# FINAL REPORT

## Relations among cheatgrass-driven fire, climate, and sensitive-status birds across the Great Basin

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# Abbreviations and Acronyms

AGL. Above ground level.
AVHRR. Advanced Very High Resolution Radiometer.
BLM. Bureau of Land Management.
BUGS. Bayesian Inference Using Gibbs Sampling.
CNN. Convolutional neural network.
FCN. Fully connected neural network.
GIS. Geographic information system.
JAGS. Just Another Gibbs Sampler.
JFSP. Joint Fire Science Program.
MODIS. Moderate Resolution Imaging Spectroradiometer.
NAIP. National Agriculture Imagery Program.
NDVI. Normalized difference vegetation index.
UAV. Unmanned aerial vehicle.
USDA. United States Department of Agriculture.
USFS. United States Forest Service.

# Keywords

# Acknowledgments

# Abstract

The principal aim of this project was to project changes in fuels, fire dynamics, and associated responses of vegetation and breeding birds that might inform selection and prioritization of management actions in the Great Basin. Our original six objectives were to model percent cover of cheatgrass (*Bromus tectorum*) across the Great Basin and project changes in cheatgrass cover as a function of precipitation; increase the accuracy of models of percent cover of sagebrush and herbaceous vegetation; use field data to train and validate models of vegetation cover and to relate cheatgrass cover and biomass; model probability of fire across the Great Basin as a function of percent cover of cheatgrass and precipitation; project changes in habitat quality and occupancy for sensitive-status birds given changes in vegetation; and test whether ecological thresholds (values of an environmental pressure at which ecosystem state changes abruptly and nonlinearly) occur in projected future vegetation cover, habitat quality, and occupancy.

We established study sites in four biogeographically distinct regions of the Great Basin. We collected field data on cheatgrass cover and biomass and other aspects of vegetation composition and structure, captured ultra-high resolution aerial images, and collected point-count data on breeding birds and their habitat.

The current body of public data does not allow reliable estimation of percent cover of cheatgrass as a continuous variable. Across the Great Basin, categorical percent cover of cheatgrass increased as primary productivity early in the growing season, which was correlated positively with precipitation, increased. Both the presence and proportion of years of grazing increased the probability of presence and prevalence of cheatgrass. Our results do not support the use of livestock grazing to suppress cheatgrass, and especially not in unburned areas.

Remote estimation of cheatgrass cover on the basis of visible spectral bands remains quite difficult unless the phenological stage of cheatgrass contrasts sharply with that of surrounding vegetation and cheatgrass cover exceeds about 20%. Ilastic, software with a random forest algorithm that uses spectral and texture features, proved to be a generally accurate classifier of land cover within sagebrush shrubsteppe on the basis of ultra-high resolution images.

Relations between percent cover and biomass (which is strongly related to fire likelihood) of cheatgrass were moderate to strong. We are clarifying whether the strength of the relation varies among regions or wet and dry years, or on the basis of sampling methods. From 1992–2012, about 52% of fires in the Intermountain West were human-ignited (75% in areas with cheatgrass), and that human ignitions more than doubled the length of fire season. The frequency of fires increased substantially in areas in which observed cheatgrass cover was > 1%.

Environmental associations with the abundances of individual species of breeding birds often were similar among regions, but apparent random or directional movement of individual birds during the breeding season complicates model fit. It appears that some species of birds are moving directionally along elevational gradients both within seasons and among years. The abundances of many riparian-obligate and facultative riparian species appeared to decline sharply beyond a given threshold of within-canyon riparian area.

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# Objectives

Our proposal responded to task statement 15-1-03, *Implications of changing fuels and fire regimes in selected regions*. The Great Basin was among the five selected regions. The intent of the task statement was to estimate likely changes and trends in fuels and fire regimes to approximately 2035, and to examine the potential implications of these changes and trends for management programs. We aimed to project future changes in fuels, fire dynamics, and associated ecological responses that might inform selection and prioritization of management actions in the Great Basin and shape structured adaptive management throughout the region.

To address the task statement, we originally established six study objectives. Our first objective was to model percent cover of cheatgrass across the Great Basin and project future changes in cheatgrass cover as a function of precipitation. Second, we proposed to use random forest models to increase the accuracy of models of percent cover of sagebrush and herbaceous vegetation. Third, we planned to use field data to train and validate models of vegetation cover and to relate cheatgrass cover and biomass. Our fourth objective was to model probability of fire across the Great Basin as a function of percent cover of cheatgrass and precipitation. Fifth, we planned to project changes in habitat quality and occupancy for Greater Sage-Grouse and other sensitive-status birds given changes in vegetation. Sixth, we proposed to test whether ecological thresholds (values of a natural or anthropogenic pressure at which abrupt, nonlinear changes in ecosystem state occur) occur in projected future vegetation cover, habitat quality, and occupancy.

Our efforts to meet the first objective yielded two peer-reviewed publications (Bradley et al. 2018, Williamson et al. 2020). As explained in Bradley et al. (2018), we found that a robust projection of percent cover of cheatgrass across the Great Basin was not possible. However, we developed a model that projected whether cheatgrass cover was $\geq 15\%$ or $< 15\%$ with moderate accuracy. Because we were unable to project percent cover of cheatgrass as a continuous variable, we were unable to project future changes in cheatgrass cover as a function of precipitation. Nevertheless, both publications clarified associations between direct and indirect measures of precipitation and presence, relative cover, and prevalence of cheatgrass.

Work toward meeting our second objective yielded a manuscript in revision (Horning et al.). It proved more challenging than we anticipated to transition from field measurements to mapping of land cover on the basis of moderate-resolution images from satellite-mounted sensors. We evaluated the accuracy of classifiers based not only on random forests but classifiers based on neural networks. Across five land-cover classes, and depending on the height above ground at which images were taken, three classifiers generally yielded overall accuracies $> 0.8$.

We found consistent relations between percent cover and biomass of cheatgrass, but it was unclear whether relations are uniform across the Great Basin and among sampling methods. Correlations between appear to be stronger when fine-resolution measures are aggregated within a moderate spatial extent (e.g., many 1m² quadrats aggregated along a 50-m transect) than when the same measures are not aggregated. We recently collected additional data to obtain greater clarity on sources of variation in the strength of the relation between percent cover and biomass.

Although it was not possible to model continuous percent cover of cheatgrass as a continuous variable, Bradley et al. (2018) and Williamson et al. (2020) yielded novel inferences on relations between fire, precipitation, and cheatgrass presence, prevalence, and cover. Balch et al. (2017) highlighted the increasing role of humans in igniting wildfires and extending the duration of the fire season across the conterminous United States.

We modeled the abundance of individual species of breeding birds in four regions of the Great Basin on the basis of vegetation and topography. The Joint Fire Science Program (JFSP) approved collection of data in the central Great Basin, which we did not originally propose. The volume of research focused on Greater Sage-Grouse is quite high, and volume of research focused on other species of breeding birds, especially those that may be affected by management actions taken in the name of conserving Greater Sage-Grouse (e.g., removal of native conifers), is relatively low. Accordingly, we concentrated on the latter species rather than Greater Sage-Grouse. Our analyses identified associations between abundance, vegetation attributes, and other environmental variables for a subset of species for which data were sufficient for modeling. Our work suggests strongly that within-season movements of birds, which violate assumptions of detection-weighted abundance models, may inhibit estimation of associations for many species, especially when relatively few years of data are available.

We found some evidence of thresholds in the abundance at which cheatgrass increases the likelihood of fire and in levels of riparian fragmentation that are associated with changes in the abundance of breeding birds.

**Working hypotheses**

Four working hypotheses served as a foundation for our work. We hypothesized that values of vegetation indexes (e.g., the normalized difference vegetation index [NDVI]) over time are positively correlated with percent cover of cheatgrass, and that growing season precipitation and NDVI in areas dominated by cheatgrass are strongly correlated. Additionally, we hypothesized that increases in percent cover of cheatgrass following wet growing seasons are positively related to the number and spatial extent of fires. We hypothesized that explanatory models of species occupancy as a function of environmental covariates would support projections to future time periods. Furthermore, we hypothesized that the state of at least some of our focal species of changes abruptly in response to abrupt or gradual changes in environmental conditions.


# Background

Increases in the distribution and abundance of non-native grasses have modified fire dynamics worldwide, often leading to loss of human life and property and to substantial financial costs (D'Antonio and Vitousek 1992, Brooks et al. 2004). As the geographic distribution and abundance of cheatgrass (*Bromus tectorum*), an annual grass native to Eurasia, increases across the Great Basin, it drives a cycle of increases in the frequency and extent of fire and further expansion of cheatgrass (Bradley et al. 2018). The area burned has increased by as much as 200% since 1980, accompanied by over US$1 billion in fire-suppression costs (Balch et al. 2013, NCEI 2018). Cheatgrass-induced changes in fire patterns are associated with loss of sagebrush

(*Artemisia* spp.), perennial grasses, and forbs that provide habitat for hundreds of plant and animal species. These species include Greater Sage-Grouse (*Centrocercus urophasianus*), which repeatedly has been considered for listing under the U.S. Endangered Species Act (Freeman et al. 2014, USFWS 2015, Germino et al. 2016), and many other sensitive-status animals and plants.

