, Guisan and Thuiller 2005). Indeed, considerable evidence suggests that such abiotic factors strongly influence or limit species distributions (Wiens 2011). However, ecological systems are complex networks of biotic and abiotic interactions, many of which contribute to structuring species distributions (e.g., Connell 1961, Pulliam 2000, Jackson et al. 2001, Soberón 2007, McGill 2010, Fisher et al. 2012, Wisz et al. 2013). Further, species abundances are likely driven by different, and perhaps more local processes relative to those driving patterns of species distributions. Boulangeat et al. (2012) documented that accessibility or dispersal limitation was more influential in describing plant distributions, whereas biotic interactions explained plant abundances. Abiotic factors such as climate and soil were important for both distribution and abundance (Boulangeat et al. 2012). Many biotic and abiotic factors interact to influence species distributions and abundances, and the strengths of these interactions are linked with scale (Wiens 1989, Guisan and Thuiller 2005, Soberón 2007, McGill 2010). Therefore, an integrated analytical approach that incorporates both distribution and abundance will likely result in a more comprehensive understanding of how ecosystem stressors and other ecological factors influence animal populations (e.g., Boulangeat et al. 2012, Ehrlén and Morris 2015).

The main ecosystem stressor in lower elevation sagebrush ecosystems (e.g., *A. t. wyomingensis*) is the fire-cheatgrass cycle, which describes a synergistic relationship between biological invasions by exotic annual grasses such as cheatgrass (*Bromus tectorum*) and changing fire regimes (Miller et al. 2011). Cheatgrass dominates $\geq 40,000$ km² of the 650,000 km² land area of the Great Basin Desert (Bradley and Mustard 2008). Cheatgrass invasion has changed fire regimes resulting in shorter fire return intervals, larger area burned, and increased probability of fire (Balch et al. 2013). Furthermore, climate projections suggest greater precipitation variability and potential for drought (Abatzoglou and Kolden 2011, Cook et al. 2015), leading to increased expansion of exotic annual grasses and continued changes in fire. The fire-cheatgrass cycle presents wildlife managers with significant conservation challenges that are spatially extensive.

Our research objective was to evaluate the relative influence of the fire-cheatgrass cycle, abiotic factors, and biotic factors on occupancy and abundance of badgers and ground squirrels within a sagebrush ecosystem. Our hypotheses reflect the relative scale of gradients influencing occupancy and abundance (Guisan and Thuiller 2005, Soberón 2007; Figure 1). For example, local-scale, biotic factors were expected to drive abundance of ground squirrels, whereas larger-scale abiotic factors were expected to influence occupancy patterns of ground squirrels. Because of the strong association between badgers and ground squirrels as predator and prey (e.g., Messick and Hornocker 1981), we expected prey distribution and abundance (i.e., local biotic factors) to influence occupancy of badgers. We separated the components of our hypotheses into abiotic and biotic themes (e.g., Guisan and Thuiller 2005, Hirzel and Lay 2008). We included soil, climate, and disturbance (i.e., fire) as our abiotic factors, while we included landscape, dispersal, disturbance (i.e., grazing), predation, prey, and forage as our

biotic factors. Embedded within disturbance and forage is the fire-cheatgrass cycle (asterisks in Figure 1); that is, changes in fire regimes and invasion of cheatgrass. We hypothesized (H1) that broader-scale abiotic gradients and dispersal potential would largely influence occupancy of ground squirrels. We predicted that soil, climate, and dispersal potential would be the strongest drivers of ground squirrel occupancy because they are important for burrow construction, forage, and site accessibility (Figure 1a). We hypothesized (H2) that biotic factors (via bottom-up processes) would largely influence occupancy of badgers in that we expected a positive association with ground squirrels (e.g., Messick and Hornocker 1981, Grassel et al. 2015) and human disturbance (i.e., irrigated agriculture; Figure 1b). Additional and temporally consistent precipitation in the form of irrigation has created resource hotspots in other desert environments (Faeth et al. 2005, Cook and Faeth 2006), and may increase biomass and population stability of alternative prey for badgers. Finally, we hypothesized (H3) biotic and disturbance factors, including forage, biological invasions, and fire history, would be the most influential on ground squirrel abundance given their high densities and nutritional demands (i.e., bottom-up forcing, Van Horne et al. 1997a; Figure 1c). Collectively, this work 1) highlights how the fire-cheatgrass cycle within sagebrush ecosystems influences a predator-prey system at the landscape level, and 2) provides recommendations for managers to conserve the functions provided by burrowing mammals in a rapidly changing environment.

Methods

Study Area and Sampling

This study was conducted on the Morley Nelson Snake River Birds of Prey National Conservation Area (BOP; Figure 2.2) in southwestern Idaho, USA (Latitude: 43.28,

Longitude: 116.20), which is a 1962 km² sagebrush-steppe ecosystem that is managed under a multiple-use framework by the U.S. Bureau of Land Management. This arid shrubland receives approximately 110–320 mm of precipitation annually, most falling between November and April (Yensen et al. 1992, Van Horne et al. 1997a). The elevation gradient (900–950 m) and topography are modest with the exception of the Snake River canyon and a few isolated buttes. The dominant plant communities have largely been shaped by increasing fires since 1980 (Kochert and Pellant 1986), and include Wyoming big sagebrush (*A. t. wyomingensis*), winterfat (*Krascheninnikovia lanata*), shadscale saltbrush (*Atriplex confertifolia*), cheatgrass, and Sandberg bluegrass (*Poa secunda*). Ground squirrel and badger densities are variable across the BOP, with some areas exhibiting exceptionally high densities (Messick and Hornocker 1981, Van Horne et al. 1997a, Van Horne et al. 1997b). The Snake River canyon in the BOP provides nesting habitat for one of the most abundant and diverse assemblages of raptors world-wide (Olendorff and Kochert 1977), which primarily forage on small mammals including ground squirrels further highlighting the importance of ground squirrel conservation (Marti et al. 1993).

To sample a gradient of native and non-native plant communities, we first delineated three strata: 1) areas that were previously burned and seeded (via aerial or drill methods) with native and non-native perennial plants (i.e., treated); 2) areas that were burned and not seeded (i.e., burned); and 3) areas that have not burned for at least the last ~30 years (i.e., unburned). We then randomly allocated 1-ha plots within each strata. We created strata in a geographic information system (GIS) by mapping the distribution (and overlap) of dominant vegetation types, fires, and seeding treatments using the Land Treatment Digital Library (Pilliod and Welty 2013; <http://dx.doi.org/10.3133/ds806>). Seeding treatments were conducted by the U.S.

Bureau of Land Management, the vast majority of which were post-fire seeding of burned areas.

Badger and ground squirrel surveys

At each 1-ha plot, we surveyed for badger digs and ground squirrel burrows during April – early June 2013 and 2014 to characterize badger and ground squirrel occupancy, and ground squirrel abundance. We indexed ground squirrel abundance based on counts of recently active burrows. Sign of digging activity has been successfully used to determine occupancy and abundance of many burrowing species (e.g., Bean et al. 2012, Lara-Romero et al. 2012, Ramesh et al. 2013). Our sampling period followed the emergence of all ages of ground squirrels (i.e., young of the year and adults) and mostly preceded estivation (Rickart 1987, Van Horne et al. 1997ab), thus capturing a reasonable representation of population activity and therefore relative abundance. Our sampling of ground squirrel burrows was informed based on previous limitations found by Van Horne et al. (1997b) in that we changed our sampling to coincide with peak activity of ground squirrels and focused on recently active burrows.

We enumerated recently active burrows for ground squirrels within three 100 m × 4 m belt-transects spaced 25 meters apart (Appendix A: Figure A1). We selected a three transect design based on a balance of statistical precision and sampling effort (see Holbrook et al. 2015). We classified a burrow as recently active if 1) the entrance was approximately 6–12 cm wide (Laundré 1989) and had ≥ 2 –3 mm of fine soil at the burrow opening (Yensen et al. 1992), 2) the burrow was >5 cm deep (Appendix A: Figure A2B), and 3) the entrance did not have characteristic sign of kangaroo rats (*Dipodomys* spp.) such as tail drags (Van Horne et al. 1997b). Previous analyses indicated high correlation among observers for counts of ground

squirrel burrows (Holbrook et al. 2015), thus we used counts from a single observer. Because of the potential issue of false positives at low densities due to classification (e.g., recent vs. old) errors, we conservatively set >3 burrows equal to occupied, and ≤ 3 equal to unoccupied. This decision was supported by visual and auditory encounters of ground squirrels at study plots. Plots with counts >3 recent burrows were included in our analyses of ground squirrel abundance. Finally, we resampled 30 plots in 2014 that we had surveyed in 2013, and assessed inter-annual variation in ground squirrel abundance using linear correlations.

We characterized badger occupancy by counting recently dug burrows or foraging digs within the three belt-transects, as well as the area between transects (Appendix A: Figure A1). We chose to survey the entire 1-ha area to increase the probability of detection because badgers use larger areas relative to ground squirrels. These additional surveys did not largely affect sampling effort because digs are conspicuous and easily detected at distances ≤ 10 – 15 m. We classified a dig as recent if 1) the entrance was circular and approximately 16–30 cm in diameter, 2) it was ≥ 25 cm deep, and 3) the mound of soil outside the entrance was fan-shaped (Appendix A: Figure A2A; Eldridge 2004, Lay 2008). Additionally, we evaluated if the mound had loose or crusted soil, cracks in the soil, or colonized vegetation; crusted and cracked soil is common after a combination of rain, wind, and sun exposure. If we observed substantial crust, cracks, or colonized vegetation we did not count the dig. We considered a plot to be occupied by badgers if ≥ 1 recent dig was recorded.

Environmental data

Abiotic and biotic factors

We characterized abiotic metrics of climate and soil texture using GIS. First, we retrieved climate data (mean annual precipitation and annual temperature) from the

Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group; <http://prism.oregonstate.edu>) during 1979–2008. We expected ground squirrels to be positively associated with mean annual precipitation, assuming generally wetter areas produce more consistent forage over time (Yensen et al. 1992). We did not expect badgers to exhibit strong associations with climate data; rather we expected climate to indirectly influence badgers through prey resources (e.g., Silva et al. 2013, Hebblewhite et al. 2014). Second, we developed an abiotic soil index describing soil texture using STATSGO (Soil Survey Staff, Natural Resources Conservation Service; <http://sdmdataaccess.nrcs.usda.gov>) data to understand how soil influenced occupancy and abundance (Appendix B: Table B1-B3). We identified the STATSGO map key at each plot, and averaged (across up to 10 soil names) the proportion of soil passing through a number 4 sieve at the first soil depth. This resulted in an index with larger numbers indicating finer-grained soils, and low numbers indicating relatively course-grained soils. We expected ground squirrels and badgers to be associated with finer-grained soils because course-grained soils 1) do not retain soil moisture as well as fine-grained soils, and 2) are less structurally sound for burrow construction due to the non-cohesive nature of sand particles (Lohr et al. 2013).

We characterized biotic components of the landscape to assess the effect of connectivity and context on ground squirrels and badgers, respectively (Appendix B: Tables B1-B3). We acquired Landfire Existing Vegetation Type data (LANDFIRE 2012; <http://www.landfire.gov/NationalProductDescriptions21.php>), and used a two-step process to reclassify the data to our desired types (Appendix B: Table B4): shrubland, grassland, and human disturbance (i.e., mostly agriculture lands, but included a few highways). For each plot, we calculated the proportion of the surrounding landscape that consisted of each type.

we used a circular area of 0.79 km² for ground squirrels to coincide with average dispersal distances of juveniles (~500 m; Olsen and Van Horne 1998), and an area of 2.40 km² for badgers, which represented an average home range for males (Messick and Hornocker 1981). We expected a negative effect of shrubland on ground squirrel occupancy and abundance because previous work indicated that high canopy shrublands can make squirrels more vulnerable to predation (Schooley et al. 1996), which might limit populations. We expected ground squirrels to be negatively associated with the human disturbance because of potential predation and/or competition from other animals attracted to irrigated agricultural (e.g., Faeth et al. 2005); both processes could reduce persistence or abundance. We expected badgers to be negatively associated with shrublands and positively associated with human disturbance because of ground squirrel presence or abundance (which is a substantial prey item; Messick and Hornocker 1981) and the additional food resources (i.e., other small mammals, reptiles, insects; Messick and Hornocker 1981) associated with irrigated agriculture, respectively.

We calculated a dispersal index to evaluate how accessibility influences ground squirrel occupancy and abundance (Appendix B: Table B1 and B3). To generate this index, we identified the nearest neighboring plot (from a focal plot) and divided the neighbor's relative abundance by the distance (m) to characterize the dispersal potential (similar in concept to Boulangeat et al. 2012). Focal plots with larger values indicate higher relative abundances as well as shorter distances to the neighbor, and consequently higher accessibility than plots with lower index values. We expected ground squirrel occupancy to be largely driven by accessibility because it is essential for occupancy to be realized (Boulangeat et al. 2012). We also expected ground squirrel abundance to be positively associated with accessibility, but to a lesser degree than occupancy because abundance is driven by more

local-level processes such as bottom-up mechanisms. Incorporating accessibility when modeling occupancy or abundance of species across landscapes is increasingly important, and provides a more realistic assessment of the relative effects of abiotic and biotic factors (Miller and Holloway, in press).

We characterized vegetation at each plot to evaluate the influence of forage and cover resources on ground squirrel occupancy and abundance (Appendix B: Table B1 and B3). At each plot, we sampled the vegetation community at 9 locations (points 1-9 in Appendix A: Figure A1) during May through August 2012–2014. At each location we took a nadir (i.e., 90°) photograph from a height of 2 m that captured an area of 1.5×2 m of ground surface (see Pilliod and Arkle 2013). We estimated percent cover by plant species using SamplePoint 1.43 software (Booth et al 2006) at 100 computer-selected grid points on each image, and we averaged proportions across the 9 points to get plot-level estimates. We further refined vegetation data into functional groups (Appendix C: Table C1) that we hypothesized would influence ground squirrel occupancy or abundance through bottom-up mechanisms. Consistent with previous work on ground squirrels (e.g., Van Horne et al. 1998, Lohr et al. 2013), we expected a strong and positive relationship with cover of Sandberg bluegrass (POSE), and a positive relationship with total species richness, non-POSE native perennial grasses (NPG), exotic (i.e., planted via restoration) perennial grasses (EPG), and native forbs (NF). In our ground squirrel occupancy analysis, we only included a few vegetation groups (i.e., POSE, EPG, and total species richness) because we expected the more abundant gradients to influence occupancy. Finally, we generated a functional group describing sagebrush (*Artemisia* spp.) and total shrub cover (Appendix C: Table C1), which we expected to increase mortality due to predation through visual and locomotive obstruction for ground

squirrels (Schooley et al. 1996). Therefore, we expected a negative relationship between plot-level shrub cover and occupancy and abundance of ground squirrels.

We developed two biotic covariates characterizing food resources for badgers (Appendix B: Table B2). We included occupancy and relative abundance of ground squirrels at the plot-level. We expected badgers to be positively associated with ground squirrels through bottom-up mechanisms (Messick and Hornocker 1981), but it was unclear whether squirrel occupancy or abundance would drive badger occupancy.

Lastly, we calculated a biotic index of grazing and an additional predation index to evaluate the effect of disturbance via herbivore competition and predation on ground squirrels (Appendix B: Table B1 and B3). At each of the 9 points within the plot (Appendix A: Figure A1), we used a point-quarter method to quantify the density of ungulate (e.g., domestic sheep and cows, deer, and pronghorn) pellets. We sampled four quadrants (NW, NE, SE, and SW) within a 12.5 m search radius and recorded the distance to nearest pellet pile of any species. We estimated density of pellets at each point as: $1/(\bar{x}d_1, d_2, d_3, d_4)^2$ where d = the point-to-pellet distance (m) for the closest pellet pile in each of the four quadrants, and \bar{x} = mean of the distances. Given the low intensities of grazing we observed, we expected the influence on ground squirrel abundance to be negligible. To generate a plot-level estimate of predation potential associated with badgers, we characterized badger intensity of use (in a spatial sense) as the total number of recent digs per plot. We expected a positive or insignificant relationship between badger intensity of use and ground squirrel occupancy and abundance because we hypothesized bottom-up processes were a stronger and more consistent driver of ground squirrel density relative to predation pressures (e.g., Yensen et al. 1992, Hubbs and

Boonstra 1997). A negative effect of badger intensity of use on ground squirrel abundance would suggest a top-down effect.

Ecosystem stressors: the fire-cheatgrass cycle

We used GIS and field data to characterize the fire-cheatgrass cycle within the sagebrush ecosystem (Appendix B: Tables B1-B3). First, we developed a raster of fire disturbance characterizing frequency from 1957–2013 using a GIS fire perimeter database developed by the U.S. Geological Survey (used in Balch et al 2013; http://rimgsc.cr.usgs.gov/outgoing/Geomac/historic_fire_data); 94% of these data were from ≥ 1981 , with only 7 observations prior to 1981. We expected ground squirrels to be negatively associated with fire frequency because of negative effects to forage, or potentially direct effects of the fire with repeat burning. We anticipated that the effect of fires on badgers would be weak and mostly mediated through ground squirrels. We expected weak direct effects of fires on badgers because larger predators such as badgers have relatively high movement potential (e.g., Messick and Hornocker 1981) and can simply relocate to areas unaffected by fires. Next, we used the vegetation community data to characterize plot-level estimates of cheatgrass (BRTE) as well as exotic forbs (EF) and non-BRTE exotic annual grasses (EAG). We expected a strong negative relationship between cheatgrass and ground squirrel occupancy and abundance because cheatgrass is annually unstable and does not support high densities of ground squirrels in drought years (Yensen et al. 1992, Van Horne et al. 1998, Lohr et al. 2013). Our data were collected from years with below average annual precipitation in the preceding year (i.e., 96 and 114 mm for 2012 and 2013, respectively). Similarly, we expected a negative relationship between squirrel abundance and exotic forbs and non-BRTE exotic annual grasses. We could not identify any direct effects of biological

invasions on badgers, thus we did not include these metrics in models of badger occupancy. We expected ground squirrels to mediate the effect of biological invasions on badgers through bottom-up processes.

Data analysis

Prior to model development and analysis, we standardized covariates and assessed multicollinearity. We standardized non-binary covariates by $(x_i - \bar{x}) / (2 \times \sigma_x)$ where x_i equals an observation at plot i . This standardization allowed for an equal comparison among non-binary and binary variables (Gelman 2008). We then evaluated collinearity among covariates and removed variables with $|r| \geq 0.60$ that were associated with the same response variable (Appendix B: Tables B1-B3). Therefore, we eliminated annual temperature, percent area grassland, and sagebrush cover at the plot-level.

We modeled occupancy of ground squirrels and badgers, and relative abundance of ground squirrels using generalized linear models with binomial and negative binomial error distributions, respectively. We used a Bayesian form of logistic regression (Gelman et al. 2008) for our ground squirrel occupancy models because of quasi-complete separation between ground squirrel occupancy and our dispersal index resulting in nonidentifiability of the maximum likelihood estimate. Following Gelman et al. (2008), we used a weakly informative Cauchy prior distribution with a center of 0 and scale of 2.5. In contrast, we evaluated badger occupancy using maximum likelihood estimation. Finally, we used a maximum likelihood approach with a negative binomial error distribution for analyses of ground squirrel abundance.

For each response variable, we developed a candidate set of models that reflected individual hypotheses along our themes of abiotic and biotic factors and ecosystem stressors

(see Figure 2.1). We also included a binary season effect for ground squirrel abundance following results from Van Horne et al. (1997b) indicating a decline in the number of active burrows after June 1. We were primarily interested in main effects, therefore we did not include interactions or non-linear terms. We implemented model selection using the Bayesian information criterion (BIC) for ground squirrel occupancy and Akaike's information criterion (adjusted for small sample size) for ground squirrel abundance and badger occupancy (AIC_c ; Burnham and Anderson 2002). We interpreted the model with the smallest BIC or AIC_c as the top model when there was clear separation from the candidate set (i.e., ΔBIC or ΔAIC_c for the second model was > 2 ; Burnham and Anderson 2002). However, when there was ambiguity (e.g., multiple models exhibiting a ΔBIC or $\Delta AIC_c \leq 2-7$; Burnham and Anderson 2002), we identified the 95% confidence set of models. We reported parameter estimates ($\pm 90\%$ credible or confidence intervals) from our top model, and our 95% confidence set using the natural averaging technique (i.e., averaging only included values where the parameter appeared; Burnham and Anderson 2002, Gruber et al. 2011). For themes with more than one covariate, we used model selection within theme to select the most parsimonious model (simplest model with ΔBIC or $\Delta AIC_c \leq 2$ was selected) for combining themes. We developed combined hypotheses beginning from the hypothesized strong effects and progressing to weak effects (Figure 2.1). For example, we evaluated whether soil, climate, or dispersal were a supported hypothesis for patterns in ground squirrel occupancy. We then combined soil and climate for a subsequent hypothesis, as well as soil, climate, and dispersal, but we did not include a soil and dispersal hypothesis.

For each model evaluated, we assessed model fit or predictive performance. For the generalized models with binomial error distributions, we tested goodness of fit (Hosmer and

Lemeshow 2000) and assessed predictive performance by calculating the area under the curve (AUC) of a receiver operating characteristic (ROC; Robin et al. 2011). A ROC plot characterizes true positives (e.g., sensitivity or omission error) against false positives (e.g., 1-specificity or commission error) as the threshold for classification changes (Robin et al. 2011). The AUC ranges from 0-1 and provides a measure of the model's ability to correctly discriminate between plots that are occupied versus unoccupied; values greater than 0.5 indicate progressively better discrimination ability (Hosmer and Lemeshow 2000). For models with negative binomial error distributions, we computed the Spearman's rank correlation coefficient between the observed and predicted counts, which provided a measure of fit. To complete these analyses, we used program R (R Development Core Team 2015) and packages 'MuMIn' (Barton 2015), 'arm' (Gelman and Su 2014), 'MASS' (Venables and Ripley 2002), 'ResourceSelection' (Lele et al. 2014), and 'pROC' (Robin et al. 2011).

Throughout our modeling, we assessed the importance of management relevant factors with the goal of providing management recommendations. For example, managers cannot reasonably manipulate some factors such as climate, soil, or distribution of agricultural lands across large spatial extents. However, they can manipulate factors such as vegetation cover or composition before or after fire. Therefore, if we documented a positive effect of a plant species, for instance, we would evaluate if field-derived classifications of burned (i.e., areas with mostly cheatgrass), treated (i.e., areas with regularly spaced NPG or EPG), or unburned (i.e., shrubs present) plots affected our animal response of interest.

Results

We enumerated 0–109 recent ground squirrel burrows within each plot, and 0–21 recent badger digs. The proportion of plots occupied by badgers was 48% compared to 75%

for ground squirrels. We sampled 134 1-ha plots for analyses of ground squirrel occupancy and vegetation data and 163 plots for badger occupancy. Of the 134 plots in which we collected vegetation and animal data, 51 plots had vegetation data from the previous year (e.g., vegetation and animal data from 2012 and 2013, respectively). The remaining 83 plots had vegetation and animal data temporally coincident. We did not observe large changes in vegetation cover within plots across 2012-2014. The sample size for ground squirrel abundance analyses was 101 plots because only those plots were classified as occupied. The Pearson's correlation between years (2013 and 2014) for ground squirrel relative abundance was high ($r = 0.90$, $n = 30$) indicating annual stability in relative abundance, and therefore we did not treat year as a fixed or random effect.

Occupancy

Patterns of ground squirrel occupancy were most strongly influenced by a combination of soil, climate, and dispersal. The model representing this hypothesis was best supported (i.e., $w_i = 0.80$), and all other models exhibited a $\Delta\text{BIC} > 2.88$ indicating relatively weak support (Table 2.1). The goodness of fit test indicated appropriate fit of our top model ($\chi^2 = 4.43$, $\text{df} = 8$, $p = 0.82$). Predictive performance of models indicated excellent discrimination (i.e., $\text{AUC} \geq 0.95$) for 5 models, and all of those models included the dispersal index (Table 2.1). All parameter estimates were positive, indicating a positive effect of soil, precipitation, and dispersal, although the credible interval for soil slightly overlapped 0 (Figure 2.3). Parameter estimates indicated a greater relative effect of dispersal on occupancy, however, there was substantial variation around the estimates. The influence of precipitation was greater than the effect of soil, and all other effects were statistically similar.

Multiple hypotheses characterizing badger occupancy were supported by our analyses. Six models had $\Delta AIC_c < 6$ ($w_i = 0.03-0.53$), and 2 models had ΔAIC_c values < 2 (Table 2.2). Our 95% confidence set of models contained the top 4 models (Table 2.2), which had 2-5 parameters including; ground squirrel occupancy, percent of landscape that was disturbed by humans, fire frequency, and soil texture. The goodness of fit test indicated appropriate fit of our top model ($X^2 = 4.97$, $df = 8$, $p = 0.76$). Predictive performance of our top 4 models suggested comparatively weak discrimination (i.e., $AUC = 0.64-0.68$). However, all models with an $AUC \geq 0.64$ included ground squirrel occupancy or relative abundance (Table 2.2). Parameter estimates from the top model and model averaged values for ground squirrel occupancy and human disturbance were similar, positive, and differed from 0 (Figure 2.4), however, the effect of ground squirrel occupancy on badger occupancy was higher than that of the human disturbance. The model averaged effect of soil and fire frequency did not differ significantly from 0.

Abundance

Multiple hypotheses were supported in terms of characterizing ground squirrel abundance. Four models had $\Delta AIC_c < 4$ ($w_i = 0.07-0.51$), and 2 models were within $\Delta AIC_c < 2$ (Table 2.3). Our 95% confidence set of models contained the top 3 models (Table 2.3), which had 10-12 parameters including; season, plot-level cover of cheatgrass, percent of landscape that was shrubland and human disturbance, dispersal index, fire frequency, grazing index, plot-level cover of shrubs, precipitation, and soil texture. Predictive performance, or model fit, as measured by Spearman's rank correlations was moderate ($\rho = 0.69$) for our top 4 models ($\Delta AIC_c < 4$), while all other models were less predictive ($\rho \leq 0.52$). Top model and model averaged parameter estimates and confidence intervals were similar (Figure 2.5). We

observed a significantly positive effect of soil, and a moderately positive effect of dispersal potential (although the model averaged estimate was insignificant). The effects of precipitation, grazing, and percent of landscape that was shrubland were statistically insignificant (i.e., overlapped 0). However, effects of cheatgrass cover, fire frequency, and plot-level shrub cover were all significantly negative; cheatgrass and shrub cover were qualitatively stronger than fire frequency.

Given the significant and negative effect of cheatgrass and shrub cover on ground squirrel abundance, and the potential to implement management actions on these features, we investigated the influence of treatment history. Not surprisingly, burned plots had the lowest shrub cover and the highest cheatgrass cover (Figure 2.6A). Successfully treated plots (i.e., burned and seeded) had less cheatgrass and more shrub cover than burned plots, but unburned plots had the lowest cheatgrass cover and the highest shrub cover (Figure 2.6A). Coupling these patterns and our modeling results, we would expect ground squirrel abundance to be highest in treated plots. Estimates of ground squirrel abundance strongly supported this expectation (Figure 2.6B). Unburned plots had a higher point estimate of ground squirrel abundance compared to burned plots, but the effect was not statistically different.

Discussion

A central objective in ecology is to evaluate the interactions that determine the distribution and abundance of organisms (Andrewartha and Birch 1954, Krebs 1972, Agrawal et al. 2007). Addressing this objective is particularly important for conservation efforts when ecosystems are experiencing significant alterations, such as the sagebrush ecosystem (Davies et al. 2011). However, understanding the processes that drive distribution or occupancy and abundance patterns requires an integrated framework. Our work assessed how biotic and

abiotic drivers as well as ecosystem stressors influence the occupancy and abundance of two burrowing mammals that serve important functional roles within sagebrush ecosystems (e.g., ecosystem engineers, and predator and prey). First, patterns of ground squirrel occupancy were best explained by long-term precipitation, dispersal potential, and soil texture. Second, abundance of ground squirrels was best explained by soil texture, shrub cover, agriculture, and biological invasions and fire. Finally, badger occupancy was most influenced by prey availability in the form of ground squirrels and alternative prey near humans (i.e., irrigated agriculture). Our results support the notion that broader-scale occupancy patterns (e.g., ground squirrels) are associated with abiotic factors and dispersal limitation for a small herbivore, but biotic factors explain variation in occupancy of a predator. Local-level variation in abundance of a small herbivore, however, was driven by a combination of biotic and abiotic factors. By directly integrating multiple factors hypothesized to influence the distribution and abundance of predator and prey, our work provided important insight needed for developing conservation plans that maintain the ecological functions of these animals within changing sagebrush landscapes.

