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

JOSEPH D. HOLBROOK,† ROBERT S. ARKLE, JANET L. RACHLOW, KERRI T. VIERLING, DAVID S. PILLIOD, AND MICHELLE M. WIEST

1Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho 83844-1136 USA
2U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, Idaho 83706 USA
3Department of Statistical Science, University of Idaho, Moscow, Idaho 83844-1104 USA

Citation: Holbrook, J. D., R. S. Arkle, J. L. Rachlow, K. T. Vierling, D. S. Pilliod, and M. M. Wiest. 2016. Occupancy and abundance of predator and prey: implications of the fire-cheatgrass cycle in sagebrush ecosystems. Ecosphere 7(6):e01307. 10.1002/ecs2.1307

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 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 1962 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, agriculture, and shrub cover. Badger occupancy was positively associated with ground squirrel occupancy and 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 (e.g., 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 postfire, may provide targeted conservation strategies that promote these species and thus preserve the burrowing and trophic functions they provide.

Key words: American badger; Artemisia tridentata; biological invasion; Bromus tectorum; burrowing mammals; cheatgrass; climate change; Idaho; Piute ground squirrel; Taxidea taxus; Urocitellus mollis; wildfire.

Received 2 September 2015; revised 18 November 2015; accepted 5 December 2015. Corresponding Editor: E. Gese.
Copyright: © 2016 Holbrook et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: jholbrook03@gmail.com
INTRODUCTION

Drylands worldwide are experiencing unprecedented climate changes, increased stressors from human activities, and biological invasions (e.g., Bestelmeyer et al. 2015, Cook et al. 2015), which have 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) 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 the development of effective management and conservation plans targeted at preserving ecosystem function (Davidson et al. 2012).

Burrowing mammals influence 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, and these digs are characterized by mound ed soil at the entrance of the excavation. Badger digs influence landscape heterogeneity directly through changes in water infiltration processes, 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 nonburrowing 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 nontrophic 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 are often 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). Furthermore, 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 ≥40,000 km$^2$ of the 650,000 km$^2$ 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 abiotic and biotic gradients influencing occupancy and abundance (Guisan and Thuiller 2005, Soberón 2007, Fig. 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 Le Lay 2008). We included soil, climate, and disturbance (i.e., fire) as our abiotic factors. 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 Fig. 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 (Fig. 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; Fig. 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, Fig. 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) implicates restoration actions that could be used 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; Fig. 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. 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, b). 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

![Fig. 2.](image-url)
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 yr (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 postfire 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. 1997a, b), thus capturing a reasonable representation of population activity and relative abundance. 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. 1997a, b), thus capturing a reasonable representation of population activity and 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 × 4 m belt-transects spaced 25 m apart (Appendix S1: Fig. S1). 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 S1: Fig. S2B), 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 S1: Fig. S1). 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 S1: Fig. S2A; 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, Oregon State University 2004) 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) data to understand how soil influenced occupancy and abundance (Appendix S2: Table S1–S3). 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 coarse-grained soils. We expected ground squirrels and badgers to be associated with finer-grained soils because coarse-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 noncohesive 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 S2: Tables S1–S3). We acquired Landfire Existing Vegetation Type data (LANDFIRE 2012), and used a two-step process to reclassify the data to our desired types (Appendix S2: Table S4): 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 occupancy 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 S2: Tables S1 and S3). 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 site occupancy (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 has recently been shown to be important, and provides a more realistic assessment of the relative effects of abiotic and biotic factors (Miller and Holloway 2015).