There also is strong evidence that regional warming and drying are linked to increased fire frequency and size and longer fire seasons in the western United States (Westerling et al. 2006, 2016; Jolly et al. 2015, Abatzoglou and Williams 2016, Williams and Abatzoglou 2016). It has been difficult to determine whether individual fires were ignited by lightning or human activity (Hawbaker et al. 2013). Humans change the distribution and density of ignitions, shift the season in which fires burn, and alter fuels (Bowman et al. 2009, 2011). Human ignitions generally are most prevalent at intermediate levels of development (Syphard et al. 2007, Bistinas et al. 2013, Balch et al. 2016). Human activity ignites fires when fuels are sufficiently dry enough to ignite and carry fire, but when lightning is rare.

**Predictors of the extent and dominance of cheatgrass**

Although the effects of cheatgrass on fire dynamics are well known, whether the distribution, abundance, and biomass of cheatgrass have predictable responses to environmental variables at large spatial extents is less clear. Several studies assessed environmental correlates of cheatgrass cover, density, or abundance in the Intermountain West (e.g., Gelbard and Belnap 2003, Bradley and Mustard 2006, Compagnoni and Adler 2014, Pilliod et al. 2017). These correlates vary across the range of cheatgrass (e.g., Bradley et al. 2016, Brooks et al. 2016), in relation to fire, and potentially over time.

Establishment of cheatgrass generally is associated with relatively high levels of precipitation during autumn or spring, which facilitate the species' germination and growth (Bradley et al. 2016). Percent cover and biomass of cheatgrass also can be highly responsive to heavy winter and spring precipitation (Knapp 1998). For example, cheatgrass biomass can increase tenfold following wet winters (Garton et al. 2011), substantially increasing fine-fuel loads and the probability of fire (Balch et al. 2013, Pilliod et al. 2017). Biomass of cheatgrass may remain high during the year following a wet winter, especially when competition from perennial grasses is low (Bradley et al. 2016). There is some evidence that the abundance of cheatgrass is less likely to increase in areas with relatively high summer precipitation and cool annual temperatures (Taylor et al. 2014, Brummer et al. 2016).

Other potential predictors of cheatgrass distribution and abundance include livestock grazing, abundance of native perennial grasses, elevation, and solar exposure. The percent cover, density, or abundance of cheatgrass can increase rapidly in areas that recently have burned or been disturbed by land uses such as road construction, maintenance, or use; agricultural activities; or grazing by domestic livestock (Mack 1981, Bradley and Mustard 2006, Banks and Baker 2011, Reisner et al. 2013, Pyke et al. 2016, Svejcar et al. 2017). Little research has quantified the links between cheatgrass and livestock grazing due to the difficulty of obtaining reliable, quantitative data regarding this land use. Yet management of livestock grazing on the public lands that cover about 75% of the Great Basin may have a substantial effect on the expansion and ecological effects of cheatgrass. Livestock trample soil crusts, which can increase potential colonization by

cheatgrass, and disperse cheatgrass seeds (Reisner et al. 2013). The abundance and percent cover of native perennial grasses that compete with cheatgrass independent of land use also are directly and negatively associated with the intensity of livestock grazing (Adler et al. 2005, Reisner et al. 2013). These grasses did not coevolve with high abundances of large ungulates (Mack and Thompson 1982). In many cases, the US Forest Service (USFS) and US Bureau of Land Management (BLM) defer continuation of livestock grazing on active allotments for two years following fire (BLM 2007). Although there are advocates for both shorter and longer exclusion periods, there are few empirical data to inform management decisions, especially in areas where cheatgrass has become widespread.

**Classification of cheatgrass and other vegetation types in sagebrush shrubsteppe**

Cheatgrass usually becomes productive earlier in spring than native grasses and shrubs in the Great Basin. As a result, it often is feasible to detect and map cheatgrass with satellite imagery (Peterson 2005, Bradley 2014). Models of the distribution of cheatgrass have been based on satellite data from Landsat, the Moderate Resolution Imaging Spectroradiometer (MODIS), and the Advanced Very High Resolution Radiometer (AVHRR) (Bradley and Mustard 2005, 2008; Peterson 2005, 2006; Clinton et al. 2010; Boyte et al. 2016, Downs et al. 2016).

Low-altitude aerial imagery can be a valuable source of data when transitioning from field measurements to predictions that are based on coarser resolution imagery collected by satellite sensors (Wang et al. 2017, Leitão et al. 2018). One can acquire digital photographs with a kite or pole aerial photography system. One also can acquire extremely close-range imagery with hand-held digital cameras. Although such platforms are valuable when unmanned aerial vehicle (UAV) flights are prohibited or for long-term monitoring, UAVs often are preferred because they are readily available, they can be programmed to fly precise autonomous missions, and systems with integrated cameras are available widely.

Hundreds of peer-reviewed papers (e.g., Horning 2018, Singh & Frazier 2018, Jiménez López & Mulero-Pázmány 2019) and books (Calvo and Lovejoy 2018, Wich and Koh 2018) illustrate realized and potential applications of UAVs in resource management, often with a focus on spatial assessment of land cover. Much of that literature emphasizes techniques that stitch together hundreds of aerial photographs to create orthophotographic mosaics that are geometrically correct and can be used in a geographic information system (GIS). Few publications provide pragmatic guidance on use of methods other than visual interpretation to extract extremely detailed land-cover information from images acquired by UAVs. Although there is tremendous value in visual or manual interpretation of true-color images, automating some of the information-extraction steps offers potential for analyzing much larger volumes of data, which might encompass larger areas, longer time periods, or more-frequent sampling.

**Relations between cheatgrass cover and biomass**

Estimates of the distribution or abundance of cheatgrass may depend on the year in which images were taken (Bradley and Mustard 2005). Additionally, relatively few data are available to train and test spatial models of cheatgrass derived from satellite imagery. The small spatial resolutions (e.g., a few square meters) or linear transects on which surveys of cheatgrass and

other vegetation often are based are not necessarily comparable to the spatial resolution of satellite images (e.g., hundreds of square meters to hectares; Bradley 2014). Moreover, the sparse training and testing data rarely include information on percent cover.

Increases in the accuracy of spatial models of cheatgrass presence and percent cover, especially at fine resolution, may increase understanding of the relations between cheatgrass and regional fire dynamics. Although the grass-fire cycle associated with cheatgrass long has been known (D'Antonio and Vitousek 1992, Brooks and Pyke 2001), its effects across the Great Basin were not estimated quantitatively until the past decade (Balch et al. 2013). Furthermore, the latter estimates were based on a remotely sensed product at 1 km resolution, with an overall accuracy of 61%, which was derived from annual variability observed during the 1990s (Bradley and Mustard 2008). Additionally, to the best of our knowledge, whether percent cover of cheatgrass is strongly correlated with biomass of cheatgrass (a fairly reliable measure of fine-fuel loads) is not well understood. A consistent relation between cover and biomass would facilitate estimates of fine-fuel loads, which are associated with the likelihood of intense fire.

**Predictors of habitat quality and occupancy of breeding birds**

Conservation of Greater Sage-Grouse is a major goal of fire and fuels management in the Great Basin, but actions intended to benefit Greater Sage-Grouse may have undesirable effects on other native species of breeding birds (Carlisle et al. 2018). Some of the species that we previously recorded in the central and western Great Basin that are considered sensitive by the Intermountain Region of the USDA Forest Service, on Partners in Flight's yellow list, or are designated by Partners in Flight as common but in steep decline, occur exclusively in from areas dominated by sagebrush (e.g., Loggerhead Shrike [*Lanius ludovicianus*], Horned Lark [*Eremophila alpestris*]). However, we have recorded the majority of these species, including Greater Sage-Grouse, in multiple vegetation types, and often at soft edges between sagebrush and woodland. Species that typically nest in sagebrush, for example, may sing from perches in nearby trees to attract mates; accordingly, the presence of both sagebrush and trees may contribute to recruitment of these species. Replacement of sagebrush by cheatgrass, natural expansion of woodlands, removal of trees or brush, and both fire and post-fire restoration may affect habitat quality and occupancy for multiple species.

Moreover, management actions conceived at the level of the Great Basin, whether aimed at Greater Sage-Grouse or other objectives, do not always recognize biogeographic differentiation. For example, Behle (1963) recognized five centers of avifaunal differentiation in the Great Basin (Warner, Sierra Nevada, western Great Basin, eastern Great Basin, and Inyo), which generally correspond to differences in climate and vegetation. Accordingly, the local habitat of a species that occurs across the region, and its response to environmental change, may vary.

From 2001–2015, we collected data in two avifaunal centers, the eastern Great Basin (Shoshone Mountains and Toiyabe, Toquima, and Monitor Ranges [Lander, Eureka, and Nye Counties, Nevada]) and the Inyo (east slope of the Sierra Nevada and the Sweetwater and Wassuk Ranges [Mono County, California and Mineral, Douglas, and Lyon Counties, Nevada]). This project allowed us to augment the regional extent of our data by conducting research in the Owyhee Uplands (southern Idaho) and the East Tintic and Sheeprock Mountains (central Utah), which

also fall within the eastern Great Basin. We aimed to compare models of detection-weighted occupancy and abundance among the four widely dispersed subregions.