Effects of abiotic and biotic factors

Our results were consistent with our theoretical hypothesis that dispersal potential would shape patterns of ground squirrel occupancy. First, we expected a positive effect of dispersal potential or accessibility on ground squirrel occupancy because, in order for a site to be occupied, it is required to be accessible (Soberón 2007). The effect of dispersal was qualitatively the highest we observed (Figure 2.3), and the predictive ability of our dispersal index (AUC of dispersal index only was 0.98) suggests that occupancy patterns for ground squirrels were largely determined by accessibility. Weddell (1991) reported a similar pattern

in that the probability of occupancy of Columbian ground squirrels (*Urocitellus columbianus*) declined with distance to nearest source population. Second, we expected and observed a positive effect of finer-grained soils relative to course-grained soils because finer-grained soils are more structurally sound and tend to retain soil moisture more effectively than course-grained soils. These characteristics have implications for burrow construction and plant productivity later in the growing season (Lohr et al. 2013). Lohr et al. (2013) found a positive effect of finer-grained soils on southern Idaho ground squirrels (*Urocitellus endemicus*) supporting the hypothesis that fine-grained soils are important for ground squirrels. Finally, we expected long-term precipitation (i.e., climate) patterns to be positively associated with ground squirrel occupancy through the mechanism of temporally consistent food. The effect of precipitation was positive and as strong as dispersal potential (Figure 2.3), indicating occupancy of ground squirrels is highly associated with precipitation. Food supplementation experiments have highlighted the positive demographic responses in reproduction, survival, and immigration rates in Columbian ground squirrels (Dobson and Kjelgaard 1985) and Arctic ground squirrels (*Spermophilus parryii*; Hubbs and Boonstra 1997). The strong effect of precipitation may indicate that temporally consistent forage results in fitness characteristics that sustain site occupancy. Because precipitation strongly influenced occupancy, changes in long-term patterns of precipitation, such as increased drought conditions in the Great Basin Desert (e.g., Cook et al. 2015), could negatively influence the distribution of ground squirrels. Together, it appears that higher precipitation and finer-grained soils promote habitats that generate site occupancy of ground squirrels, however, this is conditional on the areas being accessible to dispersers from source populations.

As hypothesized, occupancy of ground squirrels exhibited the strongest effect on badger occupancy, and our model with only ground squirrel abundance had the highest predictive performance (AUC = 0.70). Badgers in our study area appeared to make choices about space use based on the distribution and abundance of ground squirrels. Indeed, across their range, occupancy and habitat selection by badgers is strongly associated with abundance and distribution of burrowing prey (Goodrich and Buskirk 1998, Bylo et al. 2014, Grassel et al. 2015). Recently, Harris et al. (2014) provided evidence that abundance of plateau pika (*Ochotona curzoniae*) was the best predictor of occupancy of the Tibetan Fox (*Vulpes ferrilata*). Silva et al. (2013) also highlighted that the presence and diversity of prey was positively associated with occupancy of the European wildcat (*Felis silvestris silvestris*). When the interaction strength between a predator and prey is strong, either due to behavioral or evolutionary adaptations, a reasonable deduction is that the distribution or abundance of prey drives the distribution and abundance of the predator. Under these constraints, we might expect biotic processes to be the strongest predictor of occupancy and abundance, and that abiotic gradients are mediated through interactions affecting prey. This hypothesis is consistent with our badger occupancy results, and should be considered when evaluating the relative contribution of biotic and abiotic factors on predator distributions and abundances across landscapes.

In addition to the ground squirrel effects, we documented a positive effect of human disturbance (i.e., mostly agriculture) on badger occupancy. Human activities such as irrigated agriculture can provide additional and temporally consistent resources for some species (e.g., Faeth et al. 2005, Cook and Faeth 2006, Morelli et al. 2012, Oro et al. 2013), perhaps including alternative prey for badgers (insects, reptiles, or other small mammals; Messick and

Hornocker 1981). Thus, badgers might select areas such as the edges of irrigated fields that provide abundant alternative prey, particularly in drought years such as in our study. This hypothesis is consistent with our results, but additional work is needed to evaluate the mechanisms underlying the positive relationship between humans and badgers.

In contrast to the occupancy results, we identified some inconsistencies between predicted and observed patterns of ground squirrel abundance. We did not predict that soil texture would strongly influence ground squirrel abundance. However, soil texture was the only statistically positive relationship we observed, suggesting that abundance increases as soils become finer in texture (within the gradient we sampled). Retaining soil moisture and providing structurally sound burrows likely mediates the relationship between ground squirrel abundance and soil texture. Further, we did not expect shrub cover to exhibit nearly the strongest negative effect on ground squirrel abundance. We predicted that plot-level shrub cover would increase mortality associated with aerial predation through visual and locomotive obstruction (Schooley et al. 1996), however, we expected that bottom-up forces would more strongly influence the abundance of ground squirrels (e.g., Hubbs and Boonstra 1997). A strong negative effect of shrub cover may indicate that local areas dominated by shrubs are exposed to stronger predation pressure limiting ground squirrel abundance relative to areas without shrubs, or that shrub cover negatively affected nutrient availability to ground squirrels. Assessing the strength of top-down and bottom-up forcing on ground squirrels as a function of shrub cover would be insightful.

Despite these inconsistencies, expectations about the negative effects of human disturbance on ground squirrel abundance were supported by the data. Human disturbance (i.e., mostly irrigated agriculture) might be negative for ground squirrels because of human

subsidies increasing the biomass of other small mammals through numerical responses ultimately increasing interspecific competition (e.g., Oro et al. 2013). Alternatively, the increase in prey resources could be increasing predator activity or abundance and leading to a stronger top-down effect in areas near irrigated agriculture (e.g., predation-mediated apparent competition; Norbury 2001). This seems particularly plausible given the abundant assemblage of birds of prey within our study region and that perch sites are associated with human developments, both of which could facilitate an increase in kill rates (i.e., number of prey killed per predator) for avian predators. Faeth et al. (2005) highlighted instances where insect abundance was increased associated with human subsidies and that predation pressure from birds on insects was increased as well. If agricultural areas are acting as resource subsidies (particularly in drought years as in our study), biotic interactions such as predation or competition from other small mammals could contribute to the negative association between ground squirrel abundance and human disturbance; however, these mechanisms require testing.

The effect size of explanatory variables differed between ground squirrel occupancy and abundance results, emphasizing how the scale of biotic and abiotic processes influence occupancy and abundance. For example, the effect of dispersal potential on ground squirrel occupancy was much stronger than on abundance, which provides support for accessibility acting at broader extents in animals as well as plants (e.g., Boulangé et al. 2012, Miller and Holloway, in press). However, the effect of soil texture was important across extents providing support for multi-scale effects of abiotic factors. Finally, the effect of some biotic processes and human disturbance were strong for only ground squirrel abundance indicating that disturbance and biotic processes operate at relatively local extents. These contrasts

provide insight into the relative contribution of biotic and abiotic factors on ground squirrel populations, and contribute to the general understanding of multi-scale effects of biotic and abiotic processes (e.g., Guisan and Thuiller 2005, Soberón 2007, McGill 2010).

Effects of ecosystem stressors: the fire-cheatgrass cycle

Sagebrush ecosystems are threatened due to the fire-cheatgrass cycle, which characterizes the invasion of cheatgrass and associated changes in fire regimes. We predicted a negative effect of biological invasions and fire on ground squirrel occupancy and abundance, and expected ground squirrels to mediate the effects of the fire-cheatgrass cycle on badgers. We identified a strong negative effect of cheatgrass on ground squirrel abundance, but no effect on occupancy. Although ground squirrels consume cheatgrass, they prefer native bunchgrasses such as Sandberg bluegrass (Van Horne et al. 1998). Other studies have reported that areas dominated by cheatgrass support fewer ground squirrels (particularly drought years; Yensen et al. 1992), as well as other small mammals (Ostoja and Schupp 2009, Freeman et al. 2014). The reduced abundance of ground squirrels in cheatgrass areas is likely mediated through nutritional demands. Similarly, we detected a strong negative effect of fire frequency over the last ~30 years on abundance of ground squirrels. Fire frequency could directly affect ground squirrel populations through mortality, or indirectly through changes animal community composition (e.g., increased predator densities). It is more likely, however, that increases in fire frequency negatively influence ground squirrel abundance by converting native grasslands to cheatgrass-dominated grasslands (Davies et al. 2011). If this is true, then the role of fire may have reversed over time for ground squirrels. For example, we observed a strong negative effect of both shrubs and cheatgrass on ground squirrel abundance. Historically, fire presumably reduced shrub cover and promoted the cover of

native grasses ultimately benefiting ground squirrels. Currently, although fire continues to reduce shrub cover, it now promotes the expansion of exotic annual grasses such as cheatgrass (Davies et al. 2011), which negatively influences ground squirrels (Yensen et al. 1992; Figure 2.5 and 2.6). Continued increases in wildfire coupled with invasion by cheatgrass in sagebrush habitats (Abatzoglou and Kolden 2011) will likely have strong negative effects on the abundance of ground squirrels and other small mammals (Ostoja and Schupp 2009, Freeman et al. 2014), and the predators that rely on them.

As predicted, we did not detect any direct effects of the fire-cheatgrass cycle on the occupancy of badgers. We did discover a strong positive effect of ground squirrel occupancy, and to a lesser degree abundance, on badger occupancy. Therefore, consistent with our hypotheses, we found an indirect effect of the fire-cheatgrass cycle on badgers via the mediator of ground squirrel abundance. Although the effect size of ground squirrel occupancy was much stronger on badger occupancy compared to the abundance of ground squirrels, badgers and certainly other predators may still experience population-level consequences of the fire-cheatgrass cycle. By jointly assessing the effect of abiotic and biotic factors as well as ecosystem stressors on both predator and prey, we were able to develop a more complete understanding of how the fire-cheatgrass cycle directly and indirectly influences our system. Developing these links not only advances our understanding of how animal communities are being influenced by broad-scale changes (Agrawal et al. 2007), but also allows wildlife managers to develop more intricate and targeted management strategies.

Despite our detailed data on plant communities and animals at a broad spatial extent, temporal limitations remained. First, we collected data over two years, both of which were a product of below average annual precipitation (i.e., 96 and 114 mm for 2012 and 2013).

Sagebrush ecosystems can exhibit substantial inter-annual variability in precipitation, which directly and indirectly influences plant biomass and animal populations (e.g., Van Horne et al. 1997a, Bates et al. 2006). Sampling across a gradient of precipitation years and implementing an approach that extends our analyses by incorporating temporal dynamics would have improved our inferences. Second, we assessed occupancy of badgers during the spring to early summer. Additional work evaluating badger occupancy during the late summer and winter could provide insight into prey switching, or the use of anthropogenic subsidies associated with agriculture. Indeed, extending the temporal period of sampling would provide a more complete evaluation of our hypotheses, however, it would also have significant logistical costs as well.

Implications

The sagebrush-steppe ecosystem is changing due to biological invasions and shifts in fire regimes (Abatzoglou and Kolden 2011, Davies et al. 2011, Miller et al. 2011, Baltch et al. 2013). We assessed the influence of these stressors in the context of other ecological factors on the distribution and abundance of a predator and prey, both of which influence landscape heterogeneity. Cheatgrass invasion and increases in fire both had negative effects on abundance of ground squirrels. Land managers have been implementing strategies to reduce cheatgrass invasion in sagebrush landscapes, one of which is extensive reseeding treatments after fire. Our data suggest that successfully seeded areas have a strong positive effect on ground squirrel abundance (Figure 6) relative to untreated or unsuccessfully treated areas and unburned sites. This is promising because many raptors rely on ground squirrels as prey (Marti et al. 1993), and conserving the abundance and diversity of raptors is the overarching management objective on our study area. Additional research, however, would be useful to

assess the fitness consequences of ground squirrels in different areas exhibiting different fire and treatment histories because our results might not be directly linked with fitness (Van Horne et al. 1983). Moreover, our data indicate that the conservation of an apex predator, the badger, is largely associated with the conservation of ground squirrels. Indeed, it appears that implementing land management strategies to promote ground squirrels would likely have many secondary benefits to the animal community through the conservation of apex predators (e.g., Estes et al. 2011).

Our work also has implications that are broader than our study ecosystem. Extending an approach similar to Boulangeat et al. (2012) into a terrestrial animal system, we have partitioned the relative influence of abiotic and biotic factors and ecosystem stressors on distribution and abundance. Characteristics such as dispersal potential, bottom-up forcing, climate, disturbance, and soil were strongly influential for our prey species. However, the distribution of prey species was the major driver for our predator species. This work provides additional insight and hypotheses to consider when modeling the distribution or abundance of prey or predator species across landscapes. For example, predator populations that specialize on a particular species (or group of species) might be indirectly influenced by abiotic or biotic factors (climate or disturbance) via their prey (e.g., Silva et al. 2013, Harris et al. 2014, Hebblewhite et al. 2014). This hypothesis, however, extends to similar situations with interacting competitors (e.g., Fisher et al. 2012) or mutualists. Therefore, reframing hypotheses in terms of how abiotic and biotic factors influence the distribution or abundance of those species with strong interspecific interactions is likely warranted. Moreover, our work advances the general understanding of how abiotic and biotic gradients drive species distribution and abundance (e.g., Guisan and Thuiller 2005, Agrawal et al. 2007, Soberón

2007, McGill 2010, Boulangeat et al. 2012), which can be used to inform ecosystem conservation and management in the face of changing landscapes (e.g., Chen et al. 2011, Newbold et al. 2015).

References

- Abatzoglou, J. T., and C. A. Kolden. 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grass. *Rangeland Ecology and Management* 64:471-478.
- Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, K. A. Mooney, M. Power, D. Schemeske, J. Stachowicz, S. Strauss, M. G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5:145-12.
- Andrewartha, H. G., and L. C. Birch. 1954. *Distribution and abundance of animals*. University of Chicago Press, Illinois.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology* 19:173-183.
- Barton, K. 2015. MuMIn: Multi-model inference. R package version 1.13.4. <http://CRAN.R-project.org/package=MuMIn>.
- Bates, J. D., T. Svejcar, R. F. Miller, and R. A. Angell. 2006. The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* 64:670-697.
- Bean, W. T., R. Stafford, L. R. Prugh, H. S. Butterfield, and J. S. Brashares. 2012. An evaluation of monitoring methods for the endangered giant kangaroo rat. *Wildlife Society Bulletin* 36:587-593.
- Bestelmeyer, B. T., G. S. Okin, M. C. Duniway, S. R. Archer, N. F. Sayre, J. C. Williamson, and J. E. Herrick. 2015. Desertification, land use, and the transformation of global drylands. *Frontiers in Ecology and the Environment* 13:28-36.

- Booth, D. T., S. E. Cox, and R. D. Berryman. 2006. Point sampling digital imagery with "Samplepoint." *Environmental Monitoring and Assessment* 123:97-108.
- Boulangeat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15:584-593.
- Bradley, B. A., and J. F. Mustard. 2008. Comparison of phenology trend by land cover class: a case study in the Great Basin, USA. *Global Change Biology* 14:334-346.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- Bylo, L. N., N. Koper, and K. A. Molloy. 2014. Grazing intensity influences ground squirrel and American badger habitat use in mixed-grass prairies. *Rangeland Ecology and Management* 67:247-254.
- Chen, I. C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024-1026.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723.
- Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American southwest and central plains. *Science Advances* 1:e1400082.
- Cook, W. M., and S. H. Faeth. 2006. Irrigation and land use drive ground arthropod community patterns in an urban desert. *Environmental Entomology* 35:1532-1540.
- Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* 9:477-486.

- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573-2584.
- Dobson, F. S., and J. D. Kjelgaard. 1985. The influence of food resources on population dynamics in Columbian ground squirrels. *Canadian Journal of Zoology* 63:2095-2104.
- Eldridge, D. J. 2004. Mounds of the North American badger (*Taxidea taxus*): significant features of North American shrub-steppe ecosystems. *Journal of Mammalogy* 85:1060-1067.
- Eldridge, D. J. 2009. Badger (*Taxidea taxus*) mounds affect soil hydrological properties in a degraded shrub-steppe. *American Midland Naturalist* 161:350-358.
- Eldridge, D. J., and W. G. Whitford. 2009. Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem. *Journal of Arid Environments* 73:66-73.
- Ehrlén, J., and W. F. Morris. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters* 18:303-314.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soule, R. Virtanen, and R. A. Wardle. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. *BioScience* 55:399-407.

- Fisher, J. T., B. Anholt, S. Bradbury, M. Wheatley, and J. P. Volpe. 2012. Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes. *Ecography* 35:1-9.
- Freeman, E. D., T. R. Sharp, R. T. Larson, R. N. Knight, S. J. Slater, and B. R. McMillan. 2014. Negative effects of an exotic grass invasion on small-mammal communities. *PLoS ONE* 9:e108843.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27:2865-2873.
- Gelman, A., A. Jakulin, M. G. Pittau, and Y. S. Su. 2008. A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics* 2:1360-1383.
- Gelman, A., and Y. S. Su. 2014. arm: data analysis using regression and multilevel/hierarchical models. R package version 1.7-07. <http://CRAN.R-project.org/package=arm>.
- Goodrich, J. M., and S. W. Buskirk. 1998. Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex. *Journal of Mammalogy* 79:171-179.
- Grassel, S. M., J. L. Rachlow, and C. J. Williams. 2015. Spatial interactions between sympatric carnivores: asymmetric avoidance of an intraguild predator. *Ecology and Evolution* 5:2762-2773.
- Gruber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24:699-711.

- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993-1009.
- Harris, R. B., Z. Jiake, J. Yinqiu, Z. Kai, Y. Chunyan, and D. W. Yu. 2014. Evidence that the Tibetan fox is an obligate predator of the plateau pika: conservation implications. *Journal of Mammalogy* 95:1207-1221.
- Hebblewhite, M., D. G. Miquelle, H. Robinson, D. G. Pikunov, Y. M. Dunishenko, V. V. Aramilev, I. G. Nikolaev, G. P. Salkina, I. V. Seryodkin, V. V. Gaponov, M. N. Litvinov, A. V. Kostyria, P. V. Fomenko, and A. A. Murzin. 2014. Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. *Biological Conservation* 178:50-64.
- Hirzel, A. H., and G. Le Lay. 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45:1372-1381.
- Holbrook, J. D., R. S. Arkle, J. L. Rachlow, K. T. Vierling, and D. S. Pilliod. Sampling animal sign in heterogeneous environments: how much is enough? *Journal of Arid Environments* 199:51-55.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. John Wiley and Sons, New York.
- Hubbs, A. H., and R. Boonstra. 1997. Population limitation in Arctic ground squirrels: effects of food and predation. *Journal of Animal Ecology* 66:527-541.
- Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157-170.

- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jones, C., J. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946-1957.
- Jones, C., J. Gutierrez, J. Byers, J. Crooks, J. Lambrinos, and T. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. *Oikos* 12:1862-1869.
- King, R., and J. Belthoff. 2001. Post-fledging dispersal of burrowing owls in southwestern Idaho: characterization of movements and use of satellite burrows. *Condor* 103:118-126.
- Kinlaw, A. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments* 41:127-145.
- Kinlaw, A., and M. Grasmueck. 2012. Evidence for and geomorphologic consequences of a reptilian ecosystem engineer: the burrowing cascade initiated by the gopher tortoise. *Geomorphology* 157-158:108-121.
- Knick, S. T., J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. V. Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *The Condor* 105:611-634.
- Knick, S., S. Hanser, R. Miller, D. Pyke, M. Wisdom, S. Finn, E. Rinkes, and C. Henny. 2011. Ecological influence and pathways of land use in the sagebrush. Pages 203-251 in S. Knick and J. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California Press, Berkeley, California.

- Kochert, M., and M. Pellant. 1986. Multiple use in the Snake River Birds of Prey Area. *Rangelands* 8:217-220.
- Krebs, C. J. 1972. *Ecology: the experimental analysis of distribution and abundance*. Harper and Row, New York.
- Lara-Romero, C., E. Virgos, and E. Revilla. 2012. Sett density as an estimator of population density in the European badger *Meles meles*. *Mammal Review* 42:78-84.
- Laundré, J. 1989. Horizontal and vertical diameter of burrows of five small mammal species in southeastern Idaho. *Great Basin Naturalist* 49:646-649.
- Laundré, J. 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. *Oecologia* 94:43-48.
- Lay, C. 2008. The status of the American badger in the San Francisco Bay area. M.S. thesis. San Jose State University, California.
- Lele, S. R., J. L. Keim, and P. Solymos. 2014. ResourceSelection: resource selection (probability) functions for use-availability data. R package version 0.2-4. <http://CRAN.R-project.org/package=ResourceSelection>.
- Lohr, K., E. Yensen, J. C. Munger, and S. J. Novak. 2013. Relationship between habitat characteristics and densities of southern Idaho ground squirrels. *Journal of Wildlife Management* 77:983-993.
- Marti, C., K. Steenhof, M. Kochert, and J. Marks. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. *Oikos* 67:6-18.
- McGill, B. J. 2010. Matters of scale. *Science* 328:575-576.
- Messick, J., and M. Hornocker. 1981. Ecology of the badger in southwestern Idaho. *Wildlife Monographs* 76:3-53.

- Miller, J. A., and P. Holloway. In press. Incorporating movement in species distribution models. *Progress in Physical Geography*.
- Miller, R., S. Knick, D. Pyke, C. Meinke, S. Hanser, M. Wisdom, and A. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 in S.T. Knick and J.W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. *Studies in Avian Biology*, University of California Press, Berkley, California.
- Morelli, T. L., A. B. Smith, C. R. Kastely, I. Mastroserio, C. Moritz, and S. R. Beissinger. 2012. Anthropogenic refugia ameliorate the severe climate-related decline of a montane mammal along its trailing edge. *Proceedings of the Royal Society B* 279:4279-4286.
- Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Diaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. K. Harrison, T. Alhousseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. P. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. P. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. Mace, J. P. W. Scharlemann, and A. Purvis. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520:45-50.
- Norbury, G. 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direction competition with introduced rabbits. *Journal of Applied Ecology* 38:1350-1361.
- Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. *Endangered ecosystems of the United States:*

- a preliminary assessment of loss and degradation. USDI National Biological Service Biological Report 28.
- Olendorff, R., and M. Kochert. 1977. Land management for the conservation of birds of prey. Proceedings of the World Conference on Birds of Prey.
- Olsen, G. S., and B. Van Horne. 1998. Dispersal patterns of juvenile Townsend's ground squirrels in southwestern Idaho. *Canadian Journal of Zoology* 76:2084-2089.
- Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martinez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters* 16:1501-1514.
- Ostojia, S. M., and E. W. Schupp. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. *Diversity and Distributions* 5:863-870.
- Pilliod D. S., and R. S. Arkle. 2013. Performance of quantitative vegetation sampling methods across gradients of cover in Great Basin plant communities. *Rangeland Ecology and Management* 66:634-647.
- Pilliod, D. S., and J. L. Welty. 2013. Land Treatment Digital Library. U.S. Geological Survey Data Series 806, <http://dx.doi.org/10.3133/ds806>.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3:349-361.
- R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ramesh, D., C. Home, Y. V Jhala, and Q. Qureshi. 2013. Calibration of a burrow count index for the Indian desert jird, *Meriones hurrianae*. *Population Ecology* 55:241-245.

- Rickart, E. A. 1987. *Spermophilus townsendii*. *Mammalian Species* 268:1-6.
- Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. C. Sanchez, and M. Müller. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* 12:77.
- Schooley, R. L., P. B. Sharpe, and B. Van Horne. 1996. Can shrub cover increase predation risk for a desert rodent? *Canadian Journal of Zoology* 74:157-163.
- Silva, A. P., K. Kilshaw, P. J. Johnson, D. W. Macdonald, and L. M. Rosalino. 2013. Wildcat occurrence in Scotland: food really matters. *Diversity and Distributions* 19:232-243.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.
- Thuiller, W., M. B. Araújo, and S. Lavorel. 2004. Do I need land-cover data to model species distributions in Europe? *Journal of Biogeography* 31:353-361.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- Van Horne, B., G. Olson, R. Schooley, J. Corn, and K. Burnham. 1997a. Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. *Ecological Monographs* 67:295-315.
- Van Horne, B., R. L. Schooley, S. T. Knick, G. S. Olson, and K. P. Burnham. 1997b. Use of burrow entrances to indicate densities of Townsend's ground squirrels. *Journal of Wildlife Management* 61:92-101.
- Van Horne, B., R. L. Schooley, and P. B. Sharpe. 1998. Influence of habitat, sex, age, and drought on the diet of Townsend's ground squirrels. *Journal of Mammalogy* 79:521-537.

- Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth Edition. Springer, New York.
- Weddell, B. J. 1991. Distribution and movements of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands? *Journal of Biogeography* 18:385-394.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, J. J. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* 366:2336-2350.
- Wisz, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, M. C. Forchhammer, J. A. Grytnes, A. Guisan, R. K. Heikkinen, T. T. Høye, I. Kühn, M. Luoto, L. Maiorano, M. C. Nilsson, S. Normand, E. Öckinger, N. M. Schmidt, M. Termansen, A. Timmermann, D. A. Wardle, P. Aastrup, and J. C. Svenning. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88:15-30.
- Yensen, E., D. Quinney, K. Johnson, K. Timmerman, and K. Steenhof. 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. *American Midland Naturalist* 128:299-312.

Table 2.1. Hypotheses and model selection results for models assessing occupancy (ψ) of Piute ground squirrels (*Urocitellus mollis*). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. BIC and AUC represent the Bayesian information criterion and the area under the curve of the receiver operating characteristic, respectively. The number of estimated parameters and model weights for each model are indicated by k and w_i . See Appendix B: Table B1 for specific variable descriptions.

Hypothesis	Model	k	BIC	Δ BIC	w_i	AUC
Soil + Climate + Dispersal	$\psi(\text{Soil} + \text{Precipitation} + \text{DI})$	4	81.2	0	0.80	0.96
Soil + Climate + Dispersal + Fire	$\psi(\text{Soil} + \text{Precipitation} + \text{DI} + \text{FireFreq})$	5	84.0	2.88	0.19	0.96
Soil + Climate + Dispersal + Fire + Forage	$\psi(\text{Soil} + \text{Precipitation} + \text{DI} + \text{FireFreq} + \text{POSE} + \text{EPG})$	7	90.9	9.76	0.01	0.96
Soils + Climate	$\psi(\text{Soil} + \text{Precipitation})$	3	91.8	10.66	0.00	0.92
Climate	$\psi(\text{Precipitation})$	2	97.4	16.29	0.00	0.90
Soil + Climate + Dispersal + Fire + Forage + Aerial predator + Badger	$\psi(\text{Soil} + \text{Precipitation} + \text{DI} + \text{FireFreq} + \text{POSE} + \text{EPG} + \text{Shrub} + \text{Badger})$	9	99.3	18.14	0.00	0.97
Dispersal	$\psi(\text{DI})$	3	116.2	35.01	0.00	0.98
Landscape + Dispersal	$\psi(\text{Shrubland} + \text{Human} + \text{DI})$	4	121.5	40.34	0.00	0.90
Soils	$\psi(\text{SoilPS})$	2	142.2	61.04	0.00	0.37
Aerial predator + Badger	$\psi(\text{Shrub} + \text{Badger})$	3	145.1	63.95	0.00	0.78
Perennial grass	$\psi(\text{POSE} + \text{EPG})$	3	146.3	65.13	0.00	0.73
Badger	$\psi(\text{Badger})$	2	147.1	65.99	0.00	0.71
Fire	$\psi(\text{FireFreq})$	2	148.8	67.62	0.00	0.65
Perennial grass + Richness	$\psi(\text{POSE} + \text{EPG} + \text{Richness})$	4	150.0	68.85	0.00	0.73
Landscape	$\psi(\text{Shrubland} + \text{Human})$	3	151.8	70.62	0.00	0.65
Aerial predator	$\psi(\text{Shrub})$	2	153.6	72.42	0.00	0.67
Perennial grass + Richness + BRTE	$\psi(\text{POSE} + \text{EPG} + \text{Richness} + \text{BRTE})$	5	154.0	72.84	0.00	0.73

Table 2.2. Hypotheses and model selection results for models assessing occupancy (ψ) of American badgers (*Taxidea taxus*). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. AIC_c and AUC represent the Akaike's information criterion (adjusted for small sample size) and the area under the curve of the receiver operating characteristic, respectively. The number of estimated parameters and model weights for each model are indicated by k and w_i . See Appendix B: Table B2 for specific variable descriptions.