We characterized vegetation at each plot to evaluate the influence of forage and cover resources on ground squirrel occupancy and abundance (Appendix S2: Tables S1 and S3). At each plot, we sampled the vegetation community at nine locations (points 1–9 in Appendix S1: Fig. S1) during May through August 2012–2014. At each location we took a nadir 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 quantified 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 nine points to get plot-level estimates. We further refined vegetation data into functional groups (Appendix S3: Table S1) 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 functional groups to influence occupancy. Finally, we generated a functional group describing sagebrush (Artemisia spp.) and total shrub cover (Appendix S3: Table S1). We expected shrub cover to increase mortality from 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 S2: Table S2). 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 S2: Tables S1 and S3). At each of the nine points within the plot (Appendix S1: Fig. S1), 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 NW) within a 12.5 m search radius and recorded the distance to nearest pellet radius and recorded the distance to nearest pellet pile of any species. We estimated density of pellets at each point as: 1/(\(\overline{d_1^2 + d_2^2 + d_3^2 + d_4^2}\)) where \(d = \) the point-to-pellet distance (m) for the closet pellet pile in each of the four quadrants, and \(\overline{x} = \) 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 S2: Tables S1–S3). First, we developed a raster of fire disturbance characterizing frequency from 1957 to 2013 using a GIS fire perimeter database developed by the U.S. Geological Survey (used in Balch et al. 2013, http://rmgsc.cr.usgs.gov/outgoing/Geomac/historic_fire_data); 94% of these data were from ≥1981, with only seven 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 biomass is annually variable 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 nonbinary covariates by \((x_i - \bar{x})/\sigma\) where \(x_i\) equals an observation at plot \(i\). This standardization allowed for an equal comparison among nonbinary 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 S2: Tables S1–S3). 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 Fig. 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 nonlinear 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., \(\Delta\text{BIC}\) or \(\Delta\text{AIC}\(_c\)\) for the second model was >2; Burnham and Anderson 2002). However, when there was ambiguity (e.g., multiple models exhibiting a \(\Delta\text{BIC}\) or \(\Delta\text{AIC}\(_c\)\) ≤ 2–7; Burnham and Anderson 2002), we identified the 95% confidence set of models. We reported parameter estimates (±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 \(\Delta\text{BIC}\) or \(\Delta\text{AIC}\(_c\)\) ≤ 2 was selected) for combining themes. We developed combined hypotheses beginning from the hypothesized strong effects and progressing to weak effects (Fig. 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 discriminative performance. For the generalized models with binomial error distributions, we tested goodness of fit (Hosmer and Lemeshow 2000) and assessed discriminative 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 to 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 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 implications. 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 to 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., $w_1 = 0.80$), and all other models exhibited a $\Delta$BIC $> 2.88$ indicating relatively weak support (Table 1). The goodness of fit test indicated appropriate fit of our top model ($X^2 = 4.43$, df = 8, $P = 0.82$). Discriminative performance of models indicated excellent fit (i.e., AUC $\geq 0.95$) for 5 models, and all of those models included the dispersal index (Table 1). All parameter estimates were positive, indicating a positive effect of soil, precipitation, and dispersal, although the credible interval for soil slightly overlapped 0 (Fig. 3). Parameter estimates indicated a greater relative effect of dispersal on occupancy (compared to the other effects), however, there was substantial variation around the estimates. The influence of precipitation was greater than the effect of soil.

Multiple hypotheses characterizing badger occupancy were supported by our analyses. Six models had $\Delta$AIC$_c < 6$ ($w_i = 0.03–0.53$), and two models had $\Delta$AIC$_c$ values $<2$ (Table 2). Our 95% confidence set of models contained the top four models (Table 2), which had 2–5 parameters including; ground squirrel occupancy, percent of landscape that was altered 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, $P = 0.76$). Discriminative performance of our top 4 models suggested comparatively weak fit (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). Parameter estimates from the top model and model averaged values for ground squirrel occupancy and human disturbance were similar, positive, and differed from 0 (Fig. 4), however, the effect of ground squirrel occupancy on badger occupancy was higher than that of 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 ΔAIC < 4 (wᵢ = 0.07–0.51), and two models were within ΔAIC < 2 (Table 3). Our 95% confidence set of models contained the top three models (Table 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. Model fit, as measured by Spearman’s rank correlations, was moderate (ρ = 0.69) for our top four models (ΔAIC < 4), while all other models were less predictive (ρ ≤ 0.52). Top model and model averaged parameter estimates and confidence intervals were similar (Fig. 5).

We observed a significantly positive effect of soil and a moderately positive effect of dispersal potential (although the model averaged estimate...
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 (Fig. 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 (Fig. 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 (Fig. 6b). Unburned plots had a higher point estimate of ground squirrel occupancy than treated plots.

Fig. 4. Standardized parameter estimates (±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 the area burned from 1957 to 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.

Table 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. AICc 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 wi. See Appendix S2: Table S2 for specific variable descriptions.

| Hypothesis                                      | Model                                      | k | AICc | ΔAICc | wi  | AUC |
|------------------------------------------------|--------------------------------------------|---|------|-------|-----|-----|
| Ground squirrel occupancy + Human disturbance   | ψ(GSOcc + Human)                           | 3 | 202.2|       | 0.53†| 0.68|
| Ground squirrel occupancy + Human disturbance + Fire | ψ(GSOcc + Human + FireFreq)               | 4 | 204.2| 1.95  | 0.20†| 0.64|
| Ground squirrel occupancy                       | ψ(GSOcc)                                  | 2 | 205.6| 3.35  | 0.10†| 0.65|
| Ground squirrel occupancy + Human disturbance + Fire + Soil | ψ(GSOcc + Human + FireFreq + Soil) | 5 | 206.0| 3.79  | 0.08†| 0.65|
| Ground squirrel occupancy + Human disturbance + Fire + Precipitation | ψ(GSOcc + Human + FireFreq + Precipitation) | 5 | 206.3| 4.05  | 0.07†| 0.66|
| Ground squirrel occupancy + Human disturbance + Fire + Climate | ψ(GSOcc + Human + FireFreq + Precipitation + Soil) | 6 | 208.1| 5.87  | 0.03†| 0.66|
| Ground squirrel RA                               | ψ(GSRA)                                   | 2 | 216.3| 14.09 |       | 0.70|
| Soil                                            | ψ(Soil)                                   | 2 | 223.1| 20.86 |       | 0.56|
| Climate                                         | ψ(Precipitation)                          | 2 | 224.7| 22.42 |       | 0.61|
| Fire                                            | ψ(FireFreq)                               | 2 | 227.3| 25.10 |       | 0.54|
| Human disturbance                               | ψ(Human)                                  | 2 | 229.5| 27.25 |       | 0.49|
| Shrubland                                       | ψ(Shrubland)                              | 2 | 229.7| 27.48 |       | 0.52|
| Landscape                                       | ψ(Shrubland + Human)                      | 3 | 231.5| 29.25 |       | 0.48|