Furthermore, we examined some of the assumptions that are inherent in methods used to draw inference on the status of breeding birds, and their relations to environmental variables and change, across not only the Great Basin but temperate ecosystems worldwide. Abundance models widely are used to infer relations between environmental variables and populations or species (Pearce and Ferrier 2001, Joseph et al. 2009, Tingley and Beissinger 2009). Abundance models are popular in part because detection data are easier to collect than data that require discriminating each individual (e.g., mark-recapture data). However, abundance models can be biased by imperfect detection (Royle and Nichols 2003).

N-mixture models (Royle 2004) frequently are used to estimate abundance from count data. These models assume that if an individual is detected at a given site during any one of the surveys (visits) in a survey period, it is available for sampling at that site during all surveys in the period. Diverse violations of this assumption can induce bias in N-mixture models, and these biases can be difficult to detect (Dail and Madsen 2011, Duarte et al. 2018, Link et al. 2018). At the resolutions generally used to detect birds (circles of ~100-400 m radius), some temporary, random movement is expected, especially where bird territories and study plots do not fully overlap (Jirinec et al. 2015), but permanent, non-random movement of passerine birds also is possible (McClure and Hill 2012). Temporary movement refers to the exit from and re-entry into a site of individuals during the survey window. Permanent movement refers to within-survey window entry, without exit, into a site by individuals from outside of the site, or to individuals' exit, without return, from the site. Permanent, non-random movements could be driven by nest failure, distributional shifts during the breeding season (e.g., elevational migration) (Betts et al. 2008), differences in the attributes of nest sites among broods within a season (Gow and Stutchbury 2013), or other events or behaviors.

Violations of the closure assumption as a result of permanent, non-random movement could bias estimators of abundance and associations between these response variables and covariates. To evaluate the extent to which seasonal availability varies and is a realistic concern for estimation of abundance, we also applied three-level hierarchical models to our avian detection data from the Great Basin. Permanent movement is a plausible explanation for such variation. Because studies that apply N-mixture models to repeated-sampling data are common in the literature, it is relevant to examine biases in these models' estimators that are induced by assumption violations.

**Ecological thresholds**

Much research in community ecology has focused on the theory that species richness increases as the area of habitat increases, and decreases as habitat becomes fragmented. Fragmentation usually refers to separation of previously contiguous land cover or habitat by land use. Some land-cover types, however, including many riparian areas in the Great Basin, are naturally isolated and fragmented. Species that evolved in these naturally fragmented systems may have different responses to habitat area and fragmentation than species in systems that are fragmented by land-use change. In the Intermountain West, the central Great Basin has some of the region's lowest levels of fragmentation from land-use change (Reeves et al. 2018).

Andrén (1994) suggested that fragmentation is a driver of species richness in areas where habitat is <30% of land cover, but Fahrig (2013) posited that habitat area explains species richness in nearly all systems (the "habitat amount hypothesis"). Previous analyses of the response of species richness to habitat area and fragmentation in naturally fragmented riparian systems in the Intermountain West are equivocal (Strong and Bock 1990, Pavlacky and Anderson 2007, Dickson et al. 2009). Any examination of the response of species richness to habitat area and fragmentation may be confounded by sampling effects; measures of sampling effort, such as the number of samples, area sampled, or sampling intensity, may explain some or all of the variance attributed to area and configuration. Fahrig's habitat amount hypothesis (2013) suggested that variance in species richness attributed to the size or isolation of habitat patches is explained more accurately by sampling effects. By contrast, other workers found that sampling effects did not explain all variation in species richness (Cam et al. 2002, Haddad et al. 2017), and a meta-analysis of tests of the habitat amount hypothesis found weak support that patch size and fragmentation affect species richness (Martin 2018). Furthermore, many measures of habitat fragmentation and, more generally, landscape pattern are not independent of total area of habitat (Wang et al. 2014). To properly assess the influence on species richness of fragmentation or any similar concept relating to the arrangement and shape of habitat patches, it is important to choose metrics that are not highly correlated with total area of habitat.

Riparian areas in the Great Basin are priorities for conservation and management due to their limited area, relatively high species richness, and future threats (Dobkin and Wilcox 1986, Dobkin 1998, Fleishman et al. 2014). The Great Basin is a largely arid region dominated by xeric shrubland and woodland, with a small fraction of riparian cover. These riparian areas typically are concentrated along small streams in canyon bottoms or in patches around valley or canyon seeps. Riparian areas in the Great Basin are naturally isolated, but have been further fragmented and degraded in recent centuries by human activities, including grazing by domestic cows and sheep, groundwater pumping, stream diversion, and land-use change (Fleischner 1994, Knopf and Samson 1994, Saab et al. 1995, Warkentin and Reed 1999, Brown et al. 2005, Chambers and Wisdom 2009, Fleishman et al. 2014). Furthermore, the size of many riparian areas likely will decrease as aridity increases over the next century (Brinson et al. 2002, Poff et al. 2012, Garfin et al. 2013). Many native species, including 32 bird species in the central Great Basin, occur primarily in these riparian areas. Variables related to riparian vegetation are correlated with occupancy, colonization, and extinction of at least several of these riparian bird species (Dickson et al. 2009). Species that are associated with xeric land-cover types also forage in nearby, higher-productivity riparian areas (Glass and Floyd 2015). Accordingly, their abundance may respond to the spatial arrangement of riparian patches and the total area of those patches.

## Materials and Methods

### Study system

Although the Great Basin, the largest desert in the United States (>425,000 km$^2$), sometimes is assumed to be relatively homogeneous, there is considerable regional variation in climate, topography, and vegetation. We established study sites in four distinct regions of the Great

Basin, hereafter referred to as western, eastern, northern, and central (Figure 1). These regional distinctions generally are consistent with zoogeographic definitions of the Great Basin. For example, the four regions fit well with Austin and Murphy's (1987) zones of butterfly differentiation, and three of the four regions correspond with Behle's (1963) zones of avifaunal differentiation.

**Figure 1.** Hydrographic boundary of the Great Basin and locations of study areas referenced in this report.
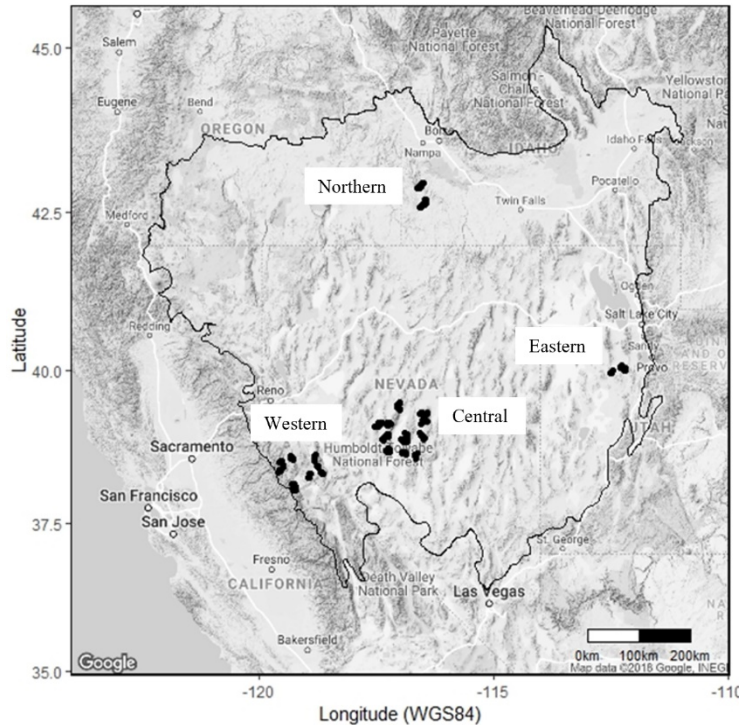


## Percent cover of cheatgrass across the Great Basin (Objective 1)

Methods are described in detail in Bradley et al. (2018). We compiled field data on percent cover of cheatgrass, including zero percent cover, from 15 sources. We aggregated these data to 250-m resolution, consistent with the finest resolution of data on phenology, measures of primary productivity (NDVI), and tree cover from MODIS. We used a random forest regression model, implemented in R, to predict percent cover of cheatgrass on the basis of 21 spatial data layers. Additionally, we predicted cheatgrass presence. We evaluated whether cheatgrass presence and percent cover were related to area burned from 2000–2014 and to the number of fires. We also tested whether ignition sources varied between fires in areas where cheatgrass was present or absent, and whether cheatgrass was more likely to be present in pixels associated with ignitions than other pixels.

**Predictors of the presence and prevalence of cheatgrass (Objective 1)**

Methods are described in detail in Williamson et al. (2020). We used two sets of data collected from 2001–2015 in 29 canyons in the central Great Basin (Fleishman 2015). Within those canyons, we sampled cheatgrass at elevations from 1886–3219 m over a range of disturbance histories. Complete vegetation data and metadata are in Chambers et al. (2010) and Fleishman (2015). Details about data collection methods also are in Urza et al. (2017).