Hypothesis	Model	k	AIC _c	Δ AIC _c	w_i	AUC
Ground squirrel occupancy + Human disturbance	$\psi(\text{GSOcc} + \text{Human})$	3	202.2	0	0.53 ^a	0.68
Ground squirrel occupancy + Human disturbance + Fire	$\psi(\text{GSOcc} + \text{Human} + \text{FireFreq})$	4	204.2	1.95	0.20 ^a	0.64
Ground squirrel occupancy	$\psi(\text{GSOcc})$	2	205.6	3.35	0.10 ^a	0.65
Ground squirrel occupancy + Human disturbance + Fire + Soil	$\psi(\text{GSOcc} + \text{Human} + \text{FireFreq} + \text{Soil})$	5	206.0	3.79	0.08 ^a	0.65
Ground squirrel occupancy + Human disturbance + Fire + Climate	$\psi(\text{GSOcc} + \text{Human} + \text{FireFreq} + \text{Precipitation})$	5	206.3	4.05	0.07	0.66
Ground squirrel occupancy + Human disturbance + Fire + Climate + Soil	$\psi(\text{GSOcc} + \text{Human} + \text{FireFreq} + \text{Precipitation} + \text{Soil})$	6	208.1	5.87	0.03	0.66
Ground squirrel RN	$\psi(\text{GSN})$	2	216.3	14.09	0	0.70
Soil	$\psi(\text{Soil})$	2	223.1	20.86	0	0.56
Climate	$\psi(\text{Precipitation})$	2	224.7	22.42	0	0.61
Fire	$\psi(\text{FireFreq})$	2	227.3	25.10	0	0.54
Human disturbance	$\psi(\text{Human})$	2	229.5	27.25	0	0.49
Shrubland	$\psi(\text{Shrubland})$	2	229.7	27.48	0	0.52
Landscape	$\psi(\text{Shrubland} + \text{Human})$	3	231.5	29.25	0	0.48

^a 95% confidence set of models

Table 2.3. Hypotheses and model selection results for models assessing relative abundance (*RA*) of Piute ground squirrels (*Urocitellus mollis*). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. AIC_c represents Akaike’s information criterion (adjusted for small sample size). The number of estimated parameters and model weights for each model are indicated by k and w_i , respectively. Spearman’s rank correlation coefficients (ρ) between predicted and observed values are also displayed. See Appendix B: Table B3 for specific variable descriptions.

Hypothesis	Model	k	AIC_c	ΔAIC_c	w_i	ρ
BRTE + Landscape + Dispersal + Disturbance + Aerial predator + Soil	$RA(\text{Season} + \text{BRTE} + \text{Shrubland} + \text{Human} + \text{DI} + \text{FireFreq} + \text{Grazing} + \text{Shrub} + \text{Soil})$	11	762.6	0	0.51 ^a	0.69
BRTE + Landscape + Dispersal + Disturbance + Aerial predator	$RA(\text{Season} + \text{BRTE} + \text{Shrubland} + \text{Human} + \text{DI} + \text{FireFreq} + \text{Grazing} + \text{Shrub})$	10	763.9	1.35	0.26 ^a	0.69
BRTE + Landscape + Dispersal + Disturbance + Aerial predator + Climate + Soil	$RA(\text{Season} + \text{BRTE} + \text{Shrubland} + \text{Human} + \text{DI} + \text{FireFreq} + \text{Grazing} + \text{Shrub} + \text{Precipitation} + \text{Soil})$	12	764.8	2.29	0.16 ^a	0.69
BRTE + Landscape + Dispersal + Disturbance + Aerial predator + Climate	$RA(\text{Season} + \text{BRTE} + \text{Shrubland} + \text{Human} + \text{DI} + \text{FireFreq} + \text{Grazing} + \text{Shrub} + \text{Precipitation})$	11	766.4	3.89	0.07	0.69
BRTE + Landscape + Dispersal + Fire + Grazing	$RA(\text{Season} + \text{BRTE} + \text{Shrubland} + \text{Human} + \text{DI} + \text{BurnFreq} + \text{Grazing})$	9	780.7	18.10	0.00	0.52
Fire + Grazing	$RA(\text{Season} + \text{FireFreq} + \text{Grazing})$	5	793.4	30.87	0.00	0.31
BRTE + Landscape + Dispersal	$RA(\text{Season} + \text{BRTE} + \text{Shrubland} + \text{Human} + \text{DI})$	7	832.7	70.11	0.00	0.46
Soil	$RA(\text{Season} + \text{Soil})$	4	835.8	73.21	0.00	0.33
Landscape + Dispersal	$RA(\text{Season} + \text{Shrubland} + \text{Human} + \text{DI})$	6	838.3	75.77	0.00	0.41
BRTE	$RA(\text{Season} + \text{BRTE})$	4	840.1	77.57	0.00	0.31
Landscape	$RA(\text{Season} + \text{Shrubland} + \text{Human})$	5	840.5	77.91	0.00	
Dispersal	$RA(\text{Season} + \text{DI})$	4	840.7	78.19	0.00	0.40
Perennial grass + BRTE	$RA(\text{Season} + \text{POSE} + \text{EPG} + \text{BRTE})$	6	841.1	78.52	0.00	0.37
Aerial predator	$RA(\text{Season} + \text{Shrub})$	4	841.3	78.78	0.00	0.16
Aerial predator + Badger	$RA(\text{Season} + \text{Shrub} + \text{Badger})$	5	841.5	78.94	0.00	0.29
Badger	$RA(\text{Season} + \text{Badger})$	4	843.9	81.32	0.00	0.27
EPG	$RA(\text{Season} + \text{EPG})$	4	844.8	82.27	0.00	0.26
Richness	$RA(\text{Season} + \text{Richness})$	4	845.3	82.73	0.00	0.27

Grass	<i>RA</i> (Season + POSE + EPG + NPG + EAG + BRTE)	8	845.5	82.90	0.00	0.40
POSE	<i>RA</i> (Season + POSE)	4	845.6	83.04	0.00	0.27
Fire	<i>RA</i> (Season + FireFreq)	4	846.6	84.03	0.00	0.21
Climate	<i>RA</i> (Season + Precipitation)	4	846.8	84.21	0.00	0.15
Perennial grass	<i>RA</i> (Season + POSE + EPG + NPG)	6	846.8	84.28	0.00	0.33
Grass + Forb	<i>RA</i> (Season + POSE + EPG + NPG + EAG + BRTE + NF + EF)	10	847.5	84.97	0.00	0.40
Perennial grass + Forb	<i>RA</i> (Season + POSE + EPG + NPG + NF + EF)	8	849.9	87.35	0.00	0.35

^a 95% confidence set of models

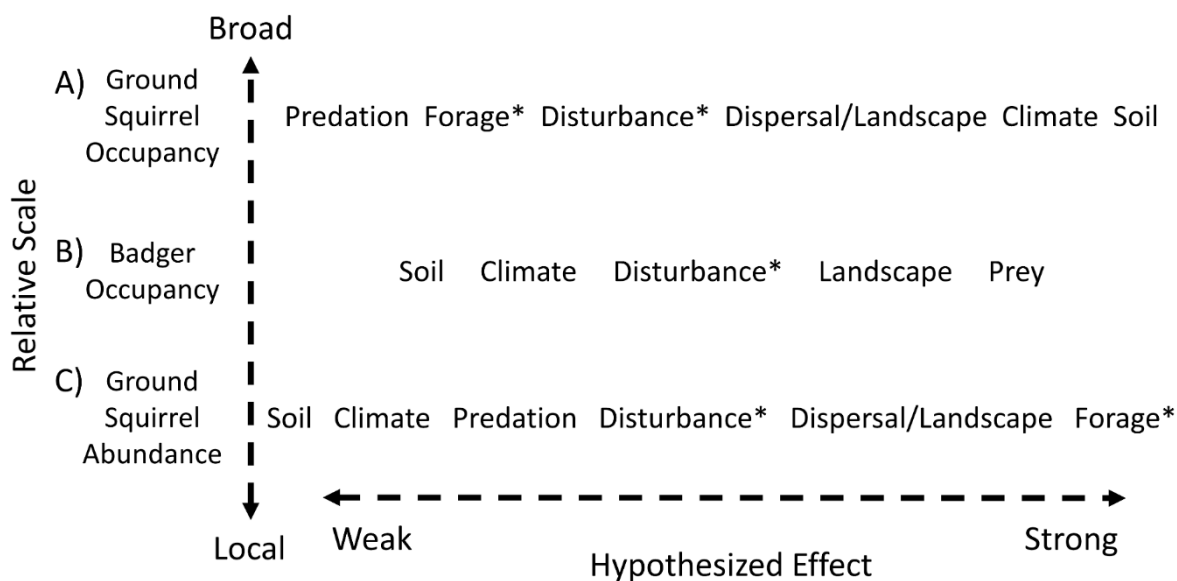


Figure 2.1. Hypothesized strength of effect across biotic and abiotic themes for occupancy of Piute ground squirrels (*Urocitellus mollis*) and American badgers (*Taxidea taxus*) and abundance of ground squirrels. Abiotic themes include soil, climate, and disturbance (i.e., fire), while biotic themes include landscape, dispersal, disturbance (i.e., grazing), predation, prey, and forage. Asterisks indicate an ecosystem stressor (i.e., biological invasions and fire) is embedded within the theme. See Appendix B: Tables B1-B3 for specific variables within biotic and abiotic themes.

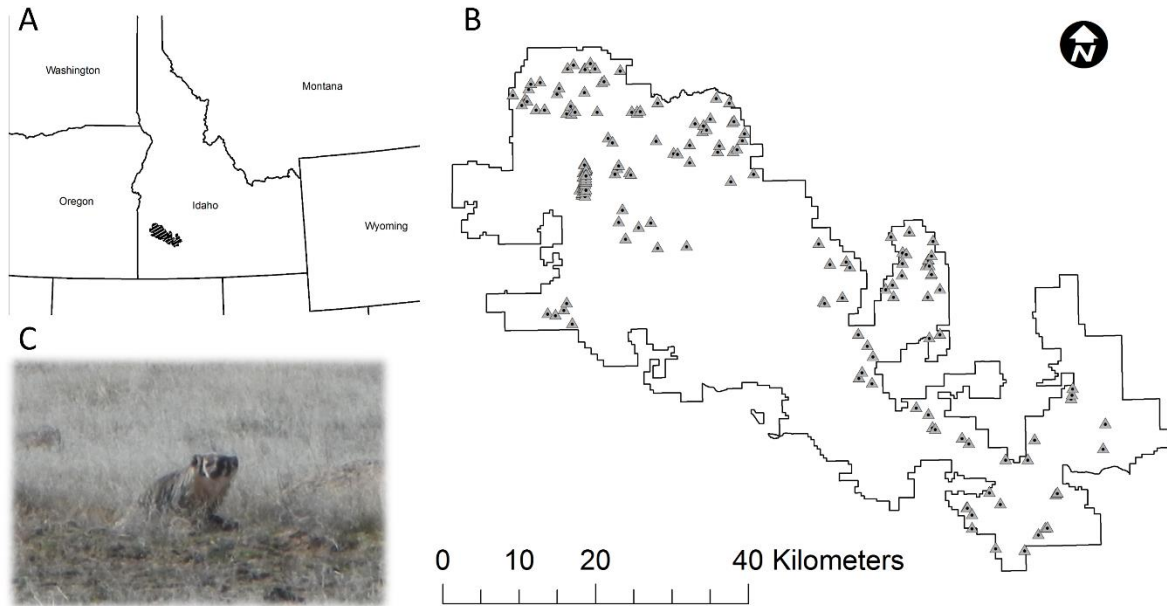


Figure 2.2. A) Location of Morley Nelson Snake River Birds of Prey National Conservation Area (i.e., study area) in southwestern Idaho, USA. B) Distribution of 1-ha plots ($n = 163$) that were sampled for Piute ground squirrels (*Uroditellus mollis*) and American badgers (*Taxidea taxus*). C) Photograph of a badger on one of our 1-ha plots (taken by J. Holbrook).

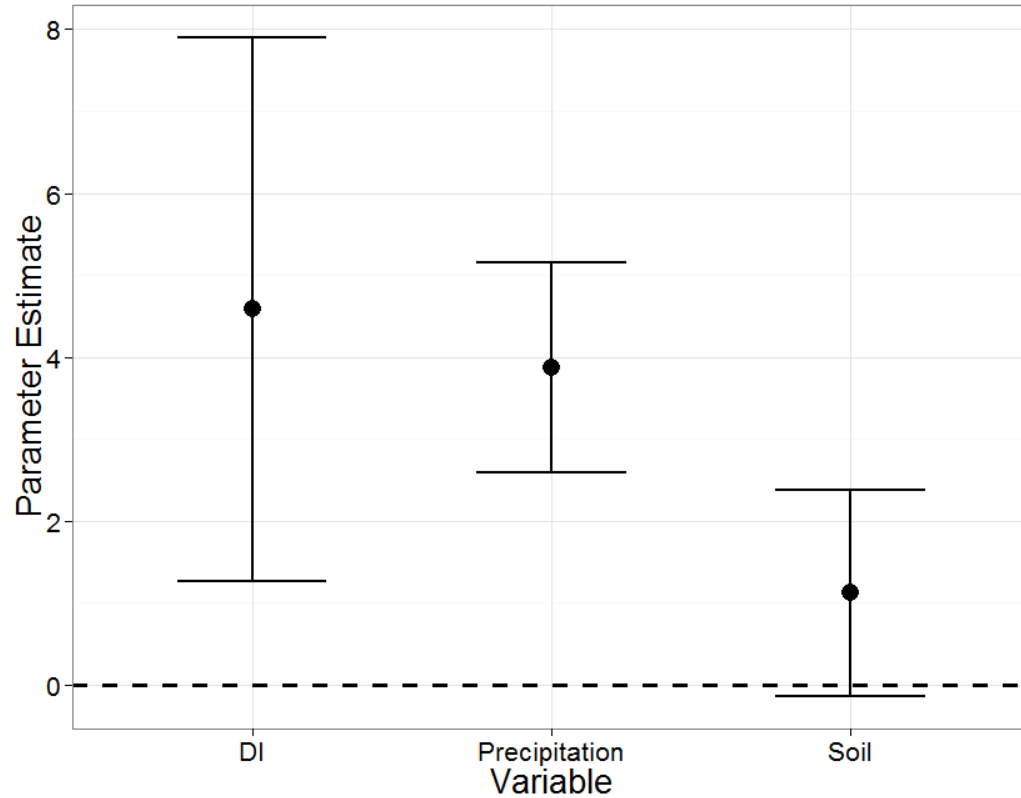


Figure 2.3. Standardized parameter estimates ($\pm 90\%$ credible intervals) describing the effect of explanatory variables (x-axis) on occupancy of Piute ground squirrels (*Urocitellus mollis*). Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. Variable descriptions are as follows: precipitation - mean annual precipitation from 1979-2008, DI – dispersal index (i.e., ratio of the numbers of burrows at the nearest sampled 1-ha plot/distance to the plot), and soil texture - % surface soil passing through a #4 sieve.

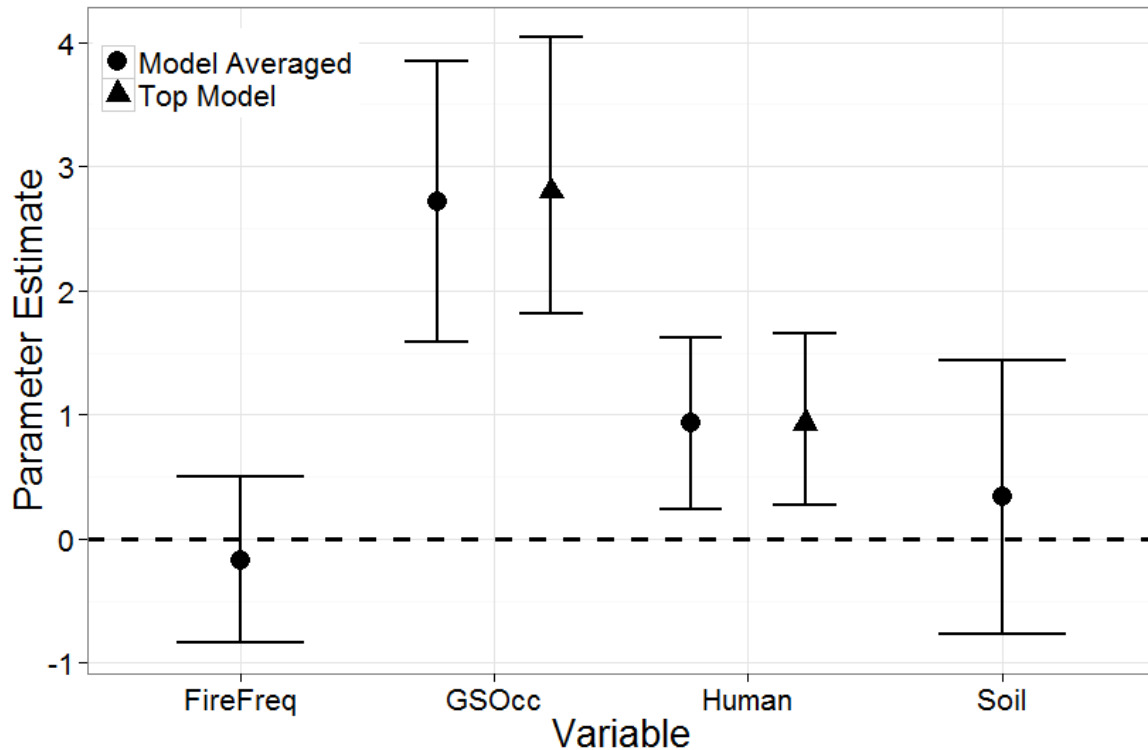


Figure 2.4. Standardized parameter estimates ($\pm 90\%$ confidence intervals) describing the effect of explanatory variables (x-axis) on occupancy of American badgers (*Taxidea taxus*). If a variable does not have a parameter estimate labeled top model it was not included. Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. Variable descriptions are as follows: firefreq - number of times area burned from 1957-2013, GSOcc – occupancy of Piute ground squirrels (*Urocitellus mollis*) at plot-level, human - % human disturbance within a 2.4 km² area, and soil texture - % surface soil passing through a #4 sieve.

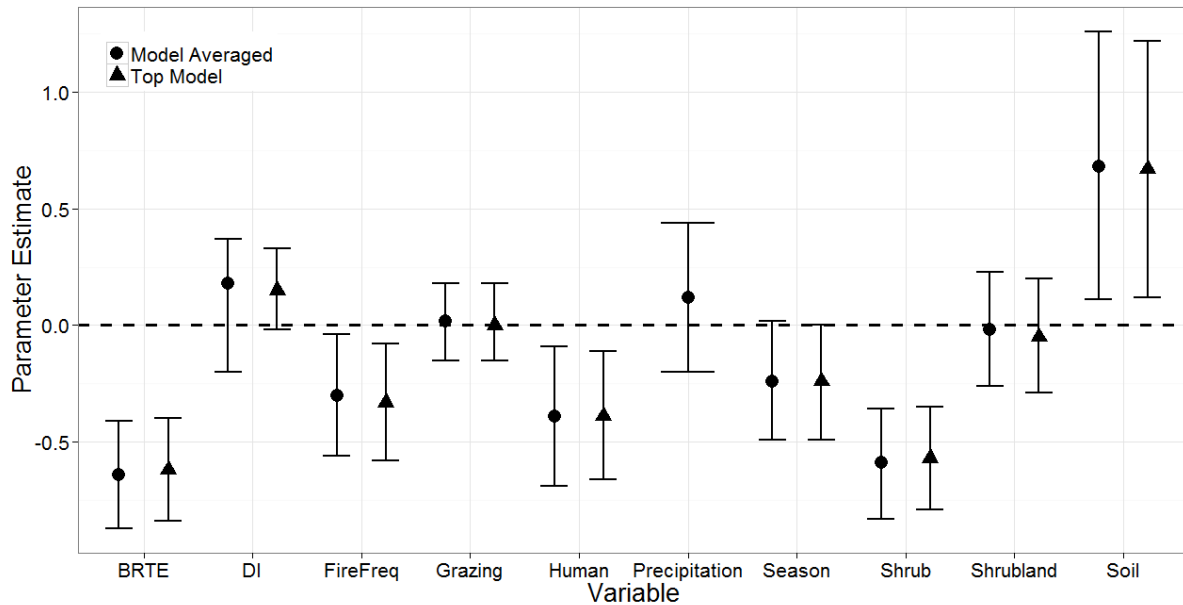


Figure 2.5. Standardized parameter estimates ($\pm 90\%$ confidence intervals) describing the effect of explanatory variables (x-axis) on relative abundance of Piute ground squirrels (*Urocitellus mollis*). If a variable does not have a parameter estimate labeled top model it was not included. Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA. Variable descriptions are as follows: BRTE – plot-level % cover of cheatgrass (*Bromus tectorum*), precipitation - mean annual precipitation from 1979-2008, DI – dispersal index (i.e., ratio of the numbers of burrows at the nearest sampled 1-ha plot/distance to the plot), firefreq - number of times area burned from 1957-2013, human - % human disturbance within a 0.79 km² area, season - binary variable to account for within season decline in active burrows (Van Horne et al. 1997b), shrub – plot-level % cover of shrub functional group, shrubland - % shrubland within a 0.79 km² area, and soil texture - % surface soil passing through a #4 sieve.

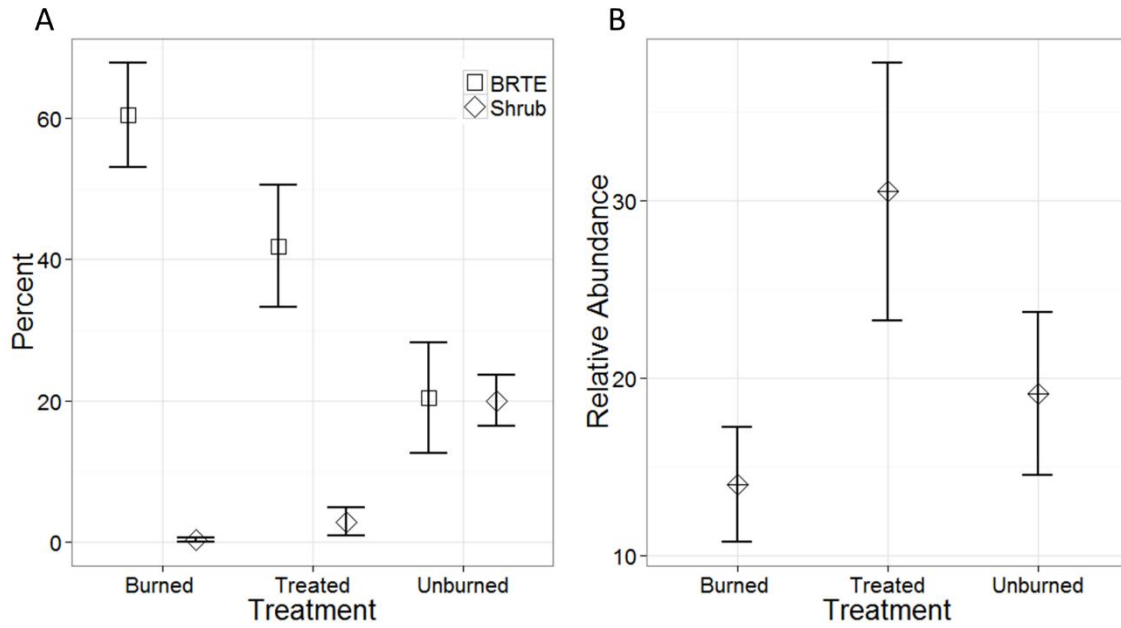


Figure 2.6. A) Cheatgrass (BRTE) and shrub cover ($\pm 90\%$ CI) as a function of treatment history (x-axis) at the plot-level ($n = 52, 38,$ and 36 for identified burned, treated, and unburned plots, respectively). B) Relative abundance of Piute ground squirrels (*Urocitellus mollis*; counts of recently active burrows, $\pm 90\%$ CI) as a function of treatment history. Data were collected on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA.

***Chapter 3: Transition of vegetation states positively affects an aridland
granivore in the Great Basin***

To be submitted to Biological Conservation

Co-authors: David S. Pilliod, Robert S. Arkle, Janet L. Rachlow, Kerri T. Vierling, and
Michelle M. Wiest

Abstract

Biological invasions by non-native plants can alter ecosystems to such an extent that new stable ecological states are reached, but less is known about how these state transitions influence animal populations. Sagebrush (*Artemisia tridentata*) ecosystems in North America, for example, have been altered by non-native annual grasses in combination with frequent fire, and in some locations have experienced complete type conversions from shrublands to annual grasslands. Our goals were to 1) assess state changes in vegetation across a gradient of time since fire, 2) evaluate the effects of state changes on an aridland granivore, the Owyhee and western harvester ants (*Pogonomyrmex salinus* and *P. occidentalis*, respectively), and 3) determine the relative importance of fire and biological invasions on harvester ant occupancy and density. We sampled 358 1-ha plots across southern Idaho and Oregon that captured a range of 1-31 years post-fire. Our results indicated an immediate and consistent change in vegetation states post-fire from shrubland to grassland, and harvester ant density qualitatively decreased with time since fire. Relationships between current vegetation states and occupancy and density of harvester ants indicated a negative effect of shrub cover and a positive effect of exotic annual grasses. Finally, we discovered that the relative importance of fire and invasion by exotic annual grasses was weak for harvester ant occupancy, but strong for density. Occupancy was positively driven by

distribution of finer-grained soils and drier locals. Density of harvester ants was positively affected by exotic annual and native perennial grasses as well as time since fire. These results suggest that fire, and the resulting native and exotic grasslands that replace sagebrush shrublands, have positive effects on harvester ant density. Although wildfire and invasion by exotic annuals may negatively affect other species in sagebrush ecosystems, our results indicate that harvester ants might benefit from the continued increase in fire frequency and biological invasion. They may indeed be one of the few winners among a sea of losers linked to vegetation state changes within sagebrush ecosystems.

Introduction

Biological invasions of non-native plants alter ecosystem processes, and thus impact native fauna in many direct and indirect ways (D'Antonio and Vitousek 1992, Litt and Pearson 2013). In some cases, non-native plants have altered ecosystems to such an extent that new, relatively stable ecological states are reached resulting in novel plant communities (Bestelmeyer et al. 2011). Ecological state transitions caused by non-native plants can change demographic rates of animals, such as survival or production, resulting in changes in occupancy and density (e.g., Ostoja et al. 2009, Ostoja and Schupp 2009, Litt and Steidl 2011). By altering population parameters of animals, biological invasions of non-native plants can cause cascading effects that change the ecosystem influence or ecological role of animals within their respective ecosystem. These cascading effects may further influence the resilience of an ecosystem to recover or resist future invasion of non-native species (e.g., Toro et al. 2015). To gain a deeper understanding of the effects of biological invasions of non-native plants on animal populations, as well as develop effective conservation strategies that

preserve the ecosystem function supported by animals, it is essential to assess how biological invasions affect animals.

Sagebrush (*Artemisia tridentata*) ecosystems in lower elevations (i.e., *A. t. wyomingensis*) throughout western North America are experiencing changes in vegetation states because of a synergy between changing fire regimes and biological invasions by exotic annual grasses such as cheatgrass (*Bromus tectorum*; Baker 2011, Davies et al. 2011, Miller et al. 2011, Chambers et al. 2014). Historically, sagebrush vegetation states were generally composed of shrublands with native perennial grasses as the dominant functional group within the understory (Miller et al. 2011). However, invasion by exotic annual grasses (due to human activity, land conversion, and grazing; Knick et al. 2011) has substantially changed fire regimes and resulted in lower fire return intervals, larger area burned per fire, and increased probability of fire (Baker 2011, Miller et al. 2011, Balch et al. 2013), all of which enhance exotic annual grass invasion (Chambers et al. 2007). Remotely sensed data indicated that the extent of cheatgrass dominance exceeded 40,000 km² of the Great Basin Desert (nearly 10%) in 2008 (Bradley and Mustard 2008), and it has likely increased since then. Indeed, the cycle of biological invasions by exotic annual grasses and subsequent changes in fire regimes are synergistically contributing to current vegetation state changes in sagebrush ecosystems; that is, transitioning from sagebrush shrublands with native perennial grasses to grasslands dominated by exotic annual grasses (Davies et al. 2011, Miller et al. 2011, Chambers et al. 2014). To understand the consequences of such changes, as well as the subsequent impact on ecosystem function, it is essential to evaluate how changes in vegetation states influence functionally important animals in sagebrush landscapes.

Considering the extent and magnitude of vegetation state changes within sagebrush ecosystems, there are surprisingly few studies assessing the effects of these state transitions on the animal community. Previous work has demonstrated negative effects of cheatgrass invasion on communities of passerines (Knick et al. 1995, 2000), small mammals (Ostoja and Schupp 2009, Rieder et al. 2010, Freeman et al. 2014), lizards (Newbold 2005, Rieder et al. 2010), and snakes (Hall et al. 2009). Contrastingly, Ostoja et al. (2009) documented an increase in density of ant assemblages in areas dominated by cheatgrass. Although this information enhances our understanding of how state changes influence animals, most of the previous studies 1) were limited in spatial extent (e.g., ≤ 5 -20 km), 2) were unable to assess how plant and animal parameters change as a function of recovery time (e.g., time since fire), and 3) could not adequately assess the relative importance of state changes in the context of other environmental gradients. Therefore, our aim was to assess the relative importance of vegetation state changes on occupancy and density of an aridland granivore across a spatial gradient capturing a range of time since fire.