† 95% confidence set of models

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 (Fig. 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 (Fig. 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 (Fig. 6b). Unburned plots had a higher point estimate of ground squirrel occupancy than treated plots.
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 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,
Fig. 5. Standardized parameter estimates (±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 to 2008, DI – dispersal index (i.e., number of burrows at the nearest sampled 1-ha plot/distance to the plot), firefreq – number of times the area burned from 1957 to 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.

Fig. 6. (a) Cheatgrass (BRTE) and shrub cover (±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, ±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.
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 and abiotic factors 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 (Fig. 3), and the discriminative 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 coarse-grained soils because finer-grained soils are more structurally sound and tend to retain soil moisture more effectively than coarse-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 endemius) 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 (Fig. 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 discriminative ability (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. Furthermore, 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 increase predator activity or abundance and lead 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 increased 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), 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., Boulangéat et al. 2012, Miller and Holloway 2015). However, the effect of soil texture was important across extents providing support for multiscale 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 multiscale 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 during 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 yr 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, Fig. 5 and 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, 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, ground squirrels. 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 2 yr, 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, Balch 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 (Fig. 6) relative to untreated or unsuccessfully treated areas and unburned sites. This is promising because many raptors rely on ground squirrels as prey (Martí 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 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).

Acknowledgments

We are sincerely grateful to D. Holbrook (JDH’s father) for the consistent willingness to help his son with field work. JDH was supported by the National Science Foundation’s IGERT program (Award 0903479), Shikar Safari Club International Scholarship, and the J. Michael and Sharon L. Scott Graduate Student Scholarship. Funding for environmental data was provided by the Joint Fire Science Program (Project ID: 11-1-2-30). We thank Steve Knick, Kurt Jenkins, and two anonymous reviewers for providing comments that improved this manuscript. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. government.

Literature Cited

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., et al. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5:145–152.

Andrewartha, H. G., and L. C. Birch. 1954. Distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

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, C. M. 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, New York, USA.

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, 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.

Cook, B. L., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American southwest and central plains. Science Advances 1:e1400082.

Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivoreous 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.

Ehtlén, J., and W. F. Morris. 2015. Predicting changes in the distribution and abundance of species under environmental change. Ecology Letters 18:303–314.

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.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Maruschich. 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. 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

Gelman, A., A. Jakulin, M. G. Pittau, and Y. S. Su. 2008. A weakly informative default prior distribution for logistic and other regression models. Annals of Applied Statistics 2:1360–1383.

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., et al. 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. 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, New York, USA.

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 semiaquatic 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. Condor 105:611–634.

Knick, S., S. Hansen, 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, USA.

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, New York, USA.

LANDFIRE. 2012. Existing Vegetation Type Layer. U.S. Department of the Interior, Geological Survey. http://landfire.cr.usgs.gov/viewer/

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.

Laudrè, J. 1989. Horizontal and vertical diameter of burrows of five small mammal species in southeastern Idaho. Great Basin Naturalist 49:646–649.

Laudrè, 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, San Jose, California, USA.

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.
Martí, 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. 2015. Incorporating movement in species distribution models. Progress in Physical Geography 39:837–849.
Miller, R., S. Knick, D. Pyke, C. Meinke, S. Hansen, 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, Berkeley, California, USA.
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., et al. 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. Biological Report 28. National Biological Service, Washington, D.C., USA.
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-Abrain. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.
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.
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
PRISM Climate Group. 2004. Oregon State University. http://prism.oregonstate.edu
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.
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. Muller. 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.
Soil Survey Staff, Natural Resource Conservation Service, United States Department of Agriculture. U.S. General Soil Map (STATSGO2). http://sdmdbdataccess.nrcs.usda.gov/
Thuiller, W., M. B. Araújo, and S. Lavoire. 2004. Do we 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, New York, USA.
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., et al. 2013. 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.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1307/supinfo