We collected data on cheatgrass and other elements of vegetation structure and composition from 30–50 m point-intercept transects along elevational gradients of the 29 canyons. We also collected vegetation data in three pairs of adjacent alluvial fans on burned and unburned sites within one watershed in the Shoshone Mountains. We established sampling plots within burned and unburned plots at each elevation. We refer to each transect or plot as a *sample point*.

We assessed cheatgrass occurrence by considering sample points at which cheatgrass was not recorded during the study period as absences, and sample points at which cheatgrass was recorded present in ≥ 1 year during the study period as presences. For each sample point at which cheatgrass was recorded present, we estimated local prevalence of cheatgrass by summing the number of point intercepts (or quadrats) where cheatgrass was recorded present and the total number of point intercepts (or quadrats) taken at each point in a given year.

We characterized the grazing and fire history of each sample point for each year. We assigned a binary value to indicate whether the allotment in which a given sample point was embedded was grazed during each year. Because data on realized (as opposed to permitted) grazing intensity are not maintained by the USFS, which manages virtually all of the land on which our sample points were located, we assumed that all active allotments were grazed. We calculated the proportion of years during which each sample point was grazed (years grazed / years during the study period prior to collection of data in a given year) to estimate levels of livestock use. We classified sampled points as burned if a fire occurred at the sample point from 2000–2015. For burned points, we calculated the number of growing seasons between the fire and a given field sample.

We modeled associations between predictors and occurrence and between predictors and annual variation in prevalence. To evaluate associations with predictors in the presence and in the absence of fire, we applied these models to all of the data, to only those points that had not been burned, and to only those points that had been burned. We did not fit occurrence models to burned points because cheatgrass was recorded present in nearly all of them, preventing the model from discriminating between the determinants of presence and absence. We classified sample points as *recorded present* if cheatgrass was detected at any time during the study period and *recorded absent* if cheatgrass was not observed during the study period.

We assessed the strength of evidence that a predictor was strongly associated with the probability of occurrence or with the prevalence of cheatgrass by calculating the proportion of the posterior probability distribution that exceeded zero for each predictor's regression coefficient. We regarded predictors for which $> 0.90$ or $< 0.10$ of the posterior predictive mass for the regression coefficient $\geq 0$, respectively, as strongly and positively or strongly and negatively associated with the response variable (Jeffreys 1961).

**Classification of cheatgrass and other vegetation types (Objective 2)**

Methods are described in detail in Horning et al. (in revision). We compared four machine-learning workflows for classifying images. The workflows are based on open-source software and can be used to create land-cover maps from ultra-high resolution aerial imagery. We focused on workflows that are applicable to imagery acquired from a UAV at flying heights $< 122$ m above ground level, an upper limit set by a US federal regulation. Images acquired with point-and-shoot or action cameras, which often are supplied with consumer UAVs at these flying heights, have a spatial resolution of 10 cm (deci-resolution) or finer.

To obtain photographs, we used the stock red-green-blue camera on a DJI Phantom 3 Pro quadcopter flown over heterogenous sagebrush shrubsteppe. For our analysis we selected three, 12 megapixel (3000 lines by 4000 columns) images, one each from a flying height of 10, 45, and

90 m above the elevation of the take-off point. Because the ground was relatively level, we refer to the flying height as above ground level (AGL), and distortion due to terrain effects was minimal. We acquired the three images on 14 June 2017 from the same area in central Nevada.

We classified images acquired from 10 m AGL into six cover types—cheatgrass, other grasses and forbs, shrub, soil and rock, litter, and shadow. We did not include litter in our classification of images from 45 and 90 m AGL because litter objects became too small to interpret visually. To increase our confidence that the training data adequately represented feature variability, we used a kmeans unsupervised classifier to partition feature space into several clusters, and then selected training data from each cluster to ensure there were no major gaps in feature variability throughout the image. We used the validation data to assess accuracy of all workflows.

Our four workflows were ilastic, software with a random forest algorithm that uses spectral and texture features (Sommer et al. 2011; www.ilastik.org); segmentation, a random forest algorithm applied to image objects that were defined with image segmentation; fully connected neural networks (FCNs), which process one-dimensional vectors; and convolutional neural networks (CNNs), which process two-dimensional image chips. Random forest (Breiman 2001) is a nonparametric, machine learning method with high classification accuracy for remote sensing applications (Rodriguez-Galiano et al. 2012). To implement FCNs and CNNs, we used the Neural Network Image Classifier (Nenetic) (https://github.com/persts/Nenetic), an open-source software package under development at the American Museum of Natural History. All of the software for these workflows is open source and available, at no cost, for Windows, Mac, and Linux operating systems.

We assessed the accuracy of each workflow on the basis of 2000 pixels selected from the original set of labeled data for each flying height. The total number of labeled pixels from the images acquired at 10 m, 45 m, and 90 m flying heights was 880267, 267195, and 230670, respectively. In all cases the number of training points equated to < 1% of the labeled data, so spatial autocorrelation between training and validation data likely was minimal.

We calculated overall accuracy at each flying height. We also assessed accuracy per class by calculating user's and producer's accuracy (Story and Congalton 1986) and balanced accuracy (Velez et al. 2007). For a given class, user's accuracy is the proportion of pixels attributed to that class that were classified correctly, whereas producer's accuracy is the proportion of reference pixels for the class that were classified correctly. Balanced accuracy, which compensates for differences in sample sizes among classes, is calculated as 0.5 * (proportion of all positives that are true positives + proportion of all negatives that are true negatives).

**Relations between cheatgrass cover and biomass (Objective 3)**

We measured cheatgrass cover and biomass from 2016–2019 in the north-central, western, central, northern, and eastern Great Basin. Within each region, precise sampling locations varied among years, but were intended to represent the full gradient of cheatgrass cover during each year. All biomass samples were placed in paper bags and delivered to the University of Colorado. We dried the samples at 60°C until the mass stabilized, and then weighed the samples.

In the north-central Great Basin (near Battle Mountain and Winnemucca, Nevada), we collected samples in 20 locations in each of 2016, 2017, and 2018. The locations were dominated by shrubs, cheatgrass, or cheatgrass and forbs at elevations from 1300–1600 m. All locations were relatively flat (< 5% slope), with similar soils and a recent history of livestock grazing. In 2016, we established three pairs of parallel 50 m transects, with 20 m between the two transects in a given pair, at each location. At 5-m intervals along each transect, we recorded an ocular estimate of percent cover in one 0.1 m² quadrat (11 estimates per transect). We then clipped the aboveground biomass of cheatgrass. In 2017 and 2018, we established a 30-m transect at each location and sampled biomass in five 0.1 m² quadrats at randomly selected positions along the transect. In 2016, we also sampled 28, 50 x 50 m plots. We established nine 1 m² quadrats at random locations within each plot and took a digital photograph of each from approximately 1.5 m above ground level. We then clipped all cheatgrass from a 0.1 m² area in the northwest corner. We aggregated biomass from the quadrats. We used Samplepoint software (Booth et al. 2006) to estimate percent cover within each quadrat, and averaged percent cover among the quadrats.

In 2016 and 2017, we collected data in the western and northern Great Basin; in 2017, we collected data in the eastern Great Basin. We sampled cheatgrass in the same general areas in which we sampled birds. In all cases, we established a 10 x 10 m plot, set 1 m² quadrats in the center and each corner, and measured maximum height (with a measuring tape) and cover (ocular estimate) of cheatgrass in each quadrat. In roughly half of the plots, we placed a 0.1 m² hoop in the middle of the upper left and lower right quadrats, and clipped all aboveground biomass of cheatgrass within the hoop. In the western Great Basin, we collected data from 24 plots in 2016 and 20 plots in 2017. In the northern Great Basin, we collected data from 31 plots in 2016 and 20 plots in 2017. We collected data from 33 plots in the eastern Great Basin in 2017.

In 2018, we collected data in the western, northern, and central Great Basin; in 2019, we collected data in the western and central Great Basin. We established 1 m² plots in which we recorded an ocular estimate of average percent cover of cheatgrass and clipped aboveground biomass in a representative 0.1 m². In all three regions, we collected data from 40 plots in 2018. In both the central and western Great Basin, we collected data from 50 plots in 2019.

**Relations between cheatgrass and fire (Objective 4)**

We derived our data from US Forest Service Fire Program Analysis – Fire Occurrence Database (Short 2014), which includes ~1.6 million federal, state, and local records of wildfires (including location, discovery date, and cause) on public and private lands that were suppressed from 1992–2012. We calculated the proportion of human-ignited versus lightning-ignited wildfires within equal-area 50 × 50-km grid cells across the conterminous United States.

We obtained daily 1,000-h dead fuel moisture data from 1992–2012 from surface meteorological data on a 4-km grid (Abatzoglou 2013). We acquired 4-km gridded monthly lightning-strike data from the Vaisala National Lightning Detection Network (www.ncdc. noaa.gov/data-access/severe-weather/lightning-products-and-services). We also obtained MODIS data on mean annual net primary productivity at 1 km resolution from 2002–2015 (Zhao et al. 2015). We assessed temporal trends in the causes of wildfires on the basis of large fires (>

12

400 ha in the western and > 200 ha in the eastern United States) that were independently verified by the Monitoring Trends in Burn Severity project (Eidenshink et al. 2007).