We selected the Owyhee and western harvester ants (*Pogonomyrmex salinus* and *P. occidentalis*, hereafter harvester ant) as target species because they are granivorous and also serve as ecosystem engineers (e.g., Jones et al 1994, 1997, 2010) in many desert environments (MacMahon et al. 2000). In many arid ecosystems seed predation and movement are arguably the most critical plant-animal interactions shaping plant communities (e.g., Brown et al. 1979, Crist and MacMahon 1992, Heske et al. 1993). Further, harvester ant activities directly and indirectly influence plant communities by removing vegetation (Carlson and Whitford 1991, Gosselin et al., in revision), and increasing soil nutrients and water absorption

(Mandel and Sorenson 1982, Blom 1990, Wagner et al. 1997, Wilby et al. 2001, Brown et al. 2012).

Our specific research objectives were to 1) assess state changes in plants as well as occupancy and density of harvester ants across a range of recovery times (i.e., time since fire), 2) determine how the plant community influenced harvester ant parameters, and 3) evaluate the relative importance of fire and biological invasions, in the context of other environmental gradients, on both occupancy and density of harvester ants. We predicted that state changes from shrublands to exotic annual grasslands would happen immediately after fire and remain for all years post-fire (e.g., Baker 2011), and that these changes would have positive effects on occupancy and density of harvester ants (Ostoja et al. 2009). Similarly, we expected the vegetation state of exotic annual grasslands to have higher ant occupancy and density (e.g., Ostoja et al. 2009). Finally, we predicted that the relative importance of fire and exotic annual grasses would be greater for harvester ant density compared to occupancy, and that the effects of both processes would be positive.

Methods

Study area and sampling

We conducted this study within publicly managed sagebrush ecosystems throughout southern Idaho and Oregon, USA (Figure 3.1). To capture a gradient of vegetation states we combined existing data sets from three separate studies of post-wildfire and seeding treatments (two studies took place in 2008-2009, and the third was conducted in 2013-2014). In each study, plant community and ant density data were collected using identical methods at sites (i.e., post-wildfire area) that were selected randomly within each study area (i.e., southeastern Oregon and southwestern Idaho). Within each site, we used GIS databases to

place plots randomly within: 1) areas that were previously burned and seeded (via aerial or rangeland drill methods by the U.S. Bureau of Land Management) with native and exotic perennial plants (i.e., treated), 2) areas that were burned and not seeded (i.e., burned), and 3) areas that have not burned for at least the last ~30 years (i.e., unburned). Sites ranged in mean annual precipitation from 20-64 cm and fire years ranged from 1957-2012. The dominant plant communities we sampled include big sagebrush, winterfat (*Krascheninnikovia lanata*), shadscale saltbrush (*Atriplex confertifolia*), Sandberg bluegrass (*Poa secunda*), and cheatgrass.

Harvester ant data

At each 1-ha plot, we surveyed for harvester ant colonies during April – August in 2008-2009 or 2013-2014. Our sampling season was coincident with harvester ant activity, allowing us to identify active colonies. To characterize harvester ant occupancy and density during 2008-2009, we enumerated active colonies within three 100 m × 2 m (600 m²) belt-transects spaced 25 m apart. During 2013-2014 we increased our survey effort to three 100 × 4 m (1200 m²) belt-transects because of relatively low ant densities at sites sampled during this time. A three transect design was an appropriate balance of statistical precision and sampling effort (Holbrook et al. 2015). We classified a colony as active if we observed individual ants in or on the nest. If no individuals were detected, observers slightly disturbed the nest and waited for up to 30 seconds to solicit a response. Previous analyses indicated high correlation of counts of harvester ant colonies between observers (Holbrook et al. 2015), thus we used the maximum count per plot. Finally, we resampled 30 plots in 2014 that we surveyed in 2013 to assess interannual variation in the density of harvester ant colonies. The

Pearson's correlation between years for colony density was high ($r = 0.95$), suggesting little annual change.

Time since fire and vegetation data

We used GIS and field data to characterize time since fire and the vegetation community (Table 3.1). First, we calculated time since fire (TSF) using a fire perimeter geodatabase described in Balch et al. (2013), and updated with subsequent fires, by subtracting the survey year from the year of the most recent fire intersecting each plot. However, because of the lack of reporting and sparse data records associated with fire perimeters before the 1980s (Miller et al. 2011), we subtracted our survey date by 1980 for plots with no fire data or much older records (e.g., ≤ 1960), which resulted in a maximum TSF of 33 years and allowed us to use the records of a fire as well as no fire ≥ 1980 . Second, we characterized vegetation at 6-9 random or systematically placed (depending on the study site) locations at each plot concurrent with ant sampling. At each location, we captured a nadir (i.e., 90°) photograph from 2 m above the ground (Pilliod and Arkle 2013). This height corresponded to a 1.5×2 m area of ground surface and provided sufficient height above shrubs. We used SamplePoint 1.43 software (Booth et al. 2006) to measure the cover of species and abiotic habitat components (e.g., rock, soil, litter) at 100 computer-selected pixels per image. We classified each pixel to a plant group (Table 3.1), which generated a percent cover measurement at the image level. We then averaged percentages across the 6-9 locations to attain plot-level percent cover estimates. Finally, when visiting each plot, we documented whether the area was consistent with successfully treated (e.g., rows of exotic or native perennials), burned or unsuccessfully treated (e.g., mostly cheatgrass or native perennial grasses without shrubs), and unburned (e.g., shrubs present) vegetation.

Other environmental data

We developed an abiotic soil index describing soil texture using STATSGO data (Table 3.1; Soil Survey Staff, Natural Resources Conservation Service; <http://sdmdataaccess.nrcs.usda.gov>). We identified the STATSGO map key at each plot, and averaged (across up to 10 soil names) the proportion of soil passing through a number 4 sieve at the first soil depth. This resulted in an index with larger numbers indicating finer-grained soils, and low numbers indicating coarse-grained soils. We expected harvester ants to be strongly associated with finer-grained soils (e.g., Johnson 1992) because they retain soil moisture better than coarse-grained soils (Johnson 2001). Soil moisture positively influences survival of harvester ant (*P. rugosus*, *P. barbatus*) foundresses, wet body mass, and brood production during colony establishment and growth (Johnson 1998), which are the most vulnerable life stages for colonies.

We used GIS databases to generate climate metrics at each plot (Table 3.1). First, we calculated mean annual precipitation and mean annual temperature from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group; <http://prism.oregonstate.edu>) during the time period 1979–2008. We expected harvester ants to be negatively associated with mean annual precipitation (over our sampled gradient) because harvester ants are evolutionarily adapted for semi-arid or arid environments (Johnson 2001) and tend to be more abundant in these locations (Hanser et al. 2011).

Data analyses

State Changes

To assess the direction and temporal trend in plant characteristics and harvester ant occupancy and density, we binned plots according to time since fire categories derived from

our fire geodatabase. We binned plots with the goal of maintaining a reasonable sample size within each TSF bin (i.e., approximately ≥ 20 observations), which resulted in 1-5 years ($n = 77$), 6-10 years ($n = 78$), 11-20 years ($n = 81$), 21-30 years ($n = 61$), ≥ 31 years ($n = 53$). We used our group of ≥ 31 years for comparisons to all other groups in that we assumed it likely contained plots that were unburned (i.e., contained shrubs), and thus would generate an average estimate of our plant groups that was closer to “control” conditions than all other bins. At each bin, we computed the mean ($\pm 90\%$ CI) for exotic annual grasses (EAG), native perennial grasses (NPG), and shrubs, as well as proportion of sites occupied and density of harvester ants. We focused on these plant groups because they are the major groups discussed in terms of vegetation state changes in sagebrush ecosystems (e.g., Chambers et al. 2014), and they were the most dominant groups in our data (see Table 3.1). Additionally, we assessed the effect of current vegetation states on harvester ant occupancy and density using our field assessment of burned ($n = 98$), treated ($n = 124$), and unburned ($n = 123$). Within this categorization, we computed the mean ($\pm 90\%$ CI) for the same plant groups aforementioned (i.e., EAG, NPG, and shrubs), as well as the proportion of sites occupied and density of harvester ants.

Relative Importance of Fire and Biological Invasions

To evaluate the relative importance of fire and biological invasions on harvester ant occupancy and density, we combined vegetation data, TSF, and other environmental factors potentially important for harvester ants (see Table 3.1) into generalized linear models. We used a nested approach similar to Boulangeat et al. (2012), within which we built one model assessing the variation in occupancy ($n = 358$), and then built a second model that modeled variation in density ($n = 171$) for those plots that were occupied. We used generalized linear

models with a binomial distribution for occupancy data, and a negative binomial error distribution for density data. In each model, we included an offset describing the difference in areas surveyed among study sites to account for differences in survey effort. Our modeling objectives were focused on general patterns, thus, we evaluated only main effects.

Prior to model development, we standardized covariates and evaluated multicollinearity. We standardized continuous covariates by $(x_i - \bar{x}) / (2 \times \sigma_x)$ where x_i equals an observation at plot i , σ is the standard deviation of covariate x , and \bar{x} is the mean of the covariate. This standardization allowed for an equal comparison among effect sizes for continuous and binary covariates (Gelman 2008), which was important for our objective of assessing relative importance of fire and biological invasions. We assessed collinearity among covariates, and removed temperature because it was correlated with precipitation ($r = -0.67$; Table 3.1).

For each response variable, we developed an initial model with all covariates except EAG and TSF (see Table 3.1). We then added EAG and TSF to the initial model, and tested the drop-in-deviance using a likelihood ratio test to evaluate if EAG and TSF increased model fit. For example,

Initial model:

$$Y_i = \beta_0 + \beta_1(x_{i1}) + \beta_2(x_{i2}) + \beta_3(x_{i3}) + \varepsilon$$

Fire and biological invasion model:

$$Y_i = \beta_0 + \beta_1(x_{i1}) + \beta_2(x_{i2}) + \beta_3(x_{i3}) + \beta_4(TSF_i) + \beta_4(EAG_i) + \varepsilon$$

where Y = response variable at plot i , β = parameter estimate associated with a particular covariate, and x = observation of a particular covariate at plot i . To provide a conservative estimate for TSF in “unburned” plots (those without fire data associated with

them), we set the TSF to 33 years, which was the maximum TSF we observed within our fire geodatabase using data from ≥ 1980 .

We assessed model fit for our most supported occupancy and density models. For our occupancy model, we tested goodness-of-fit (Hosmer and Lemeshow 2000) and assessed predictive performance by calculating the area under the curve (AUC) of a receiver operating characteristic (ROC; Robin et al. 2011). A ROC plot characterizes true positives against false positives, and the AUC ranges from 0-1 providing a measure of the model's ability to correctly discriminate between plots that are occupied versus unoccupied (Hosmer and Lemeshow 2000, Robin et al. 2011). AUC of 0.5 indicates random discrimination, whereas values greater than 0.5 indicate progressively better discrimination (Hosmer and Lemeshow 2000). For our density model, we computed the Spearman's rank correlation coefficient between the observed and predicted counts as a measure of fit. Finally, we plotted the effect sizes ($\pm 90\%$ CI) of the estimated parameters describing covariate relationships, which allowed us to assess which effects were comparatively strongest. To complete these analyses, we used program R (R Development Core Team 2015) and packages 'MASS' (Venables and Ripley 2002), 'ResourceSelection' (Lele et al. 2014), and 'pROC' (Robin et al. 2011).

Results

Across a range of 1-31 years post-fire, we observed 0-2.8 harvester ant colonies per 100 m², and 48% of the 358 plots we surveyed were occupied by ants. The effect of TSF on shrub cover was immediate and consistent in that the estimated shrub cover for years 1-30 post-fire was similar (~5%) and significantly less than shrub cover for ≥ 31 years post-fire (~15%; Figure 3.2). Native perennial grasses were consistently higher in areas 1-30 years post-fire compared to ≥ 31 years, and there was no consistent trend in EAG across TSF. The

proportion of plots occupied by harvester ants displayed no consistent pattern, although years 6-10 indicated significant low proportions relative to all other categories (Figure 3.3A).

Colony density exhibited a qualitative decrease across TSF, but no statistical changes (Figure 3.3B).

Field derived categories of vegetation (i.e., burned, treated, and unburned) produced significant differences in plant groups and harvester ant parameters (Figure 3.4, Figure 3.5A and 5B). Burned plots had the highest cover of EAG, followed by treated plots and unburned plots (Figure 3.4). Burned plots and treated plots had similar and lower NPG relative to unburned plots. Finally, treated and burned plots had much lower shrub cover compared to unburned plots. Both the proportion of plots occupied and density of harvester ant colonies were statistically similar in burned and treated plots and were higher relative to unburned plots (Figure 3.5A and 3.5B), suggesting a positive effect of EAG and negative effect of shrub cover.

Evidence from our drop-in-deviance indicated there was support for biological invasions by EAG, and the effect of TSF, improved model fit for both occupancy ($X^2 = 5.35$, $df = 2$, $p = 0.07$) and density ($X^2 = 16.94$, $df = 2$, $p < 0.01$) of harvester ants, however, results for occupancy data were not as strong as for density. For our occupancy model, the goodness-of-fit test indicated appropriate fit ($X^2 = 14.35$, $df = 13$, $p = 0.35$), and predictive performance was high (AUC = 0.90); although, the predictive performance of the reduced model (without EAG and TSF) was essentially equivalent (AUC = 0.89). Our density model suggested reasonable model fit as measured by Spearman's rank correlation coefficient ($\rho = 0.58$).

The strongest positive effect size we observed in our occupancy model was associated with soil texture, and the strongest negative effect was associated with precipitation (Figure 3.6A). These results indicated that the variation in harvester ant occupancy was largely influenced by finer-grained soils and drier locals across our sampling extent. Next, we observed a relatively strong and positive effect of native forbs on harvester ant occupancy, followed by a comparatively weak and negative effect of shrub cover. Effects associated with EAG and TSF were negative (i.e., positive fire effect) and different from 0, but were among the weakest effects observed. All other effects were statistically insignificant.

Similar to our occupancy model, our strongest (and negative) effect from our density model was associated with precipitation, reinforcing the positive effect of relatively drier locales on harvester ants (Figure 3.6B). In contrast, however, we observed a positive and significant effect of EAG and a stronger negative effect of TSF indicating colony density was related to increasing EAG and decreasing TSF, which was consistent with the qualitative patterns observed when evaluating differences among vegetation states and density (Figure 3.2, 3.3B, and 3.5B). We also documented a positive effect of NPG on colony density, suggesting an increase in harvester ants in areas with more native perennial grasses. We observed no effect of soil texture, native forbs, or shrub cover on density, which contrasted with our occupancy model results (Figure 3.6A and 3.6B). Similarly, we discovered no effect of exotic forbs or exotic perennial grasses.

Discussion

Our results suggest that vegetation states are changing from what were historically shrublands to native perennial and exotic annual grasslands, and that harvester ant density is more associated (and in a positive direction) with those changes compared to occupancy.

Harvester ant occupancy appears to be driven by more extensive ecological gradients such as climate and soil texture, relative to effects of fire or changes in vegetation states.

Collectively, this work emphasizes the importance of assessing changes of vegetation states on multiple population parameters to gain a better understanding of the relative effects of environmental change on animal species. For example, in sagebrush systems both fire and biological invasions are rapidly changing landscapes, and in our case, these changes are positively affecting the density of harvester ants, which are a functionally important ecosystem engineer and granivore.

State Changes

Similar to previous work in sagebrush ecosystems (e.g., Baker 2011), we quantitatively documented an immediate and relatively consistent change from shrublands to grasslands 30 years post fire. However, we predicted that EAG would be the dominant vegetation state after fire (Miller et al. 2011), but we found evidence of similar proportions between exotic annual and native perennial grasslands in most categories (Figure 3.2). Additionally, we expected both occupancy and density of harvester ants to be positively associated with time since fire and EAG (Ostoja et al. 2009), but we only observed a qualitative pattern consistent with our predictions in harvester ant density. The qualitative signal we observed in vegetation changes and harvester ant parameters post-fire were likely highlighting the enduring weaknesses of using a TSF approach (e.g., Keeley et al. 2005, Swan et al., in press). For example, a TSF framework assumes that spatially disparate locations that are within the same time since fire category are reasonable replicates. In other words, a TSF approach does not account for different trajectories of the plant community that occur post-fire in spatially disparate locations, which undoubtedly occur, thus correlation between

vegetation states and time since fire may be weak at best (Swan et al., in press). Despite these limitations, however, we documented a state change that was abrupt, consistent, and statistically significant from shrublands to grasslands suggesting that the ecological signal for this characteristic was strong.

To mediate the weaknesses of a TSF approach in our assessment of animal responses to vegetation states, we complemented our analyses by assessing differences in current vegetation states based on field observations. By using current vegetation states, we did not assume that spatially disparate locations exhibited similar plant community responses post-fire. Here, our observations were consistent with a statistically positive effect of EAG and reduced shrub cover on both occupancy and density of harvester ants, providing evidence for a positive effect of vegetation state changes. We predicted this relationship because EAG produce many seeds (i.e., harvester ant food), which might facilitate high colony densities (Ostoja et al. 2009). Previous work has indicated much higher densities of harvester ants in areas that are dominated by exotic annual grasses (Ostoja et al. 2009, Gosselin et al., in revision). Although harvester ants generally do not prefer cheatgrass seeds (Crist and MacMahon 1992, Ostoja et al. 2013), cheatgrass and other exotic annuals provided an abundant food resource for harvester ants that may support high colony densities.

Relative influence of fire, biological invasions, and other ecological factors

Although we documented a pattern consistent with a positive effect of EAG and reduced shrub cover due to fire on both occupancy and density of harvester ants when assessing vegetation state changes, analyses assessing the relative importance of fire and EAG provided a more resolved conclusion in that it was comparative. The influence of EAG and TSF on occupancy of harvester ants ranked ~4th in terms of importance (i.e., effect sizes),

while these factors ranked ~2nd concerning their influence on harvester ant density. This disparity was also supported by the results from our likelihood ratio test, with much more statistical support for the effect of EAG and TSF on density compared to occupancy of harvester ants. Thus, we placed relatively little weight on the effect sizes describing the effects of EAG and TSF on occupancy, and more weight on the effects characterizing the influence of EAG and TSF on density.

Variation in density of harvester ant was best characterized by precipitation gradients, native perennial grasses, EAG, and TSF. The effect of precipitation was negative, substantiating previous analyses indicating a biogeographical affinity and evolutionary adaptations of harvester ants for arid locations (e.g., Johnson 2001, Hanser et al. 2011). We predicted a positive effect of native perennial grasses and (as aforementioned) EAG because of production of preferred and abundant seed resources, respectively (Crist and MacMahon 1992, Ostoja et al. 2013). Finally, a negative effect of TSF on density of harvester ants (indicating an increase in density for years immediately post-fire) was expected because fires reduce shrub and other surface cover, and consequently increase availability of potential nest and foraging sites (e.g., Zimmer and Parmenter 1998, Ratchford et al. 2005, Arnan et al. 2006, Matsuda et al. 2011). The occurrence of fire might indeed trigger a colonization response from harvester ants.

In contrast, variation in occupancy was best explained by precipitation gradients, soil texture, and native forbs; although, effects of EAG, shrub cover, and TSF were also significant. The negative effect of precipitation, which was stronger for occupancy relative to density, further substantiated the affinity of harvester ants for arid locations (Johnson 2001). Additionally, the positive effect of finer-grained soils on occupancy was expected because

they retain soil moisture better than coarse-grained soils, and soil moisture is related to foundress survival and brood production (Johnson 1998, Johnson 2001). The positive effect of fire and lower shrub cover was consistent with our prediction that fire may initiate a colonization response, and that vegetation state changes would increase occupancy; however, as aforementioned, these effects were comparatively weak. Lastly, we observed a positive effect of native forbs and a *negative* effect of EAG on occupancy of harvester ants. Native forb species in our study area, such as slickspot peppergrass (*Lepidium papilliferum*), provide fruits and seeds that harvester ants consume in large quantities when present, consistent with a positive effect of native forbs on occupancy of harvester ants (White and Robertson 2009). The negative effect from EAG was unintuitive in that it was contrary to our predictions, initial plotting of the data, and all other pieces of observed evidence. Thus, *post-hoc* we examined if there was evidence of confounding, or other effect modifications (e.g., Arah 2008, Tu et al. 2008), within our full model (i.e., included biological invasions and fire). We sequentially removed all variables other than EAG to examine how the effect of EAG changed. The effect remained negative across the removal of each variable, however, the unconditional effect of only EAG on variation in occupancy was *positive* ($\beta = 0.21$, $df = 357$, $p = 0.32$). Thus, it appeared there was indeed a *negative* effect of EAG on harvester ant occupancy, conditioned on accounting for other sources of variation such as precipitation gradients and soil texture. The negative effect of EAG on occupancy could be related to our TSF and shrub effects in that they all may be suggesting the availability of nest locations is important for colonization. For example, in those areas with longer times since fire, cover of EAG may exceed a threshold whereby foundresses are unable to identify and initiate a nest, and thus colonization becomes unlikely. This would suggest that reduced cover of EAG and/or recent fire are

important for colonization of harvester ants, which is consistent with the effects we documented; however, additional work is needed to evaluate the mechanisms associated with colonization processes.

Combining our occupancy and density results from our generalized linear models, we observed that effect sizes for a particular variable changed depending on the response, and the changes were generally consistent with predictions derived from ecological theory. For example, many authors have provided evidence that broader scale environmental gradients better predict variation in occupancy patterns, whereas local level dynamics better explain variation in density (e.g., Soberón 2007, Wiens 2011, Boulangéat et al. 2012). Indeed, our data contribute to the weight of evidence suggesting that different environmental factors have disproportionate effects on variation in occupancy and density, and emphasize the importance of testing alternative hypotheses concerning each parameter. These multi-level approaches provide a more complete understanding of how animals are affected by landscape change, which can be directly applied for more precise management actions (Ehrlén and Morris 2015).

Implications

To our knowledge, our work is one of the first to evaluate the relative influence of changes in vegetation states on multiple population parameters of animals in sagebrush ecosystems. We demonstrated changes from shrublands to grasslands, and that these changes are strong predictors of density (but not occupancy) of an important granivore. Land managers throughout the sagebrush ecosystem are highly concerned with the conversion to exotic annual grasslands, but as with many environmental changes, there will be winners and losers (e.g., Knick et al. 2014). In our context, harvester ant density will likely continue to increase following more drought, expansion of exotic annual grasses, and increased wildfire

in the Great Basin (Abatzoglou and Kolden 2012, Cook et al. 2015), while occupancy may be relatively independent of these state changes. This suggests that harvester ants are likely winners considering the large-scale state changes within sagebrush ecosystems, which might be somewhat advantageous for restoration efforts. For example, given that harvester ants can reduce cheatgrass cover near their nests (Gosselin et al., in revision) and harvest cheatgrass seeds (Ostoja et al. 2013), harvester ants may help delay the transition from native grasslands to exotic annual grasslands in some locations by removing or reducing seed sources. This process may be increasingly facilitated provided that occupancy of harvester ants is independent of state changes, and thus ants can occupy many locations across a landscape and take advantage of those areas that begin to experience state changes. Insights such as these provide unique opportunities for restoration ecologists to “take advantage” of the ecological roles of animals to assist in achieving management objectives (*sensu* Byers et al. 2006). Overall, our work provides a unique assessment of how state changes are positively influencing an aridland granivore and ecosystem engineer, which may have implications for future conservation efforts.

References

- Abatzoglou, J. T., and C. A. Kolden. 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grass. *Rangeland Ecology and Management* 64:471-478.
- Arah, O. A. 2008. The role of causal reasoning in understanding Simpson's paradox, Lord's paradox, and the suppression effect: covariate selection in the analysis of observation studies. *Emerging Themes in Epidemiology* 5:5.
- Arnan, X., A. Rodrigo, and J. Retana. 2006. Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. *Journal of Biogeography* 33:1246-1258.
- Baker, W. L. 2011. Pre-Euro-American and recent fire in sagebrush ecosystems. Pages 185-201 in S. Knick and J. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California Press, Berkley, CA.
- Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology* 19:173-183.
- Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, K. B. Gorman, S. J. Holbrook, C. M. Laney, M. D. Ohman, D.P.C Peters, F.C., Pillsbury, A. Rassweiler, R. J. Schmitt, and S. Sharma. 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere* 2: art129.
- Byers, J.E., K. Cuddington, C.G. Jones, T.S. Talley, A. Hastings, J.G. Lambrinos, J.A. Crooks, and W.G. Wilson. 2006. Using ecosystem engineers to restore ecological

- systems. *Trends in Ecology and Evolution* 21:493–500.
- Blom, P. 1990. Potential impacts on radioactive waste disposal situations by the harvester ant, *Pogonomyrmex salinus* Olsen (Hymenoptera: Formicidae). M.S. thesis. University of Idaho, Moscow, Idaho, USA.
- Booth, D. T., S. E. Cox, and R. D. Berryman. 2006. Point sampling digital imagery with “Samplepoint.” *Environmental Monitoring and Assessment* 123:97-108.
- Boulangeat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15:584-593.
- Bradley, B. A., and J. F. Mustard. 2008. Comparison of phenology trend by land cover class: a case study in the Great Basin, USA. *Global Change Biology* 14:334-346.
- Brown, G., C. Scherber, P. Ramos, and E. K. Ebrahim. 2012. The effects of harvester ant (*Messor ebeninus* Forel) nests on vegetation and soil properties in a desert dwarf shrub community in north-eastern Arabia. *Flora* 207:503-511.
- Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* 10:201-227.
- Carlson, S. R., and W. G. Whitford. 1991. Ant mound influence on vegetation and soils in a semiarid mountain ecosystem. *The American Midland Naturalist* 126:125-139.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77:117-145.
- Chambers, J. C., R. F. Miller, D. I. Board, D. A. Pyke, B. A. Roundy, J. B. Grace, E. W. Schupp, and R. J. Tausch. 2014. Resilience and resistance of sagebrush ecosystems:

- implications for state and transition models and management treatments. *Rangeland Ecology and Management* 67: 440-454.
- Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American southwest and central plains. *Science Advances* 1:e1400082.
- Crist, T. O., and J. A. MacMahon. 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. *Ecology* 73:1768-1779.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573-2584.
- Ehrlén, J., and W. F. Morris. 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters* 18:303-314.
- Freeman, E. D., T. R. Sharp, R. T. Larson, R. N. Knight, S. J. Slater, and B. R. McMillan. 2014. Negative effects of an exotic grass invasion on small-mammal communities. *PLoS ONE* 9:e108843.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27:2865-2873.
- Gosselin, E. N., J. D. Holbrook, K. Huggler, E. Brown, K. T. Vierling, R. S. Arkle, and D. S. Pilliod. In revision. Ecosystem engineering of harvester ants: effects on vegetation in a sagebrush-steppe ecosystem. *Western North American Naturalist*.

- Hall, L. K., J. F. Mull, and J. F. Cavitt. 2009. Relationship between cheatgrass coverage and the relative abundance of snakes on Antelope Island, Utah. *Western North American Naturalist* 69:88-95.
- Hanser, S. E., M. Leu, C. L. Aldridge, S. E. Nielsen, M. M. Rowland, and S. T. Knick. 2011. Occurrence and abundance of ants, reptiles, and mammals. Pages 221-314 in S. E. Hanser, M. Leu, S. T. Knick, and C. L. Aldridge, editors. *Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins*. Allen Press, Lawrence, KS.
- Heske, E. J., J. H. Brown, and Q. Guo. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan desert. *Oecologia* 95:520-524.
- Holbrook, J. D., R. S. Arkle, J. L. Rachlow, K. T. Vierling, and D. S. Pilliod. 2015. Sampling animal sign in heterogeneous environments: how much is enough? *Journal of Arid Environments* 199:51-55.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. John Wiley and Sons, New York.
- Johnson, R. A. 1992. Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. *Oecologia* 89:118-124.
- Johnson, R. A. 1998. Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae). *Insectes Sociaux* 45:255-266.
- Johnson, R. A. 2001. Biogeography and community structure of North American seed-harvester ants. *Annual Reviews of Entomology* 46:1-29.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos*

69:373-386.

- Jones, C., J. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946-1957.
- Jones, C., J. Gutierrez, J. Byers, J. Crooks, J. Lambrinos, and T. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. *Oikos* 12:1862-1869.
- Keeley, J.E., C.J. Fotheringham, and M. Baer-Keeley. 2005. Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecological Applications* 15:151-1534.
- Knick, S., J. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conservation Biology* 9:1059-1071.
- Knick, S., J. Rotenberry. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. *Ecology* 81:220-227.
- Knick, S., S. Hanser, R. Miller, D. Pyke, M. Wisdom, S. Finn, E. Rinkes, and C. Henny. 2011. Ecological influence and pathways of land use in the sagebrush. Pages 203-251 in S. Knick and J. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology, University of California Press, Berkeley, CA.
- Knick, S., S. Hanser, and M. Leu. 2014. Ecological scale of bird community response to pinyon-juniper removal. *Rangeland Ecology and Management* 67:553-562.
- Lele, S. R., J. L. Keim, and P. Solymos. 2014. ResourceSelection: resource selection (probability) functions for use-availability data. R package version 0.2-4. <http://CRAN.R-project.org/package=ResourceSelection>.