**Predictors of habitat quality and occupancy of breeding birds (Objective 5)**

We collected point-count data on breeding birds and their habitat in the eastern, northern, and western Great Basin during the breeding seasons (mid May through early July) of 2016 and 2017, and in the central and western Great Basin during the breeding seasons of 2018 and 2019. Adding the central Great Basin to the project allowed us to capitalize on up to 15 years of existing data on breeding birds and vegetation. In 2016, we visited each point-count location in the western Great Basin four times (see below). In all other locations and years, we visited each point three times. We recorded all species of birds detected by sight or sound.  At all points in the eastern, northern, and western Great Basin, we collected data on vegetation structure and composition, focusing on trees and shrubs. We collected similar data in the central Great Basin in 2013; because values of most of our vegetation variables were unlikely to change appreciably over less than a decade, we did not repeat these measurements during the study period.

We compared estimates of single-season occupancy models that were based on three and four visits. We had sufficient data to build models for 45 species; one or both models for two species with few detections did not converge. Occupancy estimates for 41 of the remaining 43 species did not differ significantly between the three-visit and four-visit models, although precision of estimates based on four visits was higher than that based on three visits. Given constraints on the duration of the breeding season and on the number of observers we could employ, we decided that our inferences would be stronger if we visited a greater number of locations three times rather than fewer locations four times.

We conducted heads-up digitization of National Agriculture Imagery Program images of our western Great Basin and long-term central Great Basin study areas to quantify the extent and configuration of hard and soft edges among major land-cover or vegetation types (shrubs, conifers, riparian woody vegetation, riparian meadows, and aspen).

In 2018, we implemented a new method for collection of bird data in which we broke our 8-minute sample period into four consecutive 2-min periods (removal intervals). Individual birds only were recorded during the first interval in which they were detected. This allowed us to estimate whether apparent absence of a species at a given location during a given survey reflected failure to detect individuals that were present or true absence (Chandler et al. 2011), likely resulting from movement of birds between successive surveys.

**Relations between abundance and environmental variables.** We used Bayesian methods to fit single-species, N-mixture models to multiple years of abundance data from the western (2012–2019), central (2014, 2015, 2018, 2019), eastern (2016–2017), and northern (2016–2017) Great Basin. Computational requirements prevented us from including all years of central Great Basin data in the models. We calculated annual abundance as the maximum number of detections on any visit within the season. We removed the data from the second visit to each point from the 2016 western Great Basin data (in 2016, we visited each point four times).

In the majority of cases, we modeled the abundance of species for which the number of detections in two or more years exceeded 50. We modeled the abundance of each species as a function of year, elevation, and other environmental covariates that we selected on the basis of the species' ecology (Appendix C). We included canyon or area and point as random effects in all models, and included observer as a random effect in models for the western and central Great Basin. We removed covariates with variance inflation factors > 4. If the correlation between two covariates was > 0.75, we removed the covariate with the higher variance inflation factor.

We used latent indicator variables to select models and covariates (Kery and Royle 2016). Indicator variables typically are used to track the posterior probability of the inclusion of a given predictor in good models. The indicators for predictors that strongly are associated with the response variable often will be included, whereas those for predictors that are not associated with the response variable rarely will be included.

We first ran 100,000 iterations of each single-species model with all covariates and indicator variables included. We implemented models in BUGS (Bayesian Inference Using Gibbs Sampling) with JAGS (Just Another Gibbs Sampler) and the R package *jagsUI*, and ran models in R (version 3.6.1). We assessed whether models converged, and used Bayesian p-values to evaluate goodness of fit. We examined the mean of the posterior probability of each indicator variable and retained covariates for which the mean was > 0.9, indicating that the variable was included in > 90% of models. After removing all other covariates, we ran another 200,000 iterations of each model.

Outputs included the mean and standard deviation of the coefficient of the covariate, an indication of whether the covariate overlapped zero, and Bayesian p-values for the detection and abundance submodels. Means of the covariates are comparable within models but not among species. Covariates that did not overlap zero are considered highly significant, and the direction of the association with abundance is indicated by the sign of the coefficient. A Bayesian p-value ~0.5 is considered ideal, and values 0.1–0.9 are considered acceptable. It is not advisable to draw inference about strengths of association with covariates for which posterior probabilities are extremely large and overlap zero, although these covariates can improve model fit.

**Availability and detection.** Methods for evaluating the extent to which closure-assumption violations induce biases in modeled estimators are described in detail in Fogarty and Fleishman (in review) We based simulation models on count data and interpreted the response variable as abundance. We built a simulator in R that allows customization of values. These values include permanent, non-random movement terms that reflect violations of the closure assumption, and values that usually are estimated by abundance models (e.g., abundance, detection probability, and effects of environmental covariates). All simulations assumed that individuals entered from or exited to sites not included in the simulation, and that counts at sites were not spatially autocorrelated. We estimated mean abundance and the relation between abundance and an environmental covariate.

For each species and region, we used the function *gmultimix* in the R package Unmarked to fit three-level hierarchical models to our 2018 detection data from the western and central Great Basin. We selected all species that were well-distributed at study sites and for which we had ≥ 45

records (28 species in the western and 27 species in the central Great Basin) as sufficient for analysis. We estimated three processes: abundance, availability, and detection. We interpreted detection as the probability of detecting an individual that was present and available during a given visit. We interpreted availability as the probability that an individual that occupied a given site at some point during the season was detectable, on the basis of both presence and behavior, during a given visit, and abundance as the total number of individuals that occupied a site for the full duration of the breeding season in which we conducted surveys.

**Ecological thresholds (Objective 6)**

Our analyses included point-count data collected in the central Great Basin from 2001–2015 and in 2018. Steep, high canyon walls covered by relatively xeric land-cover types tend to isolate the riparian areas at the bottom of individual canyons from those in neighboring canyons. Our point-count data include bird detections from 320 points in 27 canyons in the four mountain ranges.

We detected a total of 126 species. Because our survey effort included 16 years and a high density of points, we believe that few breeding species were undetected, and therefore did not apply data augmentation or other forms of rarefaction to these data. We fit abundance models to all species that we detected at least 400 times across all years and in at least 20% of our sites (32 species). We characterized each species as riparian or non-riparian (i.e., generally breed in coniferous woodland or sagebrush shrubsteppe).

We derived riparian area and fragmentation at the canyon level from National Agricultural Imagery Program (NAIP) images. To calculate riparian area, we delineated a buffer (500 meters from the canyon bottom) that was sufficiently large to encompass all riparian vegetation in most canyons and to extend beyond the expected territorial boundaries of riparian bird species. We mapped riparian land cover within the buffer for all study canyons, and classified riparian as wet meadows (little to no perennial woody vegetation; dominated by grasses, sedges, and forbs) or woody riparian (extensive cover of perennial woody vegetation, primarily *Betula occidentalis*, *Populus* spp., *Prunus virginiana*, *Salix* spp., or *Rosa woodsii*) in QGIS. We were not confident in our ability to visually discern between structural classes (e.g., trees versus shrubs) or individual woody species in the NAIP images, and therefore did not sub-classify the cover types.

We selected the Normalized Landscape Shape Index (nLSI) (McGarigal et al. 2012) as our measure of fragmentation. This nLSI assesses the shape of all focal patches and is not highly correlated with total area of the focal land-cover type when they represent < 30% of a given study area, as was the case in our system (Wang et al. 2014). The other fragmentation metrics identified by Wang et al. (2014) as not highly correlated with total area of the focal land-cover type are less intuitive measures of variance, require a minimum number of patches, or require user delineation of core focal land-cover. We calculated nLSI and total riparian area for all of our canyons with the program FragStats (McGarigal et al. 2012). We also calculated total canyon length and proportion of canyon bottom. We included these covariates in models to ensure that inferences about riparian area and fragmentation were not conflated with canyon size. We defined canyon bottom as flat areas (≤ 10°) between the inflection points of a concave canyon profile, derived from a 10-m digital elevation model, every 25 m along a line perpendicular to the canyon flow line. We calculated proportion of canyon bottom as the area of canyon bottom

divided by the total area within the a 500-m buffer surrounding the sampling route (the access road or trail near which points were established). For non-riparian species models, we also calculated the distance from each survey point to the nearest riparian patch in QGIS.

We fit mixed-effect, Bayesian N-mixture models (Royle 2004, Kéry and Royle 2016) with R and JAGS to examine the abundance relations described above. In each model, we included linear and quadratic forms of four standardized covariates on the abundance process: riparian area, nLSI, proportion of canyon bottom, and canyon length. In each of the non-riparian species models, we also fit a covariate for distance to the nearest riparian patch. In all models, we included varying intercepts for each point to account for repeated surveys across years. We fit standardized linear and quadratic terms on the observation process for time of survey and date of survey, and a varying intercept for observer identity. We used weakly informative priors (normal distributions with a mean of 0 and variance of 1) for all non-varying parameters, and used a uniform distribution with a mean of 0 and variance of 10 for the variance of each varying intercept. We used the indicator variable method (Kuo and Mallick 1998, Kéry and Royle, 2016) to evaluate posterior model probabilities and perform model selection. We evaluated goodness-of-fit by calculating Bayesian p-values for both the abundance and observation processes of the model. We rejected any models that had Bayesian p-values $< 0.5$ or $> 0.95$.