- Litt, A. R., and D. E. Pearson. 2013. Non-native plants and wildlife in the intermountain west. *Wildlife Society Bulletin* 37:517-526.
- Litt, A. R., and R. J. Steidl. 2011. Interactive effects of fire and nonnative plants on small mammals in grasslands. *Wildlife Monographs* 176:1-31.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* 31:265-291.
- Mandel, R. D. and C. J. Sorenson. 1982. The role of the western harvester ant (*Pogonomyrmex occidentalis*) in soil formation. *Soil Science Society of America* 46:785-788.
- Matsuda, T., G. Turschak, C. Brehme, C. Rochester, M. Mitrovich, and R. Fisher. 2011. Effects of local-scale wildfires on ground foraging ants (Hymenoptera: Formicidae) in southern California. *Environmental Entomology* 40:204-216.
- Miller, R., S. Knick, D. Pyke, C. Meinke, S. Hanser, M. Wisdom, and A. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 *in* S.T. Knick and J.W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. *Studies in Avian Biology*, University of California Press, Berkley, CA.
- Newbold, T. A. S. 2005. Desert horned lizard (*Phrynosoma platyrhinos*) locomotor performance: the influence of cheatgrass (*Bromus tectorum*). *The Southwestern Naturalist* 50:17-23.

- Ostoja, S. M., and E. W. Schupp. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. *Diversity and Distributions* 5:863-870.
- Ostoja, S. M., E. W. Schupp, and K. Sivy. 2009. Ant assemblages in intact big sagebrush and converted cheatgrass-dominated habitats in Tooele County, Utah. *Western North American Naturalist* 69:223-234.
- Ostoja, S. M., E. W. Schupp, and R. Klinger. 2013. Seed harvesting by a generalist consumer is context dependent: interactive effects across multiple spatial scales. *Oikos* 122:563-574.
- Pilliod D. S., and R. S. Arkle. 2013. Performance of quantitative vegetation sampling methods across gradients of cover in Great Basin plant communities. *Rangeland Ecology and Management* 66:634-647.
- R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ratchford, J. S., S. E. Wittman, E. S. Jules, A. M. Ellison, N. J. Gotelli, and N. J. Sanders. 2005. The effects of fire, local environment and time on ant assemblages in fens and forests. *Diversity and Distributions* 11:487-497.
- Rieder, J. P., T. A. S. Newbold, and S. M. Ostoja. 2010. Structural changes in vegetation coincident with annual grass invasion negatively impacts sprint velocity of small vertebrates. *Biological Invasions* 12:2429-2439.
- Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. C. Sanchez, and M. Müller. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* 12:77.

- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.
- Swan, M., F. Christie, Holly Sitters, A. York, and J. Di Stefano. In press. Predicting faunal fire responses in heterogeneous landscapes: the role of habitat structure. *Ecological Applications*.
- Toro, I.D., R.R. Ribbons, and A.M. Ellison. 2015. Ant-mediated ecosystem functions on a warmer planet: effects on soil movement, decomposition and nutrient cycling. *Journal of Animal Ecology* 84:1233-1241.
- Tu, Y., D. Gunnell, and M. Gilthorpe. 2008. Simpson's paradox, Lord's paradox, and suppression effects are the same phenomenon – the reversal paradox. *Emerging Themes in Epidemiology* 5:2.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Fourth Edition. Springer, New York.
- Wagner, D., M. Brown, and D. Gordon. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia* 112:232-236.
- White, J.P, and I.C. Robertson. 2009. Intense seed predation by harvester ants on a rare mustard. *Ecoscience* 16:508-513.
- Wilby, A., M. Shachak, and B. Boeken. 2001. Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* 92:436-444.
- Wiens, J. J. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* 366:2336-2350.
- Zimmer, K., and R. R. Parmenter. 1998. Harvester ants and fire in a desert grassland: ecological responses of *Pogonomyrmex rugosus* (Hymenoptera: Formicidae) to

experimental wildfires in central New Mexico. *Environmental Entomology* 27:282-287.

Table 3.1. Covariate descriptions, correlations, and collection methods for the variables used in analyses of vegetation states and harvester ant (*Pogonomyrmex* spp.) occupancy and density.

Variable	Units	Mean (Range)	Description	Correlated	Method
Soil	%	85 (62.5-98.25)	Mean % surface soil passing through a #4 sieve within each mukey code	NA	STATSGO (1:250,000)
Precipitation	mm	325 (199-639)	Mean annual precipitation from 1979-2008	Correlated with mean annual temperature from 1979-2008 ($r = -0.67$)	PRISM (800 m)
Time Since Fire (TSF)	years	15 (1-33)	Number of years since a fire burned an area using data beginning at 1980, or using 1980 as a reference time for areas without fire data	NA	GIS (90 m)
NPG	%	20 (0-68)	Mean % cover of native perennial grass at the plot level	NA	PhotoPoint
EPG	%	3 (0-51)	Mean % cover of exotic perennial grasses at the plot level	NA	PhotoPoint
EF	%	2 (0-24)	Mean % cover of exotic forbs at the plot level	NA	PhotoPoint
NF	%	1 (0-32)	Mean % cover of native forbs at the plot level	NA	PhotoPoint
EAG	%	28 (0-96)	Mean % cover of exotic annual grasses at the plot level (mostly cheatgrass; <i>Bromus tectorum</i>)	NA	PhotoPoint
Shrub	%	6 (0-54)	Mean % cover of shrubs at the plot level	NA	PhotoPoint

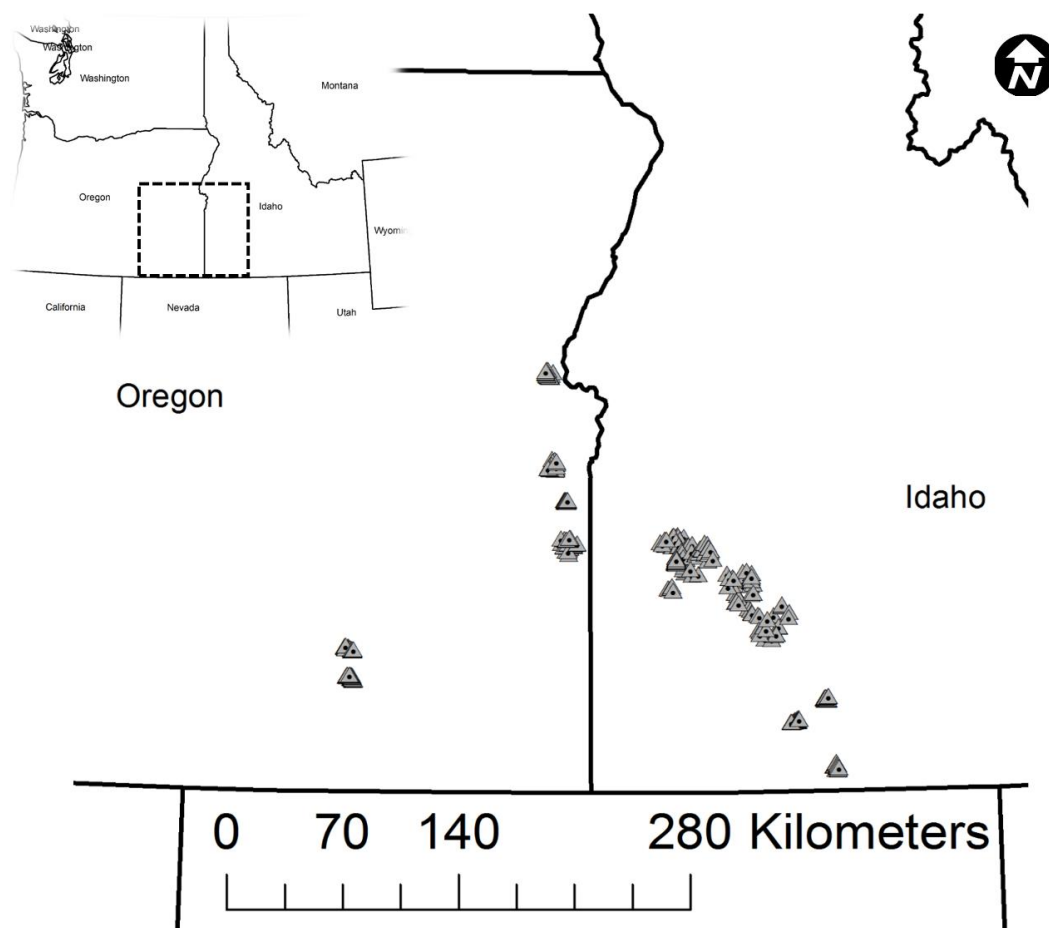


Figure 3.1. Triangles indicate the distribution of 1-ha plots ($n = 358$) that were sampled for harvester ants (*Pogonomyrmex* spp.) within southern Oregon and Idaho, USA, during 2008-2009 and 2013-2014. Inset shows the approximate extent of sampling.

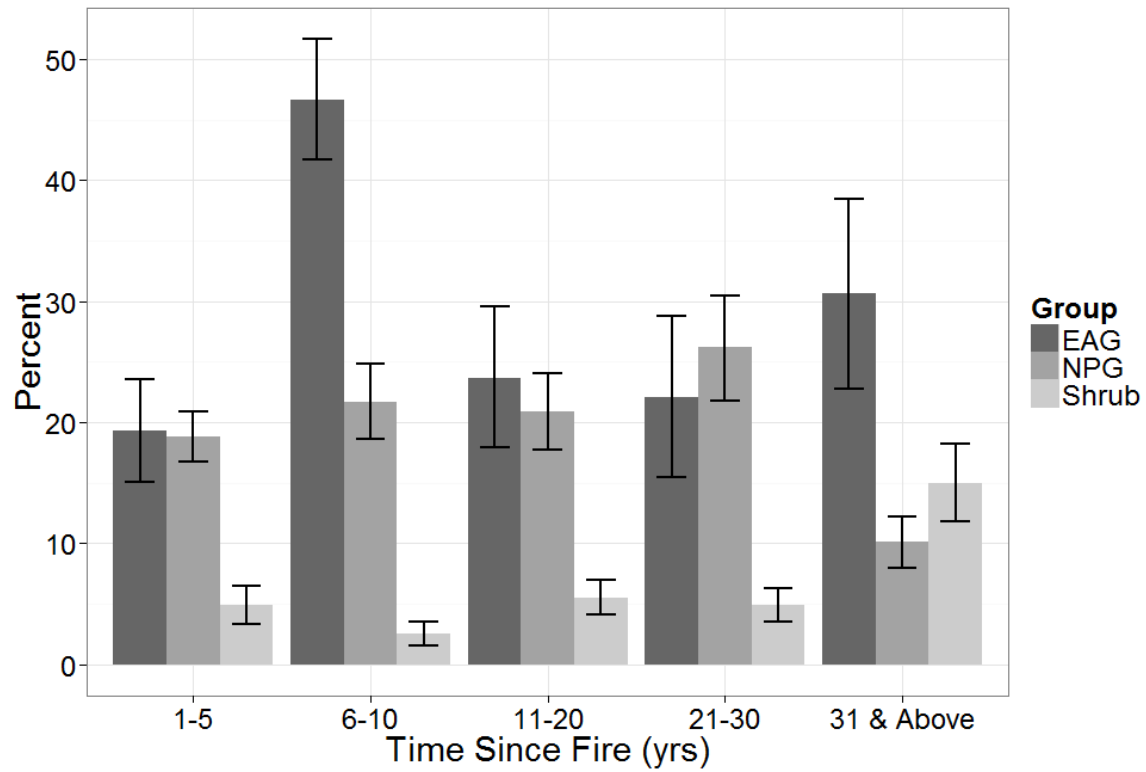


Figure 3.2. Percent cover of exotic annual grass (EAG), native perennial grass (NPG), and shrubs as a function of time since fire (x-axis). Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.

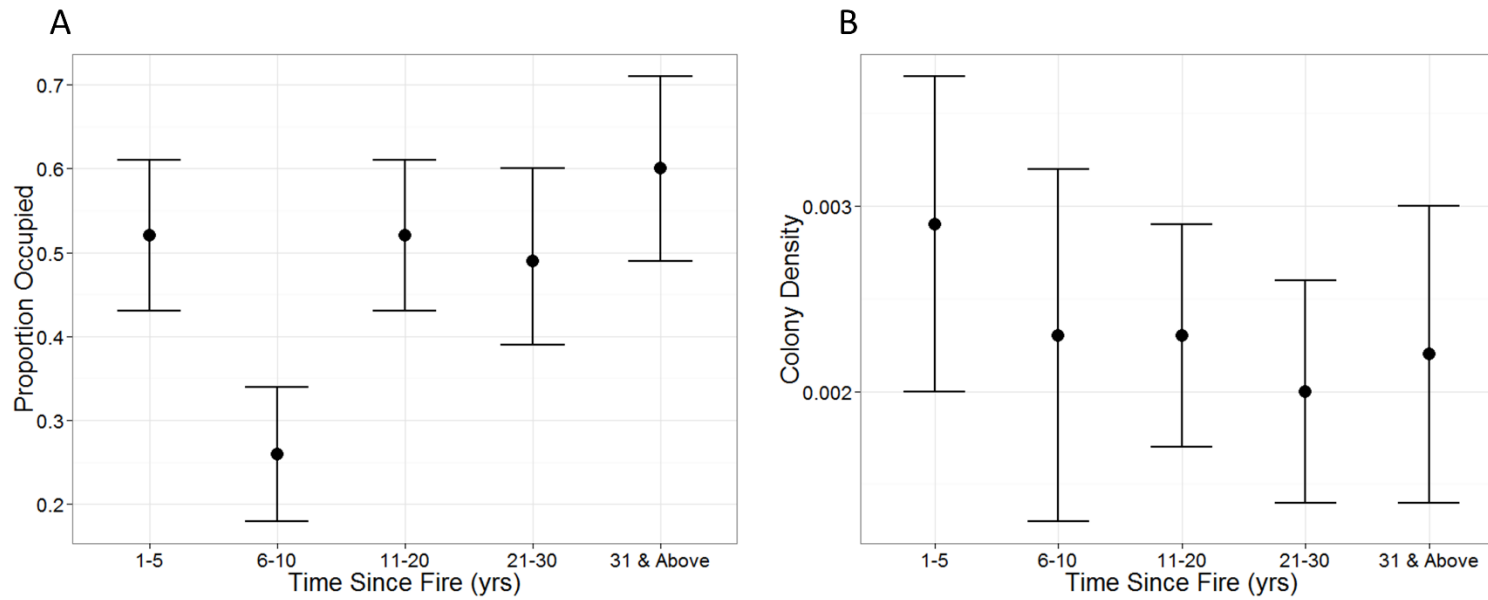


Figure 3.3. A) Proportion of plots occupied, and B) density (colony/100 m²) of harvester ant (*Pogonomyrmex* spp.) colonies as a function of time since fire (x-axis). Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.

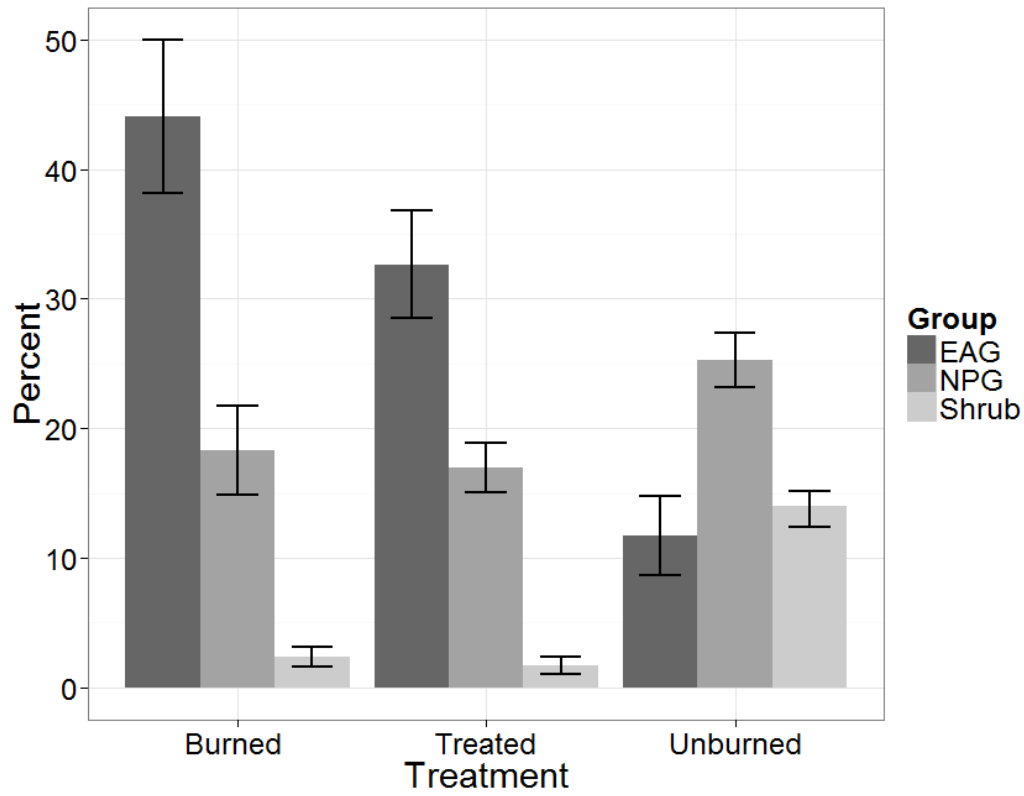


Figure 3.4. Percent cover of exotic annual grass (EAG), native perennial grass (NPG), and shrubs as a function of realized vegetation state (x-axis). Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.

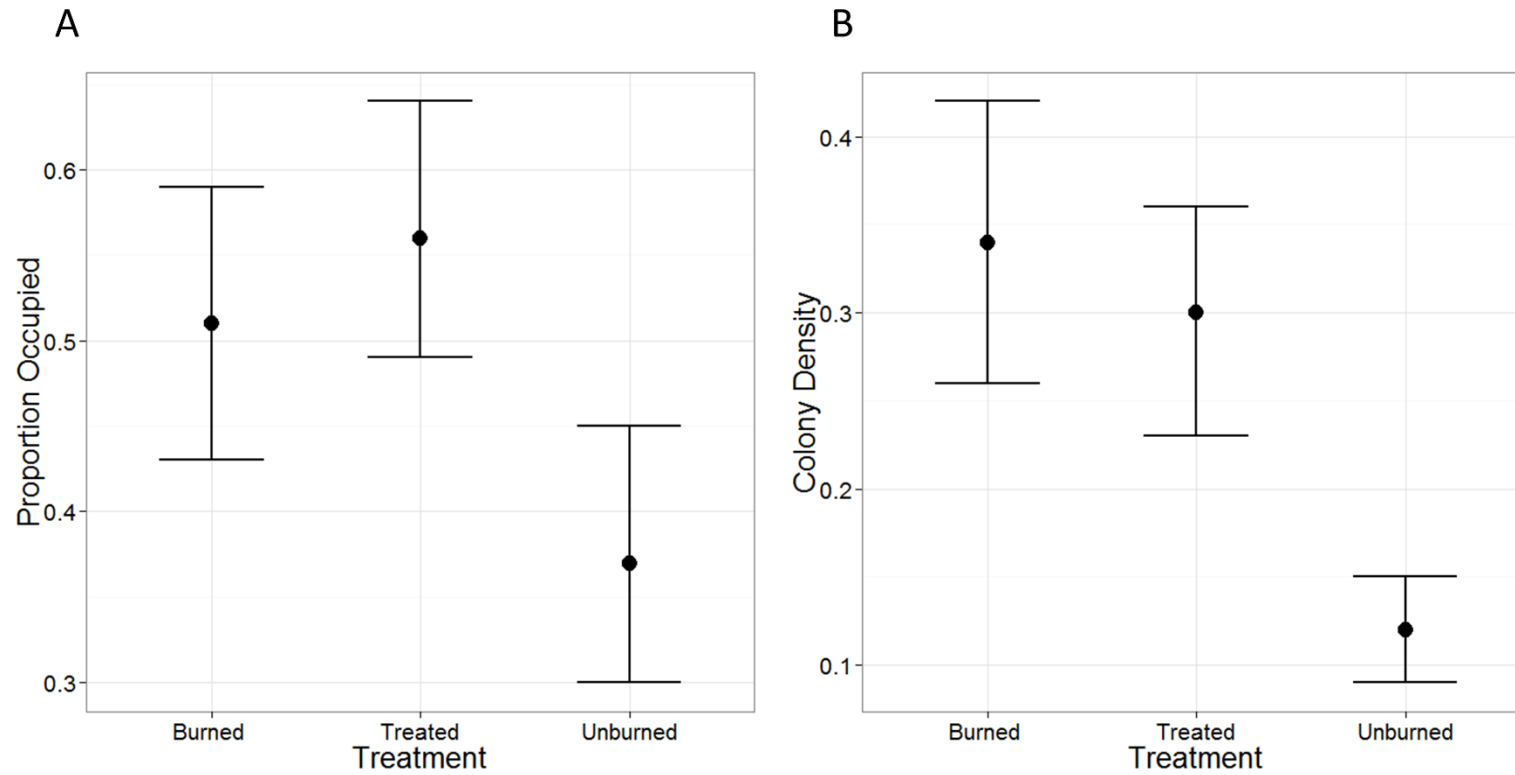


Figure 3.5. A) Proportion of plots occupied by harvester ants, and B) density (colony/100 m²) of harvester ant (*Pogonomyrmex* spp.) colonies as a function realized vegetation state. Error bars are 90% CIs. Data were collected throughout southern Oregon and Idaho, USA.

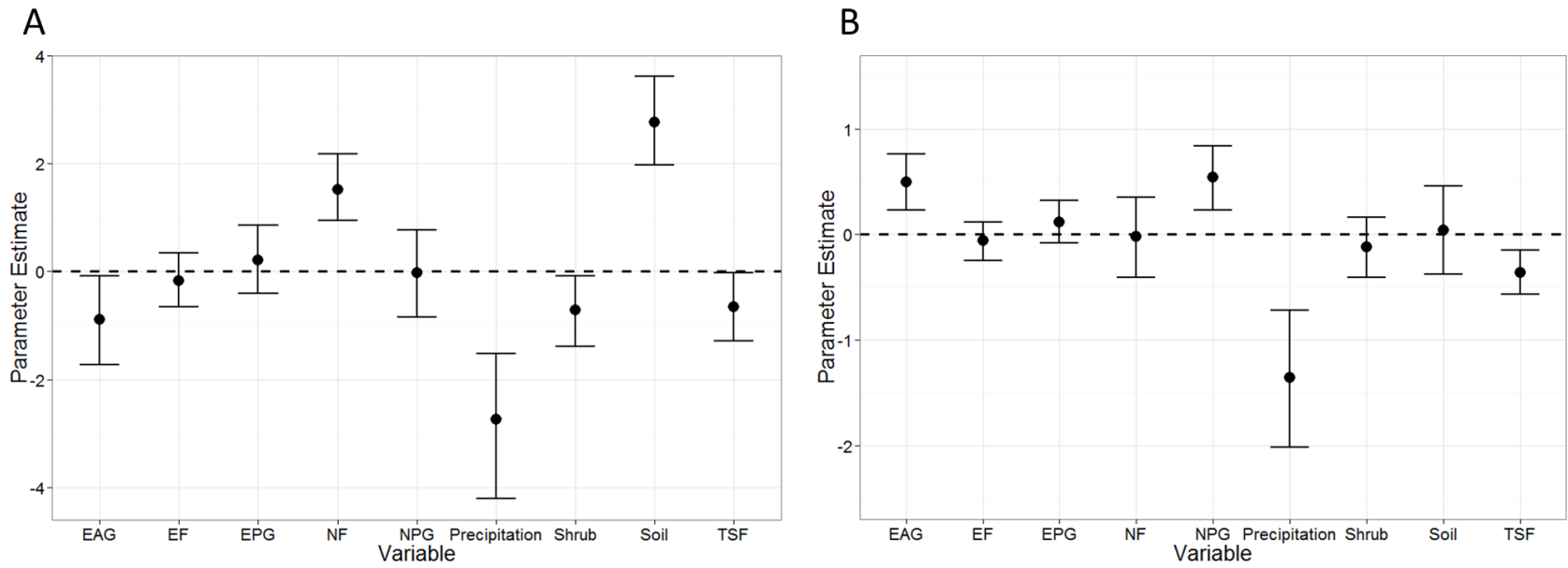


Figure 3.6. Standardized parameter estimates ($\pm 90\%$ CIs) from our A) occupancy model and B) density model that described the effect of covariates (x-axis) on harvester ants (*Pogonomyrmex* spp.). Data were collected from sites throughout southern Oregon and Idaho, USA. See Table 3.1 for variable descriptions.

***Chapter 4: A social-ecological impact assessment for public land
management: application of a conceptual and methodological framework***

Submitted to Ecology and Society

Co-authors: Amanda L. Bentley Brymer, Ryan J. Niemeyer, Alex A. Suazo, J.D. Wulfhorst, Kerri T. Vierling, Beth A. Newingham, Timothy E. Link, and Janet L. Rachlow

Abstract

According to the U.S. National Environmental Policy Act of 1969 (NEPA), federal action to manipulate habitat for species conservation requires an environmental impact statement (EIS), which should integrate natural and social sciences in planning and decision-making. Nonetheless, most impact assessments focus disproportionately on ecological impacts rather than an integration of ecological and socio-economic components. We developed a participatory social-ecological impact assessment (SEIA) that addresses the requirements of NEPA and integrates social and ecological concepts for impact assessments. We cooperated with the Bureau of Land Management in Idaho (USA) on a project designed to restore habitat for the Greater sage-grouse (*Centrocercus urophasianus*), which is a candidate species for listing under the Endangered Species Act. We employed questionnaires, workshop dialogue, and participatory mapping exercises with stakeholders to identify potential environmental changes and subsequent impacts expected to result from the removal of western juniper (*Juniperus occidentalis*). Via questionnaires and dialogue, stakeholders identified 46 environmental changes and associated positive or negative impacts to people and communities in Owyhee County. Results of the participatory mapping exercises showed that the spatial distribution of social, economic, and ecological values throughout Owyhee County

are highly associated with the two main watersheds, wilderness areas, and the historic town of Silver City, Idaho. Our SEIA framework also highlighted that perceptions of spatial and temporal scale varied among participants, emphasizing that specificity in scales is needed when discussing proposed projects. Overall, our SEIA framework generated substantial information concerning spatial and temporal impacts associated with habitat treatments for greater sage-grouse. Our SEIA is transferable to other conservation contexts, and by applying our framework land managers will better satisfy the requirements of NEPA as well as develop a more effective management plan to achieve their conservation goals.

Introduction

When federal actions aimed at species conservation are anticipated to cause significant impacts to the environment, land and resource managers in the U.S. are required by the National Environmental Policy Act of 1969 (NEPA) to assess potential impacts, develop mitigation strategies, and report their findings in an environmental impact statement (EIS). NEPA stipulates an interdisciplinary approach so that the entire environment is included in planning and decision-making (CEQ 2007). Even so, a typical EIS tends to comprise more ecological than social impacts; integrated assessments that include primary social science data are uncommon (see Burdge 2002; Whitfield et al. 2011).

A social impact is defined as a physical or cognitive effect experienced by humans and their communities and caused by a change in the social or ecological environment (Vanclay 2002). Traditionally, secondary sources such as Census data were analyzed to identify potential social impacts (Becker 1997), but secondary data can be inappropriate when sources are outdated or lack information on specific community needs or cultural issues (Esteves et al. 2012). Consequently, typical social impact assessments (SIA) often lack current, primary data

(Lockie 2001) and rarely invite stakeholders to actively engage in planning or assessment processes (Vanclay & Esteves 2011). The deficiency in SIA for fulfilling the NEPA requirements not only contradicts NEPA's objectives, but also limits the efficacy of management plans to achieve conservation goals.

Effective SIA facilitates the evaluation and management of social issues associated with planned interventions (e.g., management or land use change) and are participatory, supportive of populations affected by interventions, and increase the populations' capacity to respond to change (Vanclay 2003; Esteves et al. 2012). However, Esteves et al. (2012) identified a set of issues that persist in SIA, including inadequate public participation and analyses that do not identify spatial or temporal distributions of impacts. Research has demonstrated that dialogue-based approaches to SIA such as interactive community forums and participatory modeling can help to overcome these limitations by providing a more comprehensive and deeper understanding of social values, sense of place, and perceived impacts (Becker et al. 2003; Harris et al. 2012; Whitfield & Reed 2012). Rather than predicting impacts from secondary data sources, an emerging paradigm of SIA seeks a community-based process that empowers affected people with 1) improved understanding of a project, and 2) increased capacity to negotiate outcomes with the project managers or developers (Vanclay & Esteves 2011).

Reconciling the shifting SIA paradigm and the requirements for NEPA processes highlights the need for novel methodological approaches that can capture social dynamics like political tensions among different interest groups, as well as diverse perspectives on changing ecological conditions. The development of such approaches should assist public land managers in developing socially and ecologically comprehensive management plans that aid

in decision-making and ultimately help achieve conservation goals. Our research objective was to develop a social-ecological impact assessment (SEIA) framework and that addresses the requirements of NEPA and embodies the emerging SIA paradigm calling for more participatory, dialogue-based approaches. Our conceptual framework builds on previous work (i.e., Sloomweg et al. 2001; de Groot et al. 2002, 2010; Vanclay 2002) by merging ecosystem service concepts with social process concepts to better represent the interdependent relationships between humans and ecosystems. The methodological approach directly engages diverse stakeholders and builds on previous work (i.e., Becker et al. 2003; Gunderson & Watson 2007; Harris et al. 2012; Lowery & Morse 2013; Whitfield & Reed 2012) by deliberating project alternatives to identify stakeholders' perceptions of potential impacts, and by adding a spatial dimension with participatory mapping to include values across the landscape and project area.

We apply our SEIA framework to a high-profile conservation context in the western U.S., greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) habitat restoration. As of January 2015, the Bureau of Land Management (BLM) has been developing a draft EIS focused on improving habitat for sage-grouse by removing conifer trees. Sage-grouse are a sagebrush ecosystem obligate currently being considered for listing under the Endangered Species Act (USFWS 2010) due to >50% habitat loss since the mid-1800s (Knick et al. 2003). We embedded our integrated SEIA into the BLM's active NEPA process, illustrating the potential of this approach for other EIS processes aimed at species conservation on public lands.

Proposed Action: Sage-Grouse Habitat Restoration

The proposed study region for the treatments of sage-grouse habitat was in Owyhee County in southwestern Idaho, USA (Figure 4.1). Owyhee County is comprised of 76% public land (managed mostly by BLM), 2,092 km² (11%) of which is designated wilderness (Owyhee Initiative 2012). Agriculture comprises 26.1% of total employment in Owyhee County with two-thirds of that sector engaged in ranching (University of Idaho Extension 2015). Most ranches are not economically viable with private land alone; these operations rely on permitted grazing on BLM allotments (Bartlett et al. 2002). Although the Owyhee region is vast and rural, it is in close proximity to the greater Boise metropolitan area (Mackun & Wilson 2011), from where many people travel for hunting, fishing, rafting, bird watching, hiking, and off-highway vehicle riding.

The habitat treatment plan proposed by the BLM was termed the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project, and the goal for the project is to improve or maintain sage-grouse breeding habitat (i.e., area surrounding leks) by removing junipers (*Juniperus* spp.) that are expanding. Conifers, including junipers and pinyon pines (*Pinus* spp.), are dominant trees in Great Basin woodlands that have expanded into sagebrush habitats (Tausch et al. 1981; Romme et al. 2009). Tree expansion can negatively affect sage-grouse breeding habitat (e.g., Baruch-Mordo et al. 2013), which has prompted management actions to remove conifers.

The BOSH project proposes to remove low-density western juniper (*Juniperus* spp.) stands that are within 10 km of 63 active sage-grouse leks within Owyhee County (Figure 4.1). The BLM and Idaho Department of Fish and Game (IDFG) define active leks as those that have been visited by at least two male sage-grouse in at least one of the last five years. The BLM chose the 10 km buffer because approximately 80% of hens nest within 10 km of

their lek. The proposed project boundary covered 708,200 ha (1.75 million acres) of southwestern Idaho and included 93,078 ha (230,000 acres) of wilderness. Proposed treatments included cut and scatter, mastication, and jackpot burning. Cut and scatter involves cutting down trees and scattering the branches, while mastication uses heavy machinery that shreds the above ground tree biomass and spreads the mulch (Cline et al. 2010). Jackpot burning also employs heavy machinery to stack cut trees and burn the piles when fire risk is low (Huffman et al. 2009). In accordance with NEPA, the BLM developed treatment alternatives that included: 1) no action: no juniper removal, 2) full-suite: cut and scatter, mastication, and jackpot burning where deemed necessary and appropriate, and 3) cut and scatter: cut and scatter where deemed necessary and appropriate.

SEIA Development

Conceptual Framework

To build the SEIA framework, we merged previously developed conceptual frameworks that emphasize the connection between humans and ecosystems. First, we applied concepts from the de Groot et al. (2002, 2010) ecosystem services framework that provides a standardized typology for describing and classifying ecosystem functions, goods, and services: 1) provisioning, 2) processing, 3) supporting, and 4) cultural. Second, we used Vanclay's (2002) conceptualization of social processes to integrate economics, governance, and empowerment concepts with ecosystem services concepts. The combination of these concepts provides a more comprehensive framework for assessing potential social-ecological changes and impacts in complex systems. These aforementioned concepts have been defined and discussed in community development contexts, but have rarely been integrated in a regulatory context on U.S. public lands.

We adapted a flow diagram from Slootweg et al. (2001) to serve as a guide for the identification and description of cause and effect pathways and to aid in the articulation of potential impacts to people and communities. For example, removal of juniper (*Juniperus* spp.) trees from a landscape exemplifies an intervention that causes social-ecological change (Figure 4.2). A stakeholder might perceive that a reduction in juniper cover will lead to improved sagebrush habitat for sagebrush obligate species, and for people who appreciate sagebrush obligates, an improvement in obligate species habitat might lead to a positive perception of juniper removal (Figure 4.2). Examples illustrating two additional pathways are provided and described in the flow diagram (Figure 4.2).

Methodological Approach

The SEIA approach also merges a deliberative workshop setting and participatory mapping activities to better understand differing perspectives among people who live and work in the Owyhee region and to identify spatial dimensions of their values. Public participation GIS (PPGIS) is a method to spatially represent public knowledge, sense of place, or values by including members of the public in the mapping process (Talen 2000; Brown 2005). we merged participatory, qualitative approaches to SIA (Becker et al. 2003; Harris et al. 2012) and PPGIS methods (Gunderson & Watson 2007; Lowery & Morse 2013) because 1) there is a need and legal mandate to involve the public in planning processes (Brown & Weber 2011; Brown & Donovan 2013), and 2) human-ecosystem interactions and planning are inherently geospatial. These methods have rarely been applied together to understand potential impacts as required by NEPA on U.S. public lands.

We implemented two workshops to foster discussion about the alternatives drafted by the BLM, general stakeholder values, and benefits stakeholders receive from the ecosystem

(i.e. the Owyhee region). In the first workshop, we structured questionnaires and dialogue directly around the conceptual framework and flow diagram. Using a workshop protocol similarly structured to interactive community forum formats (Becker et al. 2003), participants were prompted to deliberate the proposed juniper treatment alternatives, how each alternative might cause changes to ecosystem services, (e.g., provisioning, processing, supporting, and cultural services), and/or changes to social processes (e.g., economic, institutional and legal, or empowerment processes), and how those changes might positively or negatively impact people and communities. In the second workshop, we asked participants to spatially draw values associated with social, economic, or ecological characteristics or processes fundamental to their relationships to the ecosystem.

Methods

The sampling frame included local, state, and federal resource managers, as well as organizations involved in a long-term collaborative effort in the Owyhee region (i.e., The Owyhee Initiative), which served as a clearinghouse of parties interested in resource management in the Owyhee region. Prior to our agreement with the BLM, a stakeholder group comprising managers from the BLM and Idaho Fish and Game, restoration conservationists from non-governmental organizations, and representative from the Owyhee County Sage-grouse Local Working Group had already been formed by the project lead (Group 1). To broaden the range of perspectives for the SEIA, we purposively sampled 27 stakeholder groups whose members are concerned with ecosystem functions in the Owyhee region to create an additional workshop group (Group 2). Group 1 and Group 2 separately participated in a two-workshop series. Each workshop spanned an average of 5 hours. We

followed ethical guidelines for working with human subjects, and the University of Idaho Institutional Review Board approved our project #12-357 (Appendix F).

Deliberative Workshops

The first workshop began with an overview presentation of the BOSH project and four rounds of questionnaires with subsequent deliberation (Appendix D: Table D1). The first round assessed participants' baseline perceptions of the current structure and function capabilities of the Owyhee region in terms of ecosystem services and social processes, while the subsequent three rounds of questions revealed stakeholders' perceptions of future structure and function of the Owyhee region under the three BOSH project alternatives.

Quantitative and qualitative analytical approaches were employed. Questionnaires included seven questions related to ecosystem services and social processes. All four questionnaires were identical, but while completing the four questionnaires participants were asked to consider the structure and function in the present state (i.e. baseline) and in the future under the three project alternatives. For the present state and future conditions under each management alternative, participants rated items from 0 – “as bad as it can be” – to 10 – “as good as it can be.” To compare the perceived benefits or costs of juniper treatment, we normalized each participant's ratings by subtracting their “baseline” rating from the three alternative ratings. The last question related to the level of acceptability for each treatment in wilderness areas, which was different than the other questions because there was no baseline condition and the scale was from 0 – “extremely unacceptable” to 5 – “extremely acceptable.” Thus, we analyzed the wilderness question separately. Data were analyzed with R statistical software (R Core Team, 2014).

Workshop dialogue was recorded and transcribed for analysis in NVivo 10 (QSR International Pty Ltd. Version 10, 2012). First, the integrated social-ecological conceptual framework was used to categorize participant responses into statements about particular ecosystem services and social processes. Second, a grounded theory approach was used to review the transcriptions and allow descriptions of potential impacts to emerge from participants' deliberations. For a social-ecological impact to be included in the analysis, it had to 1) be explicitly stated, and 2) include the direction of effect (e.g., positive/better, negative/worse, no change).

PPGIS Workshop

We implemented a qualitative approach to PPGIS (e.g., Brown & Pullar 2012, Lowery & Morse 2013). We presented participants with laminated 61 × 91 cm aerial photographs (USDA, National Agriculture Imagery Program 2011) at a scale between 1:400,000 and 1:500,000. We asked each individual to map areas throughout Owyhee County that they perceived as valuable for social, economic, and ecological reasons. Next, we presented a separate set of maps that displayed the BOSH project boundary and asked participants to identify areas where they did not want the project executed and to explain why. We then took photographs of each map to create a county value map by digitizing polygons within ArcGIS 10.1 (ESRI 2012). Each polygon had attributes indicating the group and participant number and whether it was based on social, economic, or ecological justification. We analyzed overlapping polygons in ArcGIS (Honeycutt 2013) across a 30 m² grid overlaid on Owyhee County and the BOSH boundary.

Results

The sample consisted of 20 participants in total; 16 participated in the deliberative workshops and ten also participated in the PPGIS workshops. Everyone who participated in a workshop also completed the four questionnaires. Four participants completed questionnaires but were unable to participate in the workshops. As self-described, participants represented diverse user groups including conservationists (6), wildlife biologists (4), livestock ranch land owners (2), restoration coordinator (1), archaeologist (1), natural resource manager (1), land management supervisor (1), retired fire fighter (1), cartography technician (1), self-employed individual (1), and one individual who did not self-identify an occupation.

Questionnaire Results

The average observed range of responses for all four questionnaires was 81.6% (Figure 4.3), indicating that the sample of participants revealed a broad range of perspectives. On average, participants' ratings for future social-ecological conditions in the Owyhee region under the no action alternative were 1.4 points (SD = 1.9) lower than their baseline ratings. This suggests most workshop participants perceived that if there were no action to remove juniper trees, future social-ecological conditions in the Owyhee region would deteriorate. Participant ratings for the full-suite and cut and scatter alternatives were on average 1.4 points (SD = 2.8) and 0.3 points (SD = 2.3) higher than their baseline ratings, respectively. This suggests many workshop participants perceived that implementation of either treatment alternative will improve future social-ecological conditions, but for some participants the full-suite alternative will lead to a higher degree of improvement, bringing the Owyhees closer to "as good as it can be." Some social conditions (e.g., economic, institutional and legal, and empowerment processes) were rated higher in a future with either the full-suite or cut and

scatter alternative by almost all participants (Figure 4.4e, 4.4f, and 4.4g), in contrast to some ecological conditions (e.g., supporting service: open space, cultural service: opportunities for spiritual enrichment and recreation), which were rated inconsistently across participants (Figure 4.4c and 4.4d). On the acceptability of juniper removal within wilderness, participants' responses displayed substantial variation indicating little consensus.

Deliberative Workshop Results

Workshop participants described 46 environmental changes and associated positive or negative impacts that they anticipate to result from the BOSH project alternatives (see Appendix E: Table E1, Table E2, and Table E3 for example quotations). Of the 18 changes to ecosystem services and social processes anticipated from the no action alternative, fifteen changes were perceived to lead to negative impacts and three changes were perceived to lead to positive impacts to people and their sense of well-being (Table 4.1). For example, if there is no action to remove juniper from the landscape, people anticipated experiencing negative impacts due to reduction of watershed functionality, loss of biodiversity and habitat (particularly sage-grouse habitat), diminished spiritual experience, less opportunity in the local economy, and less opportunity for stakeholder collaboration. Positive impacts were expected to derive from the availability of areas without juniper removal for control group studies and from the improvement of overall enjoyment of the Owyhee region. The most striking split in opinion among participants related to perceived impacts that no action will have on their overall enjoyment of the Owyhee region. Some participants enjoy the Owyhee region when they know it is managed and junipers are removed – particularly due to the belief that reduced juniper cover improves sage-grouse habitat. Other participants emphasized that junipers are native and that we are managing too much. For them, the knowledge that nothing

is being done to remove juniper is comforting and improves their overall enjoyment of the Owyhees.

We found participants' perceptions of potential social-ecological changes and subsequent impacts from the full-suite and cut and scatter alternatives to be mostly similar, though a few key differences stood out. Workshop participants described five similar environmental changes that they perceived could be caused by both alternatives leading to negative impacts: increased fire danger, degraded wildlife habitat, diminished viewsheds, and worsened agency reputation and diminished management effectiveness, primarily for the BLM. Workshop participants described three similar environmental changes that they perceived could be caused by both alternatives leading to positive impacts: improved watershed functionality, improved wildlife habitat, and more opportunity in the local economy. For the full suite, some participants anticipated additional positive impacts, some of which included improved management, viewsheds, general enjoyment of the Owyhee region, and the maintenance of culture tied to cowboys and sage-grouse.

Contrary to those who anticipated both alternatives to cause certain social and ecological changes, other participants described that in a future under the full suite alternative, there would be no change in some stakeholders' ability to make a living, no change in management, and no change in viewshed or spiritual experience. The split in opinion about anticipated environmental changes was based on participants' varying perceptions of project scale and juniper removal tools. For example, some participants expressed concern that mastication would be applied across the entire project area, while others understood that mastication was proposed for roadsides only.

PPGIS Workshop Results

The PPGIS workshop comprised mapping activities based on two key questions: 1) “What areas across Owyhee County are important to you for social, economic, and/or ecological reasons?”, and 2) “Within the BOSH Project boundary, where do you not want juniper removed?” Results from the first mapping activity (“county values map,” hereafter) show that the overall distribution of perceived values (social, economic, and ecological combined) throughout the Owyhee region is highly associated with the two main watersheds (Owyhee and Bruneau-Jarbridge), wilderness areas (e.g., Owyhee River and near Juniper Mountain), and the town of Silver City, Idaho (Figure 4.5). Silver City is a historic mining town with a deep history and many cultural traditions. The Owyhee and Bruneau-Jarbridge watersheds are within significant portions of the Owyhee River and Bruneau-Jarbridge wilderness areas (see point 1 and 2 in Figure 4.5a).

When we separated social, economic, and ecological values into three county value maps, the social (Figure 4.5b) and ecological (Figure 4.5d) values displayed similar patterns. However, we found more polygons per participant for ecological than social values. The polygons characterizing economic values were quite different than social and ecological values, and there were fewer polygons per participant for economic values (Figure 4.5c). Economic values were mapped in a general sense (i.e., perhaps less precise) relative to the other values and were mostly associated with farming and summer grazing areas.

Justifications for the location of social, economic, and ecological polygons were diverse. Social polygons were generally drawn around areas that participants value for the ranching or cowboy culture and tradition, and watershed- or wildlife-based recreation. Economic polygons were mapped to highlight the value of the ranching and farming industry, as well as tourism and the military. Ecological polygons were drawn across areas that

stakeholders find valuable for resource connectivity, wildlife and fisheries habitat, and biodiversity.

The second mapping activity (“no treatment map,” hereafter) served as a social setting filter, much like the ecological filter that narrows the scope of issues related to an intervention (Slootweg et al. 2001). The majority of participants indicated that the BOSH project will be positive and therefore did not draw any polygons; these participants support juniper removal over the entire project area. Some suggested no treatment around Riddle, Idaho, because this area would be a lesser priority due to essentially no juniper present. Others identified areas near Juniper Mountain, Idaho, because they are culturally valuable to Native Americans. Finally, some participants indicated they are against executing the BOSH project entirely because they questioned the BLM’s ability to complete the project goals without unintended consequences (e.g., spreading invasive species and half-finished projects).

Discussion

We combined a conceptual framework and multi-method process that upholds the requirements of NEPA to generate a more intricate understanding of social-ecological impacts associated with habitat conservation plans. In the context of our project, the general discussion of perceived impacts from juniper removal alternatives were difficult to understand without incorporating spatial data. Incorporating the spatial dimension of stakeholders’ environmental values via mapping allowed land managers to understand where stakeholders’ interests and concerns were located within the Owyhee region. This information can be useful for identifying and prioritizing the most relevant issues to address with mitigation strategies. In our case, potential impacts associated with watersheds, wilderness, and historic towns were the top priorities for the BLM to address with mitigation. Mapping data can also serve project

managers as a decision-making tool concerning where to stage juniper removal phases since the 1.75 million acre project area will not be treated simultaneously. Moreover, by coupling dialogue data and spatial mapping we were able to identify the relative scope of potential impacts associated with stakeholders' values. For instance, our data suggest that the scope of impacts is narrower within the BOSH project boundary compared to the scope of potential impacts at the county level. Collectively, these data provide BLM managers with a better understanding of how proposed land actions influence social perceptions, which will allow for the development of a more holistic environmental impact statement for sage-grouse conservation.

Our SEIA process also advanced some of the major shortcomings of conventional EISs, including the lack of social-ecological integration. Rather than consider characteristics of the social system separate from the ecological system, we merged ecosystem service concepts and social process concepts to achieve an integrated framework that represents the complexity of interdependent social-ecological systems. The SEIA conceptual framework was intuitive to the study participants, and most agreed that it was a useful tool for articulating ways that juniper removal alternatives could impact their lives. The range of topics covered in the workshops demonstrated the importance of a social-ecological framework for public lands where individual and community well-being depend upon the environment. Most EIS to date are relatively devoid of social impacts, much less integrated with ecological and/or biophysical concepts in public land management contexts (Slootweg et al. 2001; Burdge 2002; Whitfield et al. 2011). Given that NEPA requires an interdisciplinary approach for the preparation of EISs (42 U.S.C. § 4331), the lack of social impacts puts current practice into question.

In addition to improving social-ecological integration, there is a need to add a spatial dimension to environmental assessments – specifically, the identification of areas that are socially, economically and ecologically valuable. Values are the fundamental building blocks of perceptions about how one might be impacted by a management intervention and environmental change, and visualizing this information on a map is helpful because public land management is done in a spatial context (Lowery & Morse 2013). During PPGIS activities, we observed workshop participants discussing areas of value and finding common ground around rivers and wilderness areas. Participatory mapping also allowed for clarification of misconceptions about the project, identification of unnecessary project boundaries, and deliberation of areas to prioritize or disregard for juniper removal. These observations are consistent with previous research on qualitative approaches to PPGIS that reported benefits, such as positive synergy among participants and clarified perceptions of project scale (Lowery & Morse 2013).

The PPGIS activities coupled with deliberative workshops also addressed the need to improve stakeholders' role in impact assessment processes. Deliberations of potential impacts revealed a key point: addressing multiple spatial and temporal scales throughout a project can clarify project purpose and inform a more comprehensive design of mitigation strategies. The benefits of these workshops are consistent with previous research that observed improved opportunities for community members to share their perceptions about proposed actions and potential futures in a deliberative setting (Becker et al. 2003; Harris et al. 2012). Typical scoping processes, during which stakeholders write or call the planning agency with their concerns, normally do not identify such nuances. A deliberative approach to SEIA can enhance scoping in a NEPA process by providing an opportunity for stakeholders to elaborate

their concerns or support for a project, as well as to identify a comprehensive list of issues to address with mitigation strategies.

The novelty and strength of this approach is the application of a social-ecological conceptual framework within a deliberative setting that includes questionnaires, dialogue, and PPGIS. By merging the integrated conceptual framework and methodological approach, the SEIA process enabled triangulation of multi-scale social-ecological impacts associated with the proposed BOSH project. In addition, discrepancies in perceptions of the scale of the project emerged from the dialogue in the deliberative setting. For example, when anticipating changes to a viewshed as a result of juniper removal, participants described different perceptions of trail-level, ridge-line, horizon and aerial views. While an agency may frame a proposed project in one scale, we observed stakeholders framing potential impacts of the BOSH project in several scales, which fostered some ongoing confusion and is indicative of how even interested publics may misgauge project goals and objectives. Precisely characterizing scale is a recognized issue in the field of ecology (e.g., Levin 1992), but our data suggest the same level of precision is needed when discussing social-ecological impacts associated with land management actions.

Our SEIA is not designed to replace a traditional ecological impact assessment for which ecological and biophysical monitoring data are analyzed, nor do we intend for SEIA to replace traditional economic impact assessments. Rather, SEIA is meant to complement other assessments by defining the connections between people and their environment and highlighting how those connections might be weakened or strengthened by land management decisions. we support the notion that impact assessments are context-dependent (Vanclay 2002), and we recommend a modification of social-ecological concepts in the framework

and/or the tools for data collection depending on environmental characteristics, politics, and power dynamics specific to the project area (Ross & McGee 2006). Continued applications of integrated frameworks such as SEIA within public land management would better satisfy NEPA requirements and facilitate more holistic mitigation strategies, both of which should assist managers achieve conservation goals. The advancement of conservation efforts relies in part on our ability to comprehensively assess social and ecological consequences of human interventions on public lands (e.g., sensu Brashares et al. 2014). The SEIA process we described contributes to this broader conservation goal.

References

- Baruch-Mordo S, Evans J, Severson J, Naugle D, Maestas J, Kiesecker J, Falkowski M, Hagen C, Reese K. 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biological Conservation* **167**:233-241.
- Bartlett ET, Torell LA, Rimbey NR, Van Tassell LW, McCollum DW. 2002. Valuing grazing use on public land. *Journal of Range Management* **55**:426-438.
- Becker DR, Harris CC, McLaughlin WJ, Nielsen EA. 2003. A participatory approach to social impact assessment: the interactive community forum. *Environmental Impact Assessment Review* **23**:367–382.
- Becker H. 1997. *Social Impact Assessment: Method And Experience In Europe, North America And The Developing World*. UCL Presse Limited, London, United Kingdom.
- Brashares, JS, Abrahms B, Fiorella KJ, Golden CD, Hojnowski CE, Marsh RA, McCauley DJ, Nunez TA, Seto K, Withey L. 2014. Wildlife decline and social conflict. *Science* **345**:376-378.
- Brown G. 2005. Mapping spatial attributes in survey research for natural resource management: methods and applications. *Society and Natural Resources* **18**:17-39.
- Brown G, Pullar D. 2012. An evaluation of the use of points versus polygons in public participation geographic information systems using quasi-experimental design and Monte Carlo simulation. *International Journal of Geographical Information Science* **26**:231-246.
- Brown G, Weber D. 2011. Public participation GIS: a new method for national park planning. *Landscape and Urban Planning* **102**:1-15.

- Brown G, Donovan S. 2013. Escaping the national forest planning quagmire: using public participation GIS to assess acceptable national forest use. *Journal of Forestry* **111**:115-125.
- Burdge RJ. 2002. Why is social impact assessment the orphan of the assessment process? *Impact Assessment and Project Appraisal* **20**:3-9.
- Cline NL, Roundy BA, Pierson FB, Kormos P, Williams CJ. 2010. Hydrologic Response to Mechanical Shredding in a Juniper Woodland. *Rangeland Ecology and Management* **63**:467-477.
- Council on Environmental Quality. 2007. A citizen's guide to the NEPA: having your voice heard. Available from https://ceq.doe.gov/publications/citizens_guide_to_nepa.html (Accessed 16 July 2015).
- de Groot RS, Wilson MA, Boumans RM. 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* **41**:393-408.
- de Groot RS, Alkemade R, Braat L, Hein L, Willemen L. 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecological Complexity* **7**:260-272.
- Esteves A, Franks D, Vanclay F. 2012. Social impact assessment: the state of the art. *Impact Assessment and Project Appraisal* **30**:34-42.
- ESRI. 2012. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, California.
- Gunderson K, Watson A. 2007. Understanding place meanings on the Bitterroot National Forest, Montana. *Society and Natural Resources* **20**:705-721.

- Harris CC, Nielsen EA, Becker DR, Blahna DJ, McLaughlin WJ. 2012. Results of community deliberation about social impacts of ecological restoration: comparing public input of self-selected versus actively engaged community members. *Environmental Management* **50**:191-203.
- Honeycutt D. 2013. Count overlapping polygons. Environmental Systems Research Institute, Redlands, California. Available from <http://www.arcgis.com/home/item.html?id=1dd4a6832b3d40b494dbf8521cc5134c> (accessed August 2014).
- Huffman DW, Fule PZ, Crouse JE, Pearson KM. 2009. A comparison of fire hazard mitigation alternatives in pinyon–juniper woodlands of Arizona. *Forest Ecology and Management* **257**:628-635.
- Knick ST, Dobkin DS, Rotenberry JT, Schroeder MA, Vander Haegen WM, and van Riper III C. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *The Condor* **105**:611-634.
- Levin SA. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73**:1943-1967.
- Lockie S. 2001. SIA in review: setting the agenda for impact assessment in the 21st century. *Impact Assessment and Project Appraisal* **19**:277-287.
- Lowery D, Morse W. 2013. A qualitative method for collecting spatial data on important places for recreation, livelihoods, and ecological meanings: integrating focus groups with public participation geographic information systems. *Society and Natural Resources* **26**:1422-1437.

- Mackun PJ, Wilson S. 2011. Population distribution and change: 2000 to 2010. United States Department of Commerce, Economics and Statistics Administration, Washington District of Columbia, United States of America.
- National Environmental Policy Act. 1969. 42 U.S.C. § 4331 *et seq.*
- QSR International Pty Ltd . 2012. NVivo qualitative data analysis software, Version 10. Burlington, Massachusetts, USA.
- Owyhee Initiative. 2012. Available from owyheeinitiative.org (accessed April 2015).
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.
- Ross H, McGee TK. 2006. Conceptual frameworks for SIA revisited: a cumulative effects study on lead contamination and economic change. *Impact Assessment and Project Appraisal* **24**:139-149.
- Romme WH, Allen CD, Bailey JD, Baker WL, Bestelmeyer BT, Brown PM, Eisenhart KS, Floyd ML, Huffman DW, Jacobs BF, et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in pinon-juniper vegetation of the western United States. *Rangeland Ecology and Management* **62**:203-222.
- Slootweg R, Vanclay F, van Schooten M. 2001. Function evaluation as a framework for the integration of social and environmental impact assessment. *Impact Assessment and Project Appraisal* **19**:19-28.
- Talen E. 2000. Bottom-up GIS: A new tool for individual and group expression in participatory planning. *Journal of the American Planning Association* **66**:279-294.
- Tausch RJ, West NE, and Nabi AA. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. *Journal of Range Management* **34**:259-264.

- University of Idaho Extension. Agriculture, Livestock and Range. Available from <http://extension.uidaho.edu/owyhee/2014/07/11/agriculture-livestock-and-range/> (accessed April 2015).
- US Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13910-14014.
- Vanclay F. 2002. Conceptualising social impacts. Environmental Impact Assessment Review **22**:183-211.
- Vanclay F. 2003. International principles for social impact assessment. Impact Assessment and Project Appraisal **21**:5-12.
- Vanclay F, Esteves AM. 2011. New directions in social impact assessment: conceptual and methodological advances. Edward Elgar Publishing, Cheltenham, United Kingdom.
- Whitfield S, Geist HJ, Ioris AA. 2011. Deliberative assessment in complex socioecological systems: recommendations for environmental assessment in drylands. Environmental Monitoring and Assessment **183**:465-483.
- Whitfield S, Reed M. 2012. Participatory environmental assessment in drylands: introducing a new approach. Journal of Arid Environments **77**:1-10.

Table 4.1. Perceived changes to social processes and ecological services, and the direction of subsequent impacts, concerning the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project in Owyhee County, USA.