## Results and Discussion

**Percent cover of cheatgrass across the Great Basin (Objective 1)**

As detailed in Bradley et al. (2018), we found that early season productivity (spring–summer NDVI), which was correlated positively with precipitation, was associated positively with percent cover of cheatgrass. Elevation was associated negatively with percent cover of cheatgrass. We were unable to classify percent cover of cheatgrass as a continuous variable. However, at a threshold of 15% cover, with $\geq 15\%$ characterized as high abundance and $< 15\%$ as low abundance, accuracies were 67% and 77%, respectively. The overall accuracy of the model is considered moderate (Landis and Koch 1977). This model estimated that cheatgrass cover is $\geq 15\%$ across about 1/3 of the Great Basin (210,000 km$^2$), especially in northern Nevada, Idaho, Oregon, and Washington. More than twice as much area within which abundance of cheatgrass was high burned from 2000–2014 than area within which abundance was low. The frequency of fires increased substantially in areas in which observed cheatgrass cover was $> 1\%$. Furthermore, human activity was associated with 75% of ignitions in areas in which cheatgrass was present, as compared with 27% of fires in areas in which cheatgrass was absent.

**Predictors of the presence and prevalence of cheatgrass (Objective 1)**

Consistent with previous studies on the cheatgrass-fire cycle (Balch et al. 2013, Germino et al. 2016, Bradley et al. 2018), we found that the probabilities of cheatgrass occurrence and prevalence were associated strongly with fire (Williamson et al. 2020). In burned points, cheatgrass prevalence increased as time since fire increased. A lag in increases in cheatgrass density and cover of one to three years after fire is common (Chambers et al. 2016).

Consistent with Reisner et al. (2013), our analyses suggest that both the presence and proportion of years of livestock grazing increase the probability of presence and prevalence of cheatgrass. This relation was particularly strong in unburned locations, which have higher resistance to cheatgrass than burned locations. It has been suggested that grazing can reduce fuel loads and the likelihood of severe fires in sagebrush ecosystems (Davies et al. 2010). However, our work suggested that grazing on burned sites may lead to an overall decrease in herbaceous cover or biomass rather than selectively suppressing cheatgrass.

The response of cheatgrass to longer-term precipitation (median winter and spring precipitation and the median proportion of precipitation falling in winter) was inconsistent. Cheatgrass prevalence tended to be lower in years in which precipitation at a given point was high relative to that point's long-term median, but higher when regional winter precipitation was high and regional spring precipitation was at or below the median for the study period. Many of our observations of high prevalence of cheatgrass that coincided with relatively high proportions of precipitation in winter were associated with water-years in which precipitation was low. Therefore, the amount of precipitation falling during periods favorable for cheatgrass establishment and growth may be more important than the total precipitation for the year (Bradley and Mustard 2005, Chambers et al. 2014, Jones et al. 2015).

Regardless of fire history, cheatgrass was more likely to be recorded present at lower elevations. However, given presence, cheatgrass prevalence was greater at higher elevations and in areas with lower solar exposure. Higher prevalence of cheatgrass at relatively high elevations at the edges of unoccupied areas suggests that cheatgrass is likely to expand to higher elevations if thermal conditions are consistent with its requirements and if ground disturbances continue.

**Classification of cheatgrass and other vegetation types (Objective 2)**

On the basis of overall accuracy, the ilastik workflow yielded the most accurate results. Accuracy as measured by the per-class metrics was more equivocal. At the 10 m flying height, the FCN workflow most accurately classified the shrub class, but the ilastic workflow generally was the most accurate classifier. At the 45 m flying height, ilastik most accurately classified all but the shrub class. At the 90 m flying height, the CNN workflow most accurately classified grasses and forbs, shrubs, and cheatgrass.

The difference between the segmentation output and the outputs of the other workflows increased as the flying height increased; as height increased, many smaller land-cover patches appeared to merge with surrounding cover types. All of the workflows have the potential to accurately classify cheatgrass when it is spectrally distinct from the surrounding vegetation. In the set of photographs we used, cheatgrass was redder than the surrounding vegetation. Classification becomes more difficult when the density of the cheatgrass within a patch is quite low or when it is shaded.

A goal of automated, ultra-high resolution mapping in the visible spectrum is to match or exceed the accuracy with which a trained human can identify and label land-cover objects, and to do so faster and more objectively. Our research indicates that automated classification of aerial photographs acquired from low flying heights with consumer UAVs and cameras remains

difficult. Although much progress has been made in leveraging deep-learning algorithms to locate and identify or label features in an image, ultra-high resolution image classification is not yet widely accessible and applicable to classification of cheatgrass, shrubs, other grasses, and forbs in sagebrush shrubsteppe.

Few existing methods for assessing the accuracy of coarse-resolution land-cover classifications (Congalton and Green 2008) are applicable to ultra-high resolution imagery (Persello and Bruzzone 2010). Other methods for selection of validation data better represent objects, but often are more subjective, especially in landscapes with cover-class gradients. In undeveloped areas, clear boundaries between cover types are uncommon, and it is much more difficult to define object boundaries when the transition between objects is a gradient rather than a sharp edge.

The gradients between some cover types become more gradual (less stark) as flying height increases, making it more difficult to segment individual cover types. Cheatgrass can occur in relatively dense monocultures, but also co-occurs with other grasses and forbs. The latter can make it quite difficult to classify cheatgrass accurately, even with visual interpretation.

**Relations between cheatgrass cover and biomass (Objective 3)**

We found fairly strong correlations between biomass and percent cover of cheatgrass at different spatial resolutions and in different years ($r^2$ 0.67–0.86) in the north-central Great Basin. A linear model with no interactions that included all data from 2016–2018 yielded an $r^2$ of 0.82.

Relations between percent cover and biomass in the western Great Basin from 2016–2018, and in the northern Great Basin in 2016 and 2017, were weaker than those in the north-central Great Basin, but fairly similar ($r^2$ 0.36–0.42) (Figure 2). However, the relation in the northern Great Basin in 2019 was much stronger ($r^2 = 0.79$). We are analyzing the 2019 data to clarify whether the difference reflects the change in sampling methods in 2018 or a difference in the relation between percent cover and biomass, perhaps reflecting that precipitation in the winter and spring preceding data collection in 2018 was much greater than during the comparable periods in 2016 and 2017.

**Relations between cheatgrass and fire (Objective 4)**

Of the 1.5 million wildfires in the conterminous United States from 1992–2012 that were included in the analysis of Balch et al. (2017), 84% were ignited by humans. The percentage of human-ignited wildfires varied among level 1 ecoregions (Wiken et al. 2011), from 97% in Mediterranean California to 34% in the temperate Sierra Nevada. Across much of the ecoregion roughly corresponding to the Intermountain West (North American Deserts), about 52% of fires were human-ignited (as compared to 44% across the country), and these fires accounted for 21% of the area burned. Human-ignited wildfires substantially increased the length of the wildfire season in the United States; in the western United States, human-ignited fires were prevalent in late summer and autumn. Across the country, the lengths of the human and lightning-ignited wildfire seasons were 154 and 46 days, respectively. In the Intermountain West, the human- and lightning-ignited seasons were 92 and 40 days, respectively.

**Figure 2.** Relation between biomass (g/m²) and percent cover of cheatgrass. gb, Great Basin.
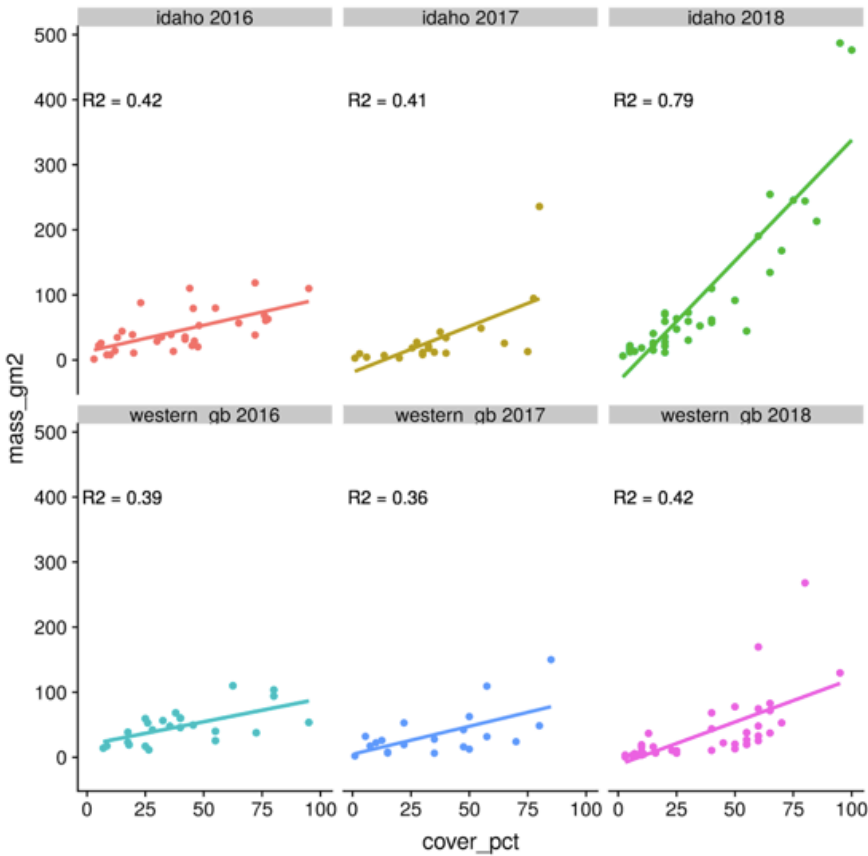