Process/Service	Direction of Effect		
	Positive	Negative	No Change
Social			
Economic processes	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -More opportunity for local economy -Ability to make a living: improved</p> <p><i>Cut and Scatter:</i> -More opportunity for local economy</p>	<p><i>No Action:</i> -Less opportunity for local economy -Tension on livestock operators</p> <p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -Weakening of local livelihoods -Reduced range and grazing</p>	<p><i>No Action:</i> -Same opportunity for local economy</p> <p><i>Full Suite:</i> -No change in ability to make a living</p> <p><i>Cut and Scatter:</i> -None described</p>
Institutional and legal processes	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -Improved management</p> <p><i>Cut and Scatter:</i> -None described</p>	<p><i>No Action:</i> -Disheartening to land managers -Endangered listing of Greater sage-grouse</p> <p><i>Full Suite:</i> -Worse management -Worsened agency reputation</p> <p><i>Cut and Scatter:</i> -Diminished management effectiveness</p>	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -No change in management</p> <p><i>Cut and Scatter:</i> -None described</p>
Empowerment processes	<p><i>No Action:</i> -None described</p>	<p><i>No Action:</i> -Less opportunity for stakeholder collaboration</p>	<p><i>No Action:</i> -Same opportunity for stakeholder collaboration</p>

	<p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -None described</p>	<p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -None described</p>	<p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -No change in stakeholder decision-making</p>
Ecological			
Provisioning	<p><i>No Action:</i> -Impact to ecosystem</p> <p><i>Full Suite:</i> -Improved range and grazing</p> <p><i>Cut and Scatter:</i> -Improved ecosystem health and characteristics -Increased water availability</p>	<p><i>No Action:</i> -Decline of historic plant communities</p> <p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -None described</p>	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -None described</p>
Processing	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -Increased watershed functionality</p> <p><i>Cut and Scatter:</i> -Increased watershed functionality</p>	<p><i>No Action:</i> -More difficult to balance or restore landscape/ecological processes -Reduced functionality of watershed</p> <p><i>Full Suite:</i> -Increased fire danger</p> <p><i>Cut and Scatter:</i> -Increased fire danger</p>	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -None described</p> <p><i>Cut and Scatter:</i> -None described</p>
Supporting	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -Increased biodiversity -Improved wildlife habitat</p>	<p><i>No Action:</i> -Loss of biodiversity and habitat -Loss of sage-grouse habitat</p> <p><i>Full Suite:</i> -Degraded wildlife habitat</p>	<p><i>No Action:</i> -None described</p> <p><i>Full Suite:</i> -None described</p>

	<ul style="list-style-type: none"> -Improved sage-grouse habitat <p style="text-align: center;"><i>Cut and Scatter:</i></p> <ul style="list-style-type: none"> -Improved wildlife habitat 	<p style="text-align: center;"><i>Cut and Scatter:</i></p> <ul style="list-style-type: none"> -Degraded sage-grouse habitat -Increased cover for sage-grouse predators 	<p style="text-align: center;"><i>Cut and Scatter:</i></p> <ul style="list-style-type: none"> -None described
Cultural	<p style="text-align: center;"><i>No Action:</i></p> <ul style="list-style-type: none"> -Availability of areas without treatment for study -Improved general enjoyment of the Owyhees <p style="text-align: center;"><i>Full Suite:</i></p> <ul style="list-style-type: none"> -Improved general enjoyment of Owyhees -Improved hunting -Improved viewshed -Improved spiritual experience -Maintained culture tied to cowboy and sage-grouse <p style="text-align: center;"><i>Cut and Scatter:</i></p> <ul style="list-style-type: none"> -None described 	<p style="text-align: center;"><i>No Action:</i></p> <ul style="list-style-type: none"> -Loss of open space -Limits on recreation -Less aesthetic enjoyment -Diminished hunting -Diminished spiritual experience <p style="text-align: center;"><i>Full Suite:</i></p> <ul style="list-style-type: none"> -Recreation: disrupted -Degraded viewshed <p style="text-align: center;"><i>Cut and Scatter:</i></p> <ul style="list-style-type: none"> -Degraded viewshed 	<p style="text-align: center;"><i>No Action:</i></p> <ul style="list-style-type: none"> -No change for general enjoyment of the Owyhees -No change in spiritual experience <p style="text-align: center;"><i>Full Suite:</i></p> <ul style="list-style-type: none"> -No change in solitude -No change in recreation -No change in viewshed -No change in spiritual experience <p style="text-align: center;"><i>Cut and Scatter:</i></p> <ul style="list-style-type: none"> -No change in general enjoyment of the Owyhees

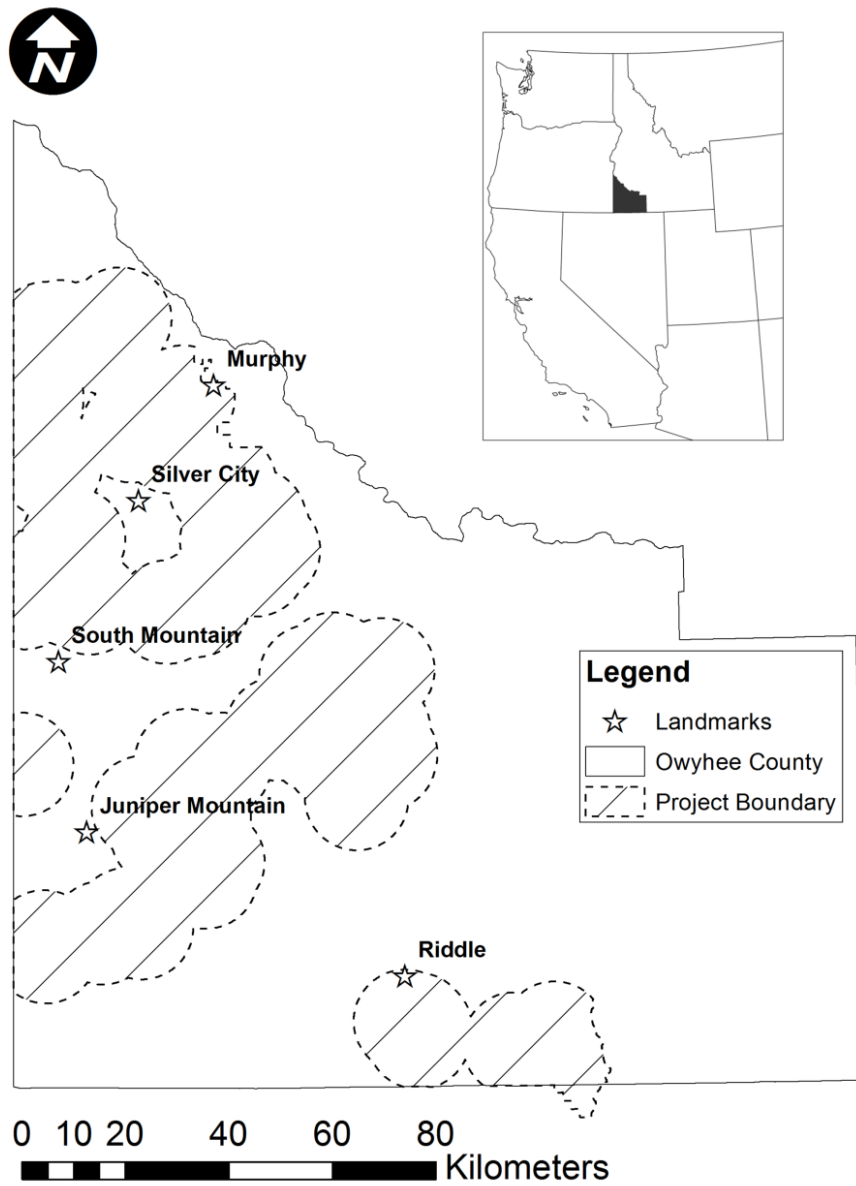


Figure 4.1. Inset map shows the western USA with Owyhee County, Idaho, in dark grey. Map of Owyhee County shows the proposed project boundary and five landmarks for the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project.

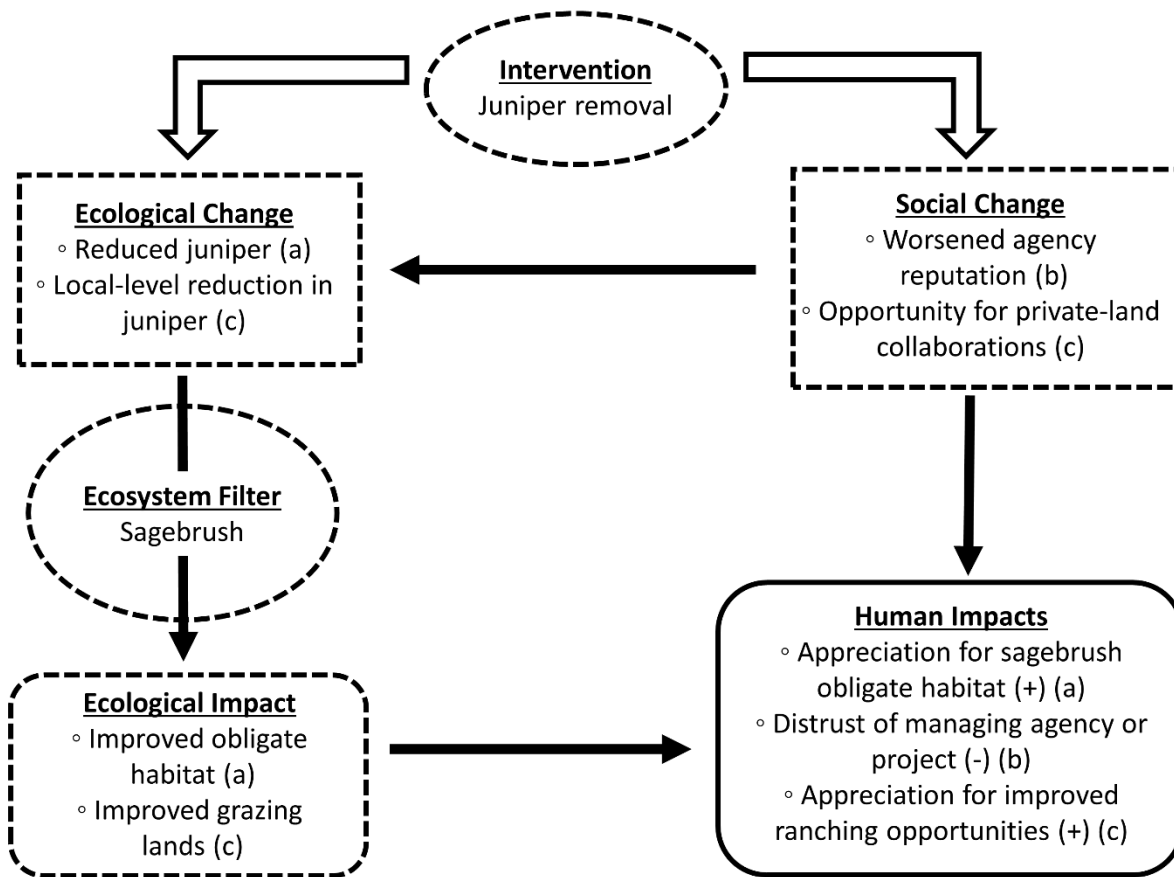


Figure 4.2. Flow diagram of the social-ecological impact assessment (SEIA) framework (modified from Slootweg et al. 2001). The diagram begins with an intervention (e.g., juniper removal), which ultimately generates social or ecological change through three pathways. (a) First, an ecological change might be a reduction in juniper. This change is filtered through an ecosystem (e.g., sagebrush) and results in an ecological impact such as improved habitat for sagebrush-obligate species. This ecological impact could then result in a positive (i.e., +) human impact in terms of appreciation of habitat for sagebrush obligates. (b) Second, an intervention might generate social change that degrades an agency's reputation, which directly generates a negative (i.e., -) human impact in terms of public distrust of the management agency. (c) Lastly, an intervention could produce social change in terms of generating opportunity for private-land collaborations. This collaboration could result in additional local-level juniper removal. This change is then filtered through the ecosystem and generates an ecological impact of improved grazing lands. The human impact via this last pathway is positive (i.e., +) in that it generated an appreciation for improved ranching opportunities. Human impacts are in solid lines and all other components are in dotted lines. All arrows represent pathways to human impacts.

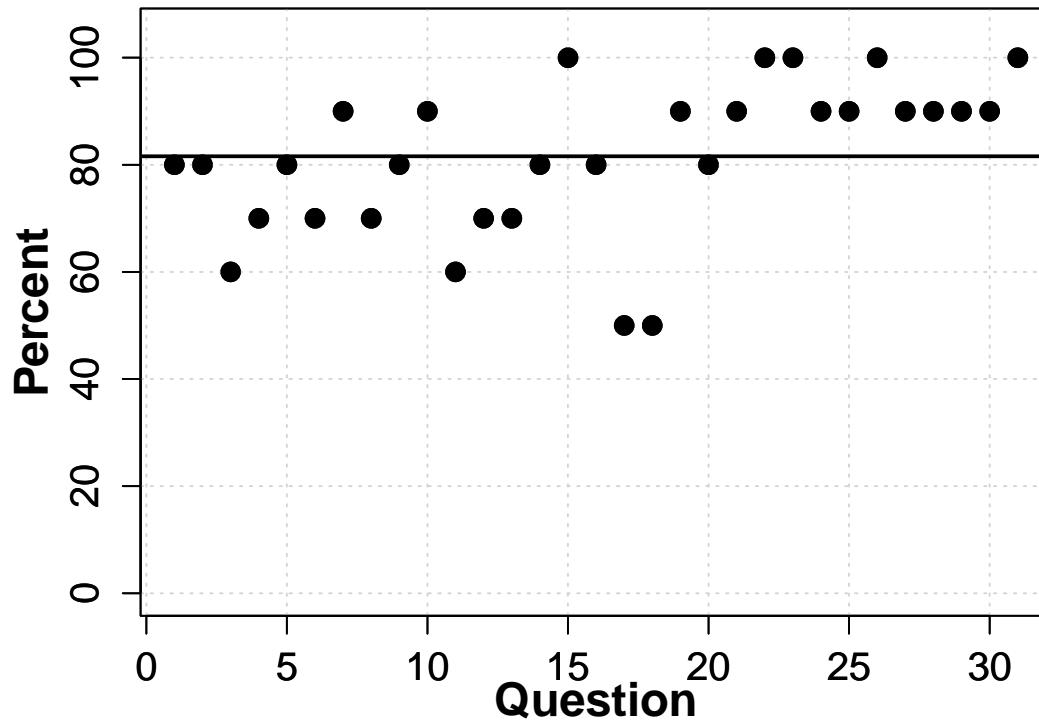


Figure 4.3. Percent of the total range observed for responses for each question. For example, for question 1 we observed a minimum score of one and a maximum score of eight, which translates to 80% range observed. Horizontal line is the average range observed across all questions.

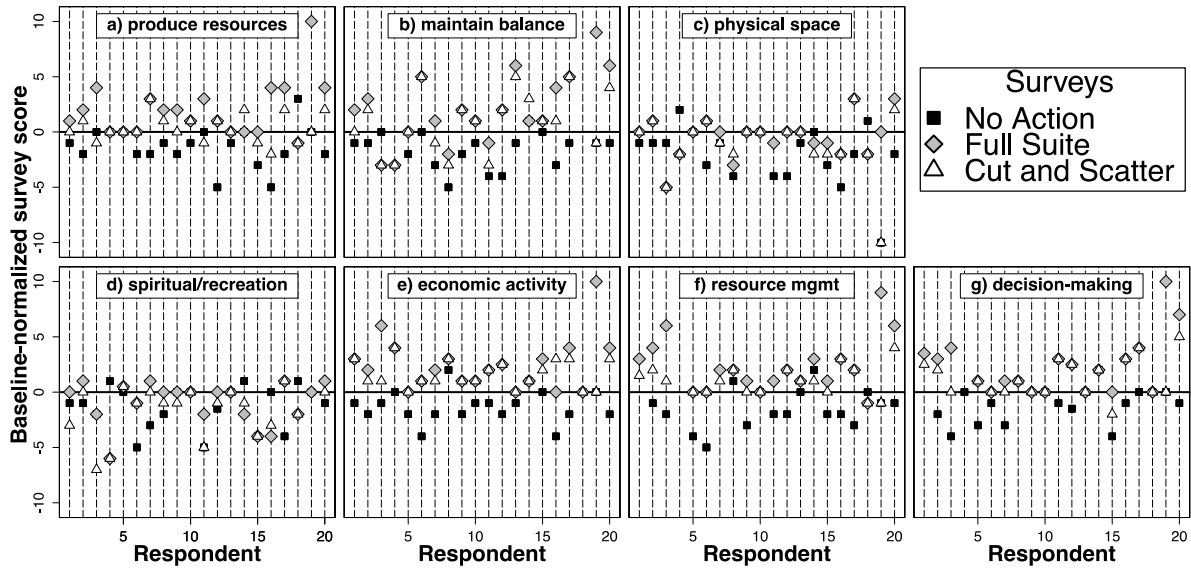


Figure 4.4. Participant responses to seven questions (Supporting Information: Table S4, except question #8) concerning the current state of Owyhee County (i.e., baseline) and the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project alternatives: no action, full suite, and cut and scatter. Displayed scored as baseline-normalized by subtracting the participant baseline score from his/her alternative score. Responses about alternatives were normalized to baseline scores (e.g. participant 1 baseline score is 7, full suite score is 8, and the baseline-normalized score is 1).

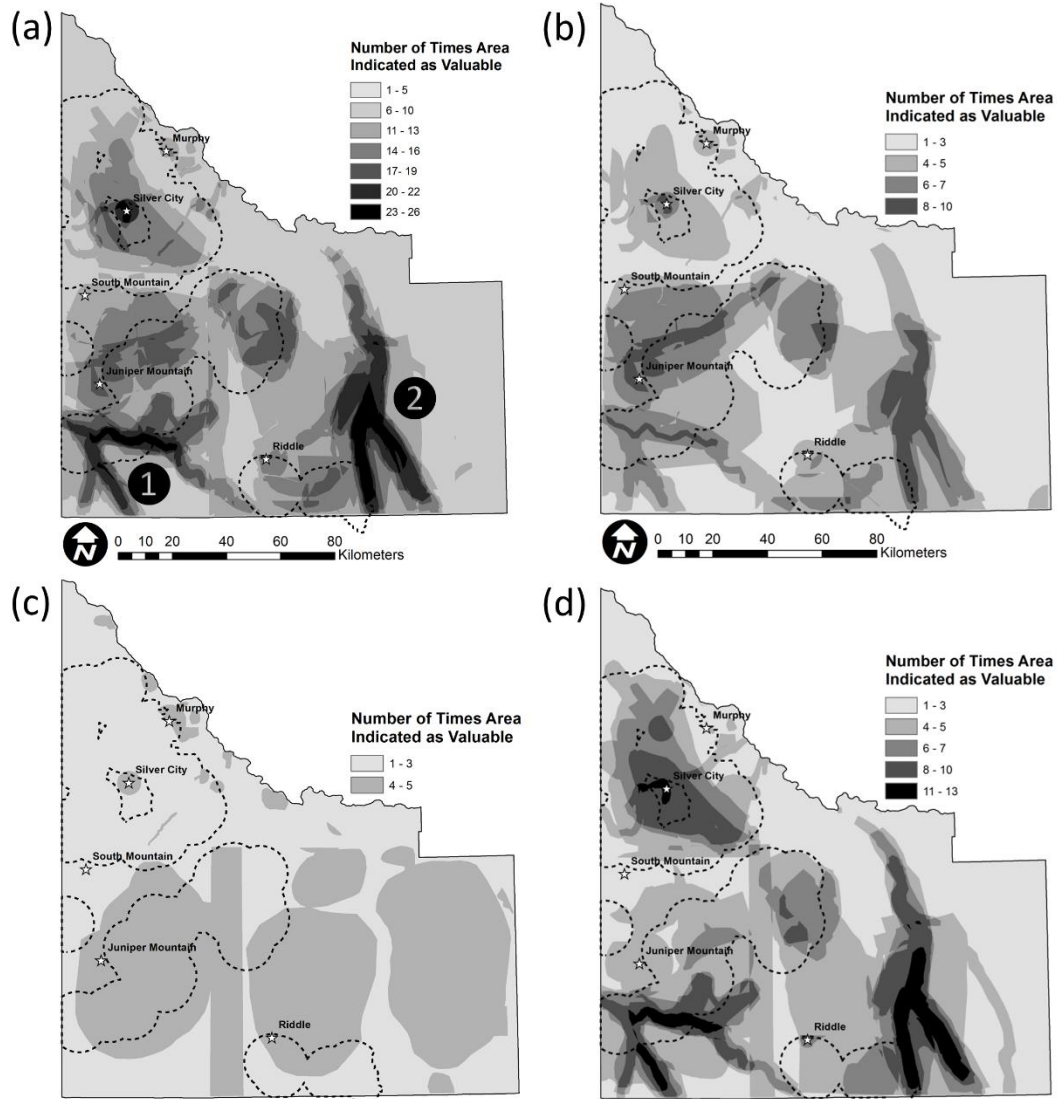


Figure 4.5. Frequency of the polygons derived for all values combined (a), social values (b), economic values (c), and ecological values (d) in Owyhee County, Idaho, USA. The proposed project boundary for the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project is indicated by the dotted lines. Point 1 and 2 in panel (a) indicate the Owyhee and Bruneau-Jarbidge watersheds and associated wilderness areas.

Dissertation Conclusion

The main objective of my dissertation was to assist management and conservation efforts in sagebrush ecosystems by 1) advancing the understanding of how landscape changes (such as fire and biological invasions) influence ecosystem engineers across trophic levels (Chapters 1, 2, and 3), and 2) developing a social-ecological framework to incorporate social dimensions of land management within the existing U.S. National Environmental Policy Act of 1969 procedures on federal lands (Chapter 4). I found that occupancy of an engineering granivore (i.e., harvester ants) was not influenced by biological invasions or fire, rather occupancy was positively driven by distribution of finer-textured soils and drier locales. Similarly, occupancy of a burrowing herbivore (i.e., Piute ground squirrels) was independent of fire and biological invasions, but positively associated with long-term precipitation, dispersal potential, and fine-textured soil. However, density of harvester ants was positively affected by exotic annual and native perennial grasses, as well as fire. Abundance of ground squirrels was positively associated with fine-textured soil, but negatively associated with cheatgrass, fire frequency, human disturbance, and shrub cover. Occupancy of a burrowing carnivore (i.e., American badger) was positively associated with ground squirrel occupancy and human disturbance (e.g., agriculture). These results suggest that the effects of fire and biological invasions are not consistent on ecosystem engineers, and that there are some winners (i.e., harvester ants) and losers (i.e., ground squirrels). Management actions targeted at conserving burrowing animals will need to be species- and parameter-specific (occupancy or abundance, as well as others such as survival and reproduction), and may or may not be associated with the large changes occurring in sagebrush systems.

Additionally, I (and my research team) partnered with the U.S. Bureau of Land Management and designed and implemented a social-ecological impact assessment associated with a project aimed at juniper tree removal for greater sage-grouse conservation. Through questionnaires, deliberative workshops, and participatory GIS, we identified a range of values and place meanings for many stakeholders from different backgrounds. These results provided clear mitigation opportunities for the Bureau of Land Management to address spatial and temporal concerns surrounding a management project on public lands. Importantly, the social-ecological impact assessment we developed could be transferred to other proposed projects on public lands throughout the U.S. that seek to better incorporate social aspects of land management in decision-making.

Appendix A: Sampling design for plants, American badgers, and Piute ground squirrels, and characteristic burrows for badgers and ground squirrels (Chapter 2)

Figure A1. Sampling scheme for environmental covariates, Piute ground squirrels (*Urocitellus mollis*), and American badgers (*Taxidea taxus*) at our 1-ha plots. Vegetation and grazing data were collected at locations 1-9 (Pt1-9); locations were ≥ 25 m apart. Ground squirrel data were collected within belt transects 1-3; transect centers were also 25 m apart. Badger data were collected within transects 1-3, as well as the interspaces between transects and the 1-ha boundary (i.e., we walked the double lined zig-zags).

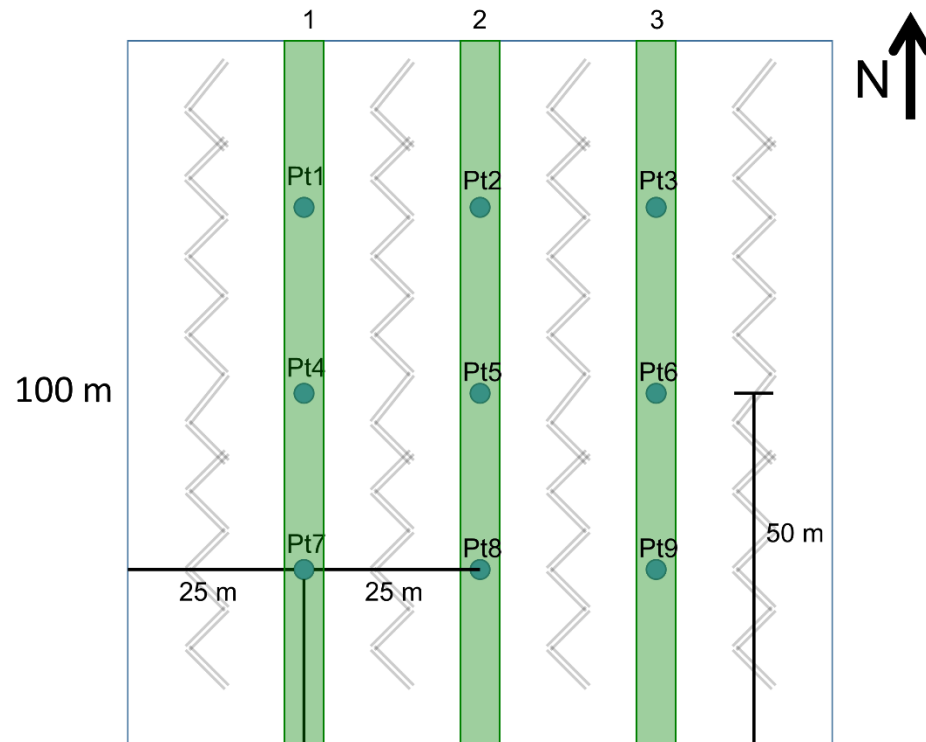


Figure A2. A) A conspicuous and recently dug American badger (*Taxidea taxus*) dig. B) A representative Piute ground squirrel (*Uroditellus mollis*) burrow that was recently used by a ground squirrel.

A



B



Appendix B: Description of covariates used in American badger and Piute ground squirrel modeling

(Chapter 2)

Table B1. Covariate descriptions, correlations, and collection methods for the variables included in our Piute ground squirrel (*Urocitellus mollis*) occupancy models.

Group	Units	Range	Description	Correlation	Method
Soil					
Soil	%	82-98	Average % surface soil passing through a #4 sieve within each mukey code	NA	STATSGO (1:250,000)
Climate					
Precipitation	mm	199-319	Mean annual precipitation from 1979-2008	Highly correlated with mean annual temperature from 1979-2008 ($r = -0.80$)	PRISM (800 m)
Dispersal/Landscape					
Shrubland	%	0-100	% shrubland within an area indicated by the average dispersal distance (500 m) juvenile Piute ground squirrels (0.79 km ²)	Highly correlated with Grassland ($r = -0.92$)	LANDFIRE (30 m) & GIS
Human	%	0-68	% human disturbance within an area indicated by the average dispersal distance (500 m) of juvenile Piute ground squirrels (0.79 km ²)	NA	LANDFIRE (30 m) & GIS
DI	NA	0-0.87	Ratio of the numbers of burrows at the nearest neighbor plot/distance to nearest neighbor	NA	Belt-transects & GIS
Disturbance					
FireFreq	count	0-7	Number of times an area burned from 1957-2013	NA	GIS (90 m)
Forage					
POSE	%	0-51	Average % (across points 1-9 in Appendix A: Figure A1) cover of <i>Poa secunda</i> at the plot level	NA	PhotoPoint

BRTE	%	0-96	Average % (across points 1-9 in Appendix A: Figure A1) cover of <i>Bromus tectorum</i> at the plot level	NA	PhotoPoint
EPG	%	0-27	Average % (across points 1-9 in Appendix A: Figure A1) cover of exotic perennial grasses at the plot level	NA	PhotoPoint
Richness	count	1-10	Number of species observed at the plot level	NA	PhotoPoint
Predation					
Shrub	%	0-54	Average % (across points 1-9 in Appendix A: Figure A1) cover of shrubs at the plot level	Highly correlated with sagebrush cover (r = 0.89)	PhotoPoint
Badger	count	0-21	Number of recent burrows dug by American badgers at plot level	NA	Census of 1 ha plot

Table B2. Covariate descriptions, correlations, and collection methods for the variables included in our American badger (*Taxidea taxus*) occupancy models.