These results are consistent with evidence that worldwide, humans tend to change the seasonality of wildfires (Le Page et al. 2010). As the climate of the western United States has become warmer and drier, the number of fires generally has increased (Westerling et al. 2006, Dennison et al. 2014, Westerling 2016). Nevertheless, human activity has increased the duration of the fire season. Lightning-ignited fires usually occurred during summer and in areas with < 15% fuel moisture, whereas, nationally, about 75% of human-ignited fires occurred during other seasons. Moreover, human-ignited fires occurred in areas with higher fuel moisture and net primary productivity than those with lighting-ignited fires. The extent of the wildland–urban interface in the Intermountain West is projected to double by 2030 (Theobald and Romme 2007). The number of ignitions, and the risk to infrastructure, also are likely to increase considerably.

**Predictors of habitat quality and occupancy of breeding birds (Objective 5)**

**Relations between abundance and environmental variables.** Of the 79 abundance models we ran, 40% did not pass goodness-of-fit tests in the initial model runs (Table 1). The goodness-of-fit of the abundance submodel usually was acceptable, but that of the detection submodel was not. We strongly suspect that the lack of fit is a consequence of violations of the closure assumption due to random or non-random movement of individuals throughout the breeding season (see below). We are developing methods to include availability in our models, which we suspect will improve the fit of many more models. We also are exploring methods to assess movement of species and of individuals (see Conclusions).

No covariates were retained in 11 of the models, indicating that those environmental attributes did not explain substantial variation in abundance. In the cases in which models for a given species in two or more regions passed goodness-of-fit tests, the retained covariates often were

similar among regions. For example, abundance of Gray Flycatchers (*Empidonax wrightii*) was positively associated with percent cover of pinyon and juniper in the central and eastern Great Basin, and abundance of MacGillivray's Warblers (*Geothlypis tolmiei*) was positively associated with the incidence of riparian trees and shrubs in both the western and central Great Basin (Appendix D). Despite recent reports that abundances of passerines are declining across the United States (Rosenberg et al. 2019), year was positively associated with abundance in all models in which it was retained and passed all inferential tests (e.g., covariates did not overlap zero and Bayesian p-values for the final model were acceptable). The latter suggests that within our study regions, abundances of at least some passerines appear to be increasing rather than decreasing over time.

Even with many years of data, many passerines in the Great Basin likely are too rare for rigorous modeling of abundance, which is considerably more informative than, and not necessarily correlated with, simple occupancy. Hierarchical models of occupancy theoretically are applicable to communities in which many species are rare. However, hierarchical models assume that species are sufficiently similar ecologically that inference on associations between occupancy of rare species and covariates can be drawn from those for common species, which we do not believe is the case in our study system.

**Table 1.** Number of single-species abundance models that met criteria for strong inference.

| Region | Passed goodness-of-fit tests, covariates retained | Passed goodness-of-fit tests, uncertain inference from some retained covariates | Passed goodness-of-fit tests, no covariates retained | Passed goodness-of-fit tests, one or more Bayesian p-values not acceptable | Did not pass goodness-of-fit tests |
|---|---|---|---|---|---|
| Western | 5 | 1 | 3 | 4 | 9 |
| Central | 9 | 3 | 3 | 4 | 13 |
| Eastern | 3 | 2 | 5 | 3 | |
| Northern | 1 | 1 | | 1 | 9 |

**Availability and detection.** In simulations, detection-weighted abundance models were sensitive to low magnitudes of assumption violations. The bias in abundance estimators induced by violations of the closure assumption increased as simulated values of either initial abundance or detection probability increased. That estimation of the abundance of abundant, easily detected species is challenging may seem counterintuitive, but reflects that it is difficult to discriminate between failures to detect individuals present at a site and absences due to movement. When detection probability is high, the ratio of missed detections to absences due to movement is low, increasing the bias in estimators of abundance.

Application of our models to field data suggested that availability was the dominant driver of imperfect detection during the breeding season. Furthermore, associations between survey date

and availability suggest that availability changed throughout the season, perhaps indicating permanent movement.

Our work suggests that lack of closure in study systems may bias inferences about abundance from detection-weighted models. Estimators of associations between environmental covariates and abundance may be more robust to violations of the closure assumption. Our results indicate that in most situations, estimators of the association between abundance and environmental covariates from detection-weighted models are minimally biased by even high levels of immigration or emigration. The exceptions are most cases with both immigration and emigration. Therefore, violations may create strong bias in some applications of abundance models (e.g., absolute or relative abundances of species, likelihood of or temporal trends in occurrence).

If detection probability is known *a priori* to be high, naïve models may be more robust than detection-weighted models to violations of the closure assumption, especially if violations largely reflect immigration. However, if detection probability is low, the resulting substantial bias in naïve models outweighs any increases in robustness.

Understanding of the potential bias created by violations of closure assumptions also was a concern for mark-recapture models (Otis 1978). Temporary, random movement did not bias estimators in mark-recapture models; some estimators were robust to either permanent immigration or permanent emigration, but not both; and other types of movement heterogeneity biased some estimators (Kendall 1999). Our results differ with respect to the effects of permanent immigration or emigration, perhaps because we modeled movement as non-random or because Kendall (1999) compared estimates of the abundance of population rather than site-level abundances. Our results are consistent with indications that permanent movement-driven violations of the closure assumption bias estimators of occupancy models (Rota et al. 2009, Hayes and Monfils 2015), and that the estimators from N-mixture models are sensitive to violations of assumptions (Dail and Madsen 2011, Duarte et al. 2018, Link et al. 2018).

Our work builds on previous studies by incorporating a more ecologically informed model of movement that is supported by field data and estimating the effect size of availability and false absence-driven biases on modeled estimators. Our results suggested that within-breeding season, non-random movement of individual birds was common, the magnitude of this movement likely would bias estimators of abundance from both detection-weighted models and naïve models that do not account for such movement, and common perceptions about seasonal closure of breeding territories in birds are too simple.

**Thresholds.** In the first iteration of our analyses, the site-level abundances of 11 of 12 species associated with riparian areas were correlated strongly with total riparian area at the canyon level; the abundances of most species appeared to decline sharply beyond a given threshold. The abundance of one species, Broad-tailed Hummingbird (*Selasphorus platycercus*), was strongly and positively related to riparian fragmentation. Information on thresholds of riparian area or fragmentation above or below which species richness or the likely abundances of species change substantially may have practical application given ongoing changes in climate and land use, which may result in riparian areas contracting and fragmenting further during the next century.

**Science delivery**

We engaged management partners throughout the project. As the project launched, we benefited from the expertise, experience, and networks of Todd Hopkins (then Science Coordinator for the Great Basin Landscape Conservation Cooperative) and Mike Pellant (an expert on cheatgrass and sagebrush steppe restoration who then was a 30-year employee of the BLM).

We discussed objectives and selected study sites in the eastern and northern Great Basin in partnership with federal and state resource managers. In autumn 2015, Fleishman and Hopkins traveled to the East Tintic and Sheeprock Mountains, Utah with staff of the Utah Division of Wildlife Resources in Salt Lake City and Springville. Additionally, Fleishman communicated with the leader of the Community-Based Conservation Program at Utah State University, and in March, 2016, attended a meeting of the West Desert Adaptive Resources Management Group in Tooele, Utah. Also in autumn 2015, Fleishman and Pellant met with project partners from the Bureau of Land Management's Boise and Bruneau, Idaho offices; Idaho Department of Fish and Game; and Mountain Home Air Force Base. This research–management group explored potential study locations in the Owyhee Uplands. Fleishman continued to communicate regularly with project partners in the western Great Basin, including the Nevada Division of Wildlife, US Forest Service, Hawthorne Army Munitions Depot, and Marine Corps Mountain Warfare Training Center. Furthermore, Fleishman met with the coordinator of the Great Basin Fire Science Exchange to discuss potential outreach opportunities.

In April 2016, Fleishman visited Corvallis, Oregon, where she delivered an invited presentation in the Department of Fisheries and Wildlife at Oregon State University. This visit also was an opportunity to meet with the director and deputy director of the Northwest Climate Science Center, which contributed support to augment the JFSP-funded project.

In mid July 2016, the project team conducted a field workshop with management partners (BLM, Idaho Department of Fish and Game, and Mountain Home Air Force Base) in the Owyhee Uplands. We also worked with management partners at the Utah Division of Wildlife Resources to convene a late July field workshop with the West Desert Adaptive Resources Management Group. Following the Utah workshop, Fleishman and project collaborator David Dobkin spent an additional day with staff from the Utah Division of Wildlife Resources. Furthermore, we met with land managers with the Austin and Tonopah Districts of the Forest Service in the central Great Basin, and with resource staff at the Hawthorne Army Munitions Depot and Marine Corps Mountain Warfare Training Center in the western Great Basin.

In June and August 2017, we conducted field workshop with management partners in Utah and Idaho (BLM and Idaho Department of Fish and Game), respectively. As the project drew to a formal close, we again met in the field with our Utah partners.

In spring 2019, Jimi Gragg (Project Leader, Utah Wildlife Action Plan, Utah Division of Wildlife Resources) and Fleishman began to plan for a July field workshop, coordinating on objectives, potential attendees, logistics, and so forth. The group ultimately included university scientists from California and Utah; staff with the US Forest Service, BLM, The Nature Conservancy, and various stage programs; and the Nevada Science Coordinator, Science

Applications, Pacific Southwest Region, US Fish and Wildlife Service. The workshop provided an opportunity for the resource managers to explain some of their priorities while visiting their project areas. For example, the group stopped in areas where conifers had been removed and where small dams recently had been placed with the aim of restoring riparian vegetation and stream banks. Additionally, the workshop allowed university scientists to demonstrate that academics are listening and seeking ways to contribute to achieving management priorities. Management personnel were frank that some actions being implemented in Utah reflect strong social objectives that may or may not coincide with ecological objectives; they indicated that certain actions, such as conifer removal, were unlikely to change regardless of the inferences from ecological research. Therefore, the project team was uncertain whether rigorous research could coincide with or inform some management actions.

In September 2019, Fleishman had a productive meeting with staff at the BLM's Boise office. Much of the meeting focused on methods for detection of cheatgrass, characterization of percent cover of cheatgrass, and challenges to estimation of bird abundance. There was considerable interest in how UAVs have been or could be used to improve detection of cheatgrass and classification of land cover.

We continue to participate in a research-management partnership, led by the USDA Forest Service's Rocky Mountain Research Station, that aims to develop methods for assessing the status and management potential of riparian and meadow ecosystems throughout the Great Basin. We also continued to collaborate and seek funding to sustain collaborations with colleagues in federal and state agencies and programs throughout the Great Basin. As this project concludes, we will share products and insights with the Northwest and Southwest Climate Adaptation Science Centers and with the Great Basin Fire Science Exchange, and anticipate several webinars, science briefs, and follow-up discussions as a result.


## Conclusions and Applications to Management, Policy, and Future Research

Our work yielded ecological inference related to changes in fuels and fire regimes in the Great Basin, insights into what currently is not feasible to infer with reasonable certainty, and potential directions for future research by the project team and the greater scientific community.

The current body of publicly available data, whether field or remotely sensed, does not allow accurate estimation of percent cover of cheatgrass as a continuous variable. Although some publications (e.g., Boyte and Wylie 2016) claimed to estimate percent cover in near-real-time with high accuracy, those models were trained and tested on previous spatial data layers with low accuracy rather than on extensive field data, and therefore are unlikely to be reliable.

Our work also suggested that remote estimation of cheatgrass cover on the basis of visible spectral bands is likely to remain quite difficult, even when images are captured 10 m above ground, unless the phenological stage of cheatgrass contrasts sharply with that of surrounding vegetation (i.e., is substantially greener or redder) and cheatgrass cover exceeds about 20%. Furthermore, the phenology of cheatgrass varies along elevational and topographic gradients, so a spatially extensive image or images captured within a relatively narrow temporal window are

unlikely to permit spectral identification in all locations. We believe that research with hyperspectral data may improve the ability to differentiate annual grasses (e.g., cheatgrass, and, where they co-occur in relatively wet, deep soils, Japanese brome [*Bromus japonicus*]) reliably. Detection of invasive bromes also would be simplified considerably if remotely sensed data facilitated discrimination throughout the snow-free period. Although the equipment necessary to collect hyperspectral data is relatively expensive, it may be worthwhile to explore the methods given our evidence that the frequency of fires increases substantially in areas in which observed cheatgrass cover is 1–5%.

Nevertheless, we identified relations between precipitation and occurrence, prevalence (given occurrence, the proportion of samples in which the cheatgrass was detected), and percent cover of cheatgrass. Across the Great Basin, percent cover of cheatgrass increased as primary productivity early in the growing season (spring–summer), which was correlated positively with precipitation, increased. In the central Great Basin, however, cheatgrass prevalence tended to increase as regional winter precipitation increased, but as regional spring precipitation decreased. The discrepancy between regional and ecosystem-level relations suggests that it may be worthwhile to explore regional variation in precipitation and productivity peaks in greater detail.

We also identified relations between elevation and occurrence, prevalence, and percent cover of cheatgrass. Elevation was associated negatively with occurrence of cheatgrass in the central Great Basin and percent cover of cheatgrass across the Great Basin. However, given presence, cheatgrass prevalence in the central Great Basin was greater at higher elevations, perhaps reflecting that precipitation generally increases as elevation increases.

Our results do not support the use of livestock grazing to suppress cheatgrass. Livestock grazing with the aim of suppressing cheatgrass may be especially counterproductive in unburned areas in which native perennial grasses may remain viable. Our discussions with some managers indicate that use of livestock grazing with the ostensible aim of cheatgrass suppression is driven as much by social aims as by ecological aims.

Correlations between biomass and percent cover of cheatgrass at different spatial resolutions and in different years generally appear to be strong. Yet our results suggest regional differences in this relation, and highlight the challenges of deriving strong inference from multiple sets of empirical data that were collected at different extents and resolutions and with different methods.

The results of our abundance models indicate that although general associations between breeding birds and land-cover types are known, even relatively detailed measures of vegetation composition and structure do not necessarily serve as reliable predictors of abundances of these birds. We believe that projections of bird distributions or abundances on the basis of simple maps of land cover, or sparse field data (e.g., Breeding Bird Surveys, one-time or one-season surveys) are unlikely to be accurate when evaluated with independent field data. Our results also may suggest that many years of data on breeding birds are necessary to account for stochastic or deterministic variation in distributions and abundances, and therefore to draw reliable inference to inform land-use decisions.

Analyses of data for this project yielded strong evidence of within-season and among-year elevational movement of breeding birds in the Great Basin. Field studies of the elevational movements of organisms as global temperatures increase indicate that a moderate proportion of species have moved upward, a smaller proportion have moved downward, and, to date, many species have not moved. Such studies largely have compared species distributions between past and contemporary time periods, within limited geographical areas, or over short temporal extents. Temporal discontinuity limits identification of mechanisms, and small spatial and short temporal extent limits the ability to generalize. Transferability further is limited because responses to environmental change vary among species and the abiotic and biotic variables that are associated with local distributions of a given species vary spatially.

Our ongoing research aims to advance mechanistic understanding of these two forms of movement, and of the role of each in distributional shifts over decades. For example, within seasons, may be associated with microclimate, the phenology of food sources, intraspecific and interspecific competition, or predation. We believe that complementary empirical and analytical work by other members of the research community would be highly fruitful. We plan to test hypotheses related to the attributes of individuals that move, the timing of movement, and the processes associated with movement. These phenomena may affect the distributions and abundances of individual species as climate and land use continue to change. Making robust and generalizable predictions about species distributions across elevations and latitudes is a major, enduring scientific challenge with mounting practical relevance. Meeting this challenge may greatly increase the likelihood that management actions achieve societal goals for conservation of species and ecosystem function, and for fiscal responsibility.

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# Appendix A
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# Appendix B

## Completed and planned scientific and technical publications and science delivery products

**Articles published or in press**

Balch, J.K., B.A. Bradley, J.T. Abatzoglou, R.C. Nagy, E.J. Fusco, and A.L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. Proceedings of the National Academy of Sciences of the United States 114:2946–2951.

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**Submitted articles**

Fogarty, F. and E. Fleishman. In review. Bias in estimated breeding-bird abundance from closure-assumption violations. Ecosphere.

Horning, N., E. Fleishman, P. Ersts, F. Fogarty, and M. Wohlfeil Zillig. In revision. Mapping of land cover with open-source software and ultra-high resolution imagery acquired with unmanned aerial vehicles. Remote Sensing in Ecology and Conservation.

**Articles anticipated and in development**

Fogarty, F., and E. Fleishman. Responses of breeding birds in the Great Basin to riparian area and riparian fragmentation.

Fogarty, F., and E. Fleishman. Variation in responses to vegetation structure and composition of the abundance and reproductive output of breeding birds.

Zillig, M.E.W., and E. Fleishman. Within-season elevational movements of passerine species in the Great Basin.

Zillig, M.E.W., and E. Fleishman. Among-year elevational movements of passerine species in the Great Basin.

Zillig, M.E.W., E. Fleishman, and F. Fogarty. Consistence of avian-vegetation associations across the Great Basin.

**Graduate theses**

Fogarty, F. Anticipated June 2020. Estimation and environmental associations of the abundance of breeding birds in the Great Basin. Ph.D. dissertation, University of California, Davis.

Zillig, M.E.W. Anticipated December 2020. Elevational shifts and vegetation associations of passerines in the Great Basin. Ph.D. dissertation, University of California, Davis.

**Presentations