Group	Units	Range	Description	Correlated	Method
Soil					
Soil	%	82-98	Average % surface soil passing through a #4 sieve within each mukey code	NA	STATSGO (1:250,000)
Climate					
Precipitation	mm	199-319	Mean annual precipitation from 1979-2008	Highly correlated with mean annual temperature from 1979-2008 ($r = -0.80$)	PRISM (800 m)
Landscape					
Shrubland	%	0-100	% shrubland within an average male American badger home range (2.4 km ²) on the BOP (Messick and Hornocker 1981)	Highly correlated with Grassland ($r = -0.84$)	LANDFIRE (30 m) & GIS
Human	%	0-68	% human disturbance within an average male American badger home range (2.4 km ²) on the BOP (Messick and Hornocker 1981)	NA	LANDFIRE (30 m) & GIS
Disturbance					
FireFreq	count	0-7	Number of times an area burned from 1957-2013	NA	GIS (90 m)
Prey					
GSOcc	binary	0-1	Presence/absence of recent Piute ground squirrel burrows at plot level. 0 = 3 recent burrows or less, and 1 = more than 3	NA	Belt-transects
GSN	count	0-109	Number of recent burrows Piute ground squirrel burrows at plot level	NA	Belt-transects

Table B3. Covariate descriptions, correlations, and collection methods for the variables included in our Piute ground squirrel (*Urocitellus mollis*) relative abundance models.

Group	Units	Range	Description	Correlated	Method
Season	binary	0-1	0 = before June 1, and 1 = at and after June 1. Van Horne et al. (1997b) indicated a decline in ground squirrel burrowing activity at June 1.	NA	NA
Soil					
Soil	%	82-98	Average % surface soil passing through a #4 sieve within each mukey code	NA	STATSGO (1:250,000)
Climate					
Precipitation	mm	199-319	Mean annual precipitation from 1979-2008	Highly correlated with mean annual temperature from 1979-2008 ($r = -0.80$)	PRISM (800 m)
Dispersal/Landscape					
Shrubland	%	0-100	% shrubland within an area indicated by the average dispersal distance (500 m) of juvenile Piute ground squirrels (0.79 km ²)	Highly correlated with Grassland ($r = -0.92$)	LANDFIRE (30 m) & GIS
Human	%	0-68	% human disturbance within an area indicated by the average dispersal distance (500 m) of juvenile Piute ground squirrels (0.79 km ²)	NA	LANDFIRE (30 m) & GIS
DI	NA	0-0.87	Ratio of the numbers of burrows at the nearest neighbor plot/distance to nearest neighbor	NA	Belt-transects & GIS
Disturbance					
FireFreq	count	0-7	Number of times an area burned from 1957-2013	NA	GIS (90 m)
Grazing	Pellet groups/m ²	0-5	Average density of domestic sheep and cow, and native ungulate pellets at plot level	NA	Point-Quarter
Forage					
POSE	%	0-51	Average % (across points 1-9 in Appendix A: Figure A1) cover of <i>Poa secunda</i> at the plot level	NA	PhotoPoint

BRTE	%	0-96	Average % (across points 1-9 in Appendix A: Figure A1) cover of <i>Bromus tectorum</i> at the plot level	NA	PhotoPoint
EPG	%	0-27	Average % (across points 1-9 in Appendix A: Figure A1) cover of exotic perennial grasses at the plot level	NA	PhotoPoint
NPG	%	0-11	Average % (across points 1-9 in Appendix A: Figure A1) cover of non-POSE native perennial grasses at the plot level	NA	PhotoPoint
EF	%	0-24	Average % (across points 1-9 in Appendix A: Figure A1) cover of exotic forbs at the plot level	NA	PhotoPoint
NF	%	0-6	Average % (across points 1-9 in Appendix A: Figure A1) cover of native forbs at the plot level	NA	PhotoPoint
EAG	%	0-27	Average % (across points 1-9 in Appendix A: Figure A1) cover of non-BRTE exotic annual grasses at the plot level	NA	PhotoPoint
Richness	count	1-10	Number of species observed at the plot level	NA	PhotoPoint
Predation					
Shrub	%	0-54	Average % (across points 1-9 in Appendix A: Figure A1) cover of shrubs at the plot level	Highly correlated with sagebrush cover ($r = 0.89$)	PhotoPoint
Badger	count	0-21	Number of recent burrows dug by American badgers at plot level	NA	Census of 1 ha plot

Table B4. Two-step process describing how Landfire data (LANDFIRE 2012; <http://www.landfire.gov/NationalProductDescriptions21.php>) were reclassified for modeling. Step One - downloaded existing vegetation type spatial information (i.e., us_130evt_2012), and used the EVT_GP_N attribute to reclassify us_130evt_2012 into 10 categories. Step Two – reclassified the 10 categories from Step One into 3 categories. Human disturbance, Grassland, and Shrubland we used in our modeling process.

Step One		Step Two	
Reclassification	Decision within EVT_GP_N – Anything including...	Reclassification	Decision
Agriculture	Agriculture	Human disturbance	Agriculture, development
Sagebrush	Big and low sagebrush	Grassland	Grassland, exotic grassland
Desert scrub	Salt desert scrub, desert scrub	Shrubland	Sagebrush, desert scrub, riparian shrubland, deciduous shrubland, greasewood shrubland
Development	Developed	NoData – Removed	Sparse vegetation
Grassland	Grassland, grassland and steppe		
Exotic grassland	Introduced annual and biennial forbland, introduced annual grassland, introduced perennial grassland and forbland		
Riparian shrubland	Western riparian woodland and shrubland		
Sparse vegetation	Sparse vegetation		
Deciduous shrubland	Deciduous shrubland		
Greasewood shrubland	Greasewood shrubland		
NoData – Removed	Forest, barren, woodland, chaparral, water, quarries – strip mines, snow-ice, western herbaceous wetland		

Appendix C: Description of plant species found at the Morley Nelson Snake River Birds of Prey National

Conservation Area in southern Idaho, USA, and that were used in Piute ground squirrel models (Chapter 2)

Table C1. Plant species characteristics and our functional group assignment for modeling Piute ground squirrel (*Urocitellus mollis*) occupancy and relative abundance. These data were collected from 134 1-ha plots on the Morley Nelson Snake River Birds of Prey National Conservation Area in southern Idaho, USA.

Scientific Name – Common Name	Nativity	Longevity	Life Form	Functional Group for Analyses
<i>Achnatherum hymenoides</i> - Indian ricegrass	Native	Perennial	Grass	NPG
<i>Achnatherum thurberianum</i> - Thurber's needlegrass	Native	Perennial	Grass	NPG
<i>Agropyron cristatum</i> - crested wheatgrass	Exotic	Perennial	Grass	EPG
<i>Amsinckia tessellata</i> - fiddleneck	Native	Annual	Forb	NF
<i>Artemisia cana</i> - silver sagebrush	Native	Perennial	Shrub	Artemisia and Shrub
<i>Artemisia tridentata</i> - big sagebrush	Native	Perennial	Shrub	Artemisia and Shrub
<i>Atriplex canescens</i> - fourwing saltbush	Native	Perennial	Shrub	Shrub
<i>Atriplex confertifolia</i> - shadscale saltbush	Native	Perennial	Shrub	Shrub
<i>Atriplex nuttallii</i> - Nutall's saltbush	Native	Perennial	Shrub	Shrub
<i>Bassia prostrata</i> - forage kochia	Exotic	Perennial	Shrub	Shrub
<i>Bromus arvensis</i> - field brome	Exotic	Annual	Grass	EAG
<i>Bromus tectorum</i> - cheatgrass	Exotic	Annual	Grass	BRTE
<i>Ceratocephala testiculata</i> - bur buttercup	Exotic	Annual	Forb	EF
<i>Chondrilla juncea</i> - rush skeletonweed	Exotic	Perennial	Forb	EF
<i>Chrysothamnus viscidiflorus</i> - green/yellow rabbitbrush	Native	Perennial	Shrub	Shrub
<i>Descurainia pinnata</i> - Pinnate/western tansymustard	Native	Annual	Forb	NF
<i>Descurainia sophia</i> - tall tansymustard / flixweed	Exotic	Annual	Forb	EF
<i>Elymus elymoides</i> - bottlebrush squirreltail	Native	Perennial	Grass	NPG
<i>Elymus lanceolatus</i> - thickspike wheatgrass	Native	Perennial	Grass	NPG
<i>Elymus multisetus</i> - big squirreltail	Native	Perennial	Grass	NPG

<i>Epilobium brachycarpum</i> - tall annual willowherb	Native	Annual	Forb	NF
<i>Erodium cicutarium</i> - redstem stork's bill	Exotic	Annual	Forb	EF
<i>Ericameria nauseosa</i> - grey/rubber rabbitbrush	Native	Perennial	Shrub	Shrub
<i>Erysimum repandum</i> - spreading wallflower	Exotic	Annual	Forb	EF
<i>Grayia spinosa</i> - spiny hopsage	Native	Perennial	Shrub	Shrub
<i>Halogeton glomeratus</i> - halogeton	Exotic	Annual	Forb	EF
<i>Hesperostipa comata</i> - needle and thread	Native	Perennial	Grass	NPG
<i>Krascheninnikovia lanata</i> - winterfat	Native	Perennial	Shrub	Shrub
<i>Lactuca serriola</i> - prickly lettuce	Exotic	Annual	Forb	EF
<i>Leymus cinereus</i> - basin wildrye	Native	Perennial	Grass	NPG
<i>Lepidium perfoliatum</i> - clasping pepperweed	Exotic	Annual	Forb	EF
<i>Lomatium dissectum</i> - fernleaf biscuitroot	Native	Perennial	Forb	NF
<i>Lomatium grayi</i> - Grays biscuitroot	Native	Perennial	Forb	NF
<i>Machaeranthera canescens</i> - hoary tansyaster	Native	Annual	Forb	NF
<i>Penstemon acuminatus</i> - sharpleaf/blue penstemon	Native	Perennial	Forb	NF
<i>Phacelia</i> sp.	Native	Annual	Forb	NF
<i>Picrothamnus desertorum</i> - bud sagebrush	Native	Perennial	Shrub	Shrub
<i>Poa secunda</i> - Sandberg bluegrass	Native	Perennial	Grass	POSE
<i>Psathyrostachys juncea</i> - Russian wildrye	Exotic	Perennial	Grass	EPG
<i>Pseudoroegneria spicata</i> - bluebunch wheatgrass	Native	Perennial	Grass	NPG
<i>Salsola tragus</i> - prickly Russian thistle	Exotic	Annual	Forb	EF
<i>Sarcobatus vermiculatus</i> - greasewood	Native	Perennial	Shrub	Shrub
<i>Sisymbrium altissimum</i> - tall tumbled mustard	Exotic	Annual	Forb	EF
<i>Sphaeralcea munroana</i> - Munro's globemallow	Native	Perennial	Forb	NF
<i>Taeniatherum caput-medusae</i> - medusahead	Exotic	Annual	Grass	EAG
<i>Tetradymia glabrata</i> - littleleaf horsebrush	Native	Perennial	Shrub	Shrub
<i>Tragopogon dubius</i> - yellow salsify	Exotic	Annual	Forb	EF

Appendix D: Questionnaire used to solicit responses from the social-ecological impact assessment (Chapter 4)

Table D1. Deliberative workshop questionnaire, including seven questions related to ecosystem services and social processes. Participants completed the same questionnaire four times while considering the present state and potential future states of the Owyhees under the three project alternatives.

1. ...the ability of the Owyhees to produce useful resources for people will be:												
As bad as can be	1	2	3	4	5	6	7	8	9	10	As good as can be	
Why?												
2. ...the ability of the Owyhees to maintain or restore its balance through physical, biological and chemical processes and interactions will be:												
As bad as can be	1	2	3	4	5	6	7	8	9	10	As good as can be	
Why?												
3. ...the availability of physical space and environmental conditions that are suitable for human activities will be:												
As bad as can be	1	2	3	4	5	6	7	8	9	10	As good as can be	
Why?												
4. ...the ability of the Owyhees to provide opportunities for spiritual enrichment, aesthetic enjoyment, contemplation, meditation and recreation will be:												
As bad as can be	1	2	3	4	5	6	7	8	9	10	As good as can be	
Why?												

5. ...the economic activity in the Owyhees – including the ways people make a living – will be:

As bad as can be 1 2 3 4 5 6 7 8 9 10 As good as can be

Why?

6. ...the efficiency and effectiveness of organization(s) in and around the Owyhees that are responsible for the management or supply of the natural resources upon which stakeholders depend will be:

As bad as can be 1 2 3 4 5 6 7 8 9 10 As good as can be

Why?

7. ...the ability of stakeholders to contribute to decision-making that affects their lives will be:

As bad as can be 1 2 3 4 5 6 7 8 9 10 As good as can be

Why?

8. Implementing this alternative in Wilderness areas within the project area boundary is (please circle one):

Extremely Unacceptable	Somewhat Unacceptable	Neutral	Somewhat Acceptable	Extremely Acceptable
Why?				

Appendix E: Summary of all responses and example quotations from the social-ecological impact assessment

(Chapter 4)

Table E1. Response to the no action alternative, including potential changes to social processes and ecosystem services with related direction of impact and quote from deliberative workshop dialogue.

Social-ecological system characteristic	Direction of Impact	Potential Change	Example Quote
Economic Processes	Negative	Local economy – less opportunity	“[Local people might be] counting on the logging jobs.”
Economic Processes	No Change	Local economy – same opportunity	“[The BOSH proposal] does not deal with economic issues driving the Owyhees.”
Economic Processes	Negative	Tension on livestock operators	“The only thing for me that I perceive changing with a no action alternative would be the future economic activity in the Owyhees, including the way people make a living. With the potential listing of sage grouse, if sage grouse are listed, that puts an added tension on especially livestock operators, which is the major economic activity in the county.”
Institutional and legal processes	Negative	Disheartening to land managers	“So if you’re not going to do anything, it’s really disheartening to everybody that worked all those years, and biologists, and it’s in every plan, the Owyhee [Initiative], the Governor’s task force, the state plan. It would be a big discouragement to everybody.”
Institutional and legal processes	Negative	Endangered listing – Greater sage grouse	“But I think there’s, what I like to say is that, the impact to the people I think may not be as much related to, okay we’re going to have more juniper out there, but it may simply be how a (sage grouse) listing decision affects the community out there.”

Empowerment processes	Negative	Stakeholder collaboration – less opportunity	“There is a lot of agreement that some action is needed and if nothing happens, folks may feel disenfranchised.”
Empowerment processes	No Change	Stakeholder collaboration – same opportunity	“Collaboration efforts exist but litigation will always be a challenge.”
Provisioning	Positive	Impact to ecosystem	“More trees – cooler streams, let nature take its course.”
Provisioning	Negative	Decline of historic plant communities	“The resources itself – historic plant communities, those types of things, they’re going to decline.”
Processing	Negative	Ability to balance or restore landscape / ecological processes – more difficult	“...the ecological site condition will continue to deviate from the historical condition affecting watershed, range & grazing, wildlife.”
Processing	Negative	Reduction of watershed functionality	“When juniper encroaches on springs and streams, it reduces their functionality. There’s at least plenty of anecdotal evidence of juniper leading to springs drying up, reducing water output.”
Supporting	Negative	Loss of biodiversity & habitat	“The area will lose diversity as juniper monocultures develop.”
Supporting	Negative	Loss of sage grouse habitat	“Are we able to actually effectively manage the habitat for sage grouse to offset these big losses we’re going to have?”
Cultural	Positive	Availability of areas without treatment for study	“And as far as not taking trees out, I think that would be great. I realize that it’s actually maybe it gives you an area that you can actually do some studies to figure out what’s going on because you haven’t messed with this, you can have this area that hasn’t had a treatment on it, maybe somebody can get in there and figure out what was really going on.”
Cultural	Positive	General enjoyment of the Owyhees – improved	“Because there won’t be this specific manipulation in wilderness.”

Cultural	No Change	General enjoyment of the Owyhees – no change	“Action or no action will have minor effect if any”
Cultural	Negative	Loss of open space	“There would be loss of open space...you would lose the sagebrush views.”
Cultural	Negative	Limits on recreation	“[Big impact to Owyhee County] on recreation...everything from motorized, which a lot of people use down there...no hunting season for the sage grouse.”
Cultural	Negative	Less aesthetic enjoyment	“Aesthetic enjoyment would decrease for me [due to] loss of sagebrush/sage-steppe.”
Cultural	Negative	Hunting – diminished	“Areas will have reduced value for human activity as juniper continues to expand = decreased recreation, hunting, decreased quality areas for wildlife.”
Cultural	Negative	Spiritual experience - diminished	“I think the [spiritual] opportunities available now are a result of the landscape available if it changes these may cease to exist,”
Cultural	No Change	Spiritual experience – no change	“You know for me with the exception of the spirituality portion because I think you can find the spirituality of it whether they’re sagebrush, sage grouse, junipers – there’s a beauty in whatever aspect of it.”

Table E2. Response to the full suite alternative, including potential changes to social processes and ecosystem services with related direction of impact and quote from deliberative workshop dialogue.

Social-ecological system characteristic	Direction of Impact	Potential Change	Quote
Economic Processes	Positive	Local economy – more opportunity	“Grazing will be improved and juniper control could hopefully prevent ESA listing thereby preventing regulation and control of producers.”
Economic Processes	Positive	Ability to make a living - improved	“More jobs for loggers.”
Institutional and legal processes	No Change	Ability to make a living – no change	“I don’t see much in that change...the ability for people to actually make a living out there. If we’re focusing on just these Phase I, Phase II [juniper stands], visually, as I go out there, I’m not going to see that much of a difference. I’m not going to experience that much change because we’re talking about small scale.”
Institutional and legal processes	Positive	Management – improved	“Management would be better through active work on the ground.”
Institutional and legal processes	Negative	Management – worse	“And we have enough problems as it is and when we do stuff like that it makes us look even worse, especially this thing here... You know we have our plan it sounds great on paper, but when we don’t get the money from Congress or whatever to follow through, then we end up dealing with this next thing that happens.”
Institutional and legal processes	No Change	Management – no change	“The future of the efficiency – of the effectiveness of the management of our supply of natural resources aren’t going to change by us simply removing the junipers...at some point in time once the juniper are gone and we’ve created this habitat for sage grouse, let’s go back to doing something that’s not going to bring the juniper back again.”

Institutional and legal processes	Negative	Worsened agency reputation	“I work for the BLM, that’s my job. I’m not here representing the BLM, but I actually work for the BLM. And we have enough problems as it is and when we do stuff like that it makes us look even worse.”
Empowerment processes	Positive	Stakeholder collaboration – more opportunity	“People will see the fruits of the labor and will want to keep collaborating if their contributions are influencing positive change.”
Provisioning	Positive	Range and grazing - improved	“I think if it’s implemented, we’re trying to get this juniper removed, that will improve range conditions, and it will improve grazing. It will improve ranching operations. And I think if we’re able to use equipment and masticators and stuff, then we can have a bigger impact on juniper encroachment and reduce it at a bigger scale than what we’re limited to hand crews and stuff.”
Processing	Positive	Increased watershed functionality	“Increased watershed and overall ecological health.”
Processing	Negative	Increased fire danger	“But when it gets down to actually implementing it I’ll bet you we end up with a bunch of dead trees out there that look like crap that maybe you’re going to end up catching or actually causing the fire because now you’ve got all this dead wood that you’ve left lying around.”
Supporting	Positive	Increased biodiversity	“Taking action in areas where we will see the most positive + cost effective benefits = more habitat for wildlife, lands for hunting/recreation; hopeful treatment/action to improve sage-grouse habitat – keeping it from being listed, and more diversity.”
Supporting	Positive	Wildlife habitat – improved	“I think it’s agreed that sage grouse is kind of a keystone species that if the habitat is improved for them, deer and elk and a vast majority of other species kind of are also positively benefitted,”
Supporting	Negative	Wildlife habitat – degraded	“A lot of blue birds, chickadees other birds that are cavity nesters, they need junipers to nest in. So they would definitely be affected...” “One of the issues, if you do have a lot of mechanical treatment, you do have to worry about noxious weeds. And hopefully the outcome is good.”

			And you do have to worry about soil disturbance. And also disruption of wildlife and if it's a sensitive nesting time or things like that.”
Supporting	Positive	Sage grouse habitat - maintained/improved	“I think it's agreed that sage grouse is kind of a keystone species that if the habitat is improved for them, deer and elk and a vast majority of other species kind of are also positively benefitted.”
Cultural	Positive	General enjoyment of the Owyhees – improved	“Increased diversity of animals and habitat will create better experiences for more people with diverse interests,”
Cultural	No Change	Solitude – no change	“I'm trying to keep in mind the scale of what we're talking about as far as Phase I, really early Phase II juniper. Yes, it'll be a success for us if we're actually able to do something out there, but as far as any other changes that are occurring, I guess personally I don't see much in that change... as far as... people's feeling of solitude.”
Cultural	Positive	Hunting – improved	“Taking action in areas where we will see the most positive + cost effective benefits = more habitat for wildlife, lands for hunting/recreation; hopeful treatment/action to improve sage-grouse habitat – keeping it from being listed, and more diversity.”
Cultural	Negative	Recreation – disrupted	“The treatment activities will be disruptive to recreationists for a period of time.”
Cultural	No change	Recreation – no change	“For instance, well it hasn't changed the future physical space that's suitable for human activities. I guess it depends on what human activity you want. If the junipers are there, there's a human activity that can still be used whether it's watching birds or it's hunting whatever the case. You remove those junipers, to some degree, those human activities are still available – may not be the <i>exact</i> same.”
Cultural	Positive	Viewshed – improved	“...for me personally, it would improve because I'd be able to go out to that lek and not see that juniper stand there anymore. So for me personally, I'm going to get to go out and be like, “Wow, this is awesome.” I feel like we accomplished exactly what we set out to do. I

			can stand and look at those birds and not see the juniper in the background.”
Cultural	Negative	Viewshed – degraded	“I know when I was at a Wildlife Refuge eight years ago, BLM came in around that area and cut down all the juniper trees, and they just laid there for years. And eventually they went and they started burning them up, but that was such a black eye for the BLM. The locals around there, they’re all like, “Freaking waste.” All these trees lay and it looked like crap.”
Cultural	No Change	Viewshed – no change	“...the average Joe is still going to drive into Mud Flat Road and see exactly what they’ve always seen. They’re not going to realize that on the ground, there have been people that have been removing junipers out there to improve sage grouse, or for whatever. Most people aren’t going to notice that.”
Cultural	Positive	Spiritual experience - improved	“But for the scope of this project, it will improve my personal spirituality or whatever, if you will, because I can actually now visually see this – no more trees within this area, this lek, these encroaching junipers are gone,”
Cultural	No Change	Spiritual experience – no change	“Again I go back to the fact that I can find beauty in a butterfly on a juniper as easily as I can find beauty in a butterfly on a sagebrush. So that aspect of my spiritual portion of it doesn’t change by the fact that we do or do nothing to it.”
Cultural	Positive	Culture tied to cowboy & sage grouse - maintained	“It’s not just the cowboy aspect. I love sage grouse, you know. And I think having all the tools available, having all the resources available is from the get-go probably the best option.”

Table E3. Response to the cut and scatter alternative, including potential changes to social processes and ecosystem services with related direction of impact and quote from deliberative workshop dialogue.

Social-ecological system characteristic	Direction of Impact	Potential Change	Quote
Economic processes	Positive	Local economy – more opportunity	“More jobs.”
Economic processes	Negative	Weakening of local livelihoods	“BLM regulations would probably still be a limiting factor in ranching operations.”
Economic processes	Negative	Range and grazing – reduced	“Ranchers/cowboys would not do well grazing would be reduced / riding the range reduced.”
Institutional and legal processes	Negative	Management effectiveness – diminished	“The efficiency of management would be reduced since mastication and jackpot burns are useful tools for juniper encroachment,” and “So if those tools aren’t available, you may not treat the acres you’d like or as effective as you’d like.”
Empowerment processes	No Change	Stakeholder decision-making – no change	“A change is not possible – unless litigation process is changed.”
Provisioning	Positive	Ecosystem health and characteristics - improved	“In 5-15 years there would be some improvement in soil and water resources. Grasses would improve also.”
Provisioning	Positive	Increased water availability	“...getting that functioning ecosystem we can pretty much all agree on...without water, nothing functions...water is the sustaining thing of life, period.”
Processing	Positive	Watershed functionality - improved	“slowed on fields and hills” and when “you get snow blowing up against the back end or on the north face, then you’ve got extra protections.”

Processing	Negative	Increased fire danger	“...increased fire danger, fuel after it dries out, which would have a big negative impact,” and “I think leaving all the wood down is a fire hazard and probably has other environmental consequences.”
Supporting	Positive	Wildlife habitat – improved	“...at least we’re getting trees cut and slashed, and that’s great. That’s a lot better than doing nothing. A whole lot better, in my book, than doing nothing,” and “We’re talking about mostly Phase 1. We’re talking small trees – those can get dropped pretty darn low to the ground, and there won’t be a lot of fuel buildup in those areas. So there are going to be a lot of positives, even if that’s what we were to do for the sage grouse.”
Supporting	Negative	Sage grouse habitat - degraded	“...if it’s [juniper branches] left lying there, the sage grouse are not going to walk through that probably either.”
Supporting	Negative	Increased cover for sage grouse predators	“...it’s cut and scatter, so that’ll take some of the cover away. It’ll leave more of the just the bowl, and the branches will be scattered out. But there’s the potential it could create more cover.”
Cultural	Negative	Viewshed - degraded	“Negative visual impact to the public. A pile of dead trees laying on the ground... it just doesn’t look natural,” and “I will see those trees still lying down in some areas that will not necessarily improve sage grouse habitat.”
Cultural	No Change	General enjoyment of the Owyhees – no change	“Landscape features would be about the same as cut trees would take a long time to decay. If trunks are used for fire wood or other purpose this would help in this area.”

Appendix F: Institutional Review Board Approval from the University of Idaho for implementing the social-ecological assessment (Chapter 4)

University of Idaho

**Office of Research Assurances (ORA)
Institutional Review Board (IRB)**

875 Perimeter Drive, MS 3010
Moscow ID 83844-3010

Phone: 208-885-6162
Fax: 208-885-5752
irb@uidaho.edu

July 10, 2013

To: Wulfhorst, JD
Cc: Bentley, Amanda; Holbrook, Joseph; Niemeyer, Ryan; Suazo, Alex
From: IRB, University of Idaho Institutional Review Board
Subject: Exempt Certification for IRB project number 12-357

Determination: July 8, 2013
Certified as Exempt under category 2 at 45 CFR 46.101(b)(2)
IRB project number 12-357: Exploring Dynamic Processes of the Sagebrush-
Steppe Using Philosophy and System Dynamics Modeling

This study may be conducted according to the protocol described in the Application without further review by the IRB. As specific instruments are developed, each should be forwarded to the ORA, in order to allow the IRB to maintain current records. Every effort should be made to ensure that the project is conducted in a manner consistent with the three fundamental principles identified in the Belmont Report: respect for persons; beneficence; and justice.

It is important to note that certification of exemption is NOT approval by the IRB. Do not include the statement that the UI IRB has reviewed and approved the study for human subject participation. Remove all statements of IRB Approval and IRB contact information from study materials that will be disseminated to participants. Instead please indicate, "The University of Idaho Institutional Review Board has Certified this project as Exempt."

Certification of exemption is not to be construed as authorization to recruit participants or conduct research in schools or other institutions, including on Native Reserved lands or within Native Institutions, which have their own policies that require approvals before Human Subjects Research Projects can begin. This authorization must be obtained from the appropriate Tribal Government (or equivalent) and/or Institutional Administration. This may include independent review by a tribal or institutional IRB or equivalent. It is the investigator's responsibility to obtain all such necessary approvals and provide copies of these approvals to ORA, in order to allow the IRB to maintain current records.

This certification is valid only for the study protocol as it was submitted to the ORA. Studies certified as Exempt are not subject to continuing review (this Certification does not expire). If any changes are made to the study protocol, you must submit the changes to the ORA for determination that the study remains Exempt before implementing the changes. The IRB Modification Request Form is available online at: <http://www.uidaho.edu/ora/committees/irb/irbforms>

***Appendix G: License agreement to reprint manuscript from the Journal of
Arid Environments (Chapter 1)***

License Number	3718450086497
License date	Sep 29, 2015
Licensed content publisher	Elsevier
Licensed content publication	Journal of Arid Environments
Licensed content title	Sampling animal sign in heterogeneous environments: How much is enough?
Licensed content author	Joseph D. Holbrook, Robert S. Arkle, Janet L. Rachlow, Kerri T. Vierling, David S. Pilliod
Licensed content date	August 2015
Licensed content volume number	119
Licensed content issue number	n/a
Number of pages	5
Type of Use	reuse in a thesis/dissertation
Portion	full article
Format	both print and electronic
Are you the author of this Elsevier article?	Yes
Will you be translating?	No
Title of your thesis/dissertation	Social-Ecological Research in the Sagebrush Ecosystem: Evaluating the Landscape Ecology of Burrowing Animals and Implementing a Social-Ecological Impact Assessment
Expected completion date	Dec 2015
Estimated size (number of pages)	180
Elsevier VAT number	GB 494 6272 12
Permissions price	0.00 USD
VAT/Local Sales Tax	0.00 USD / 0.00 GBP
Total	0.00 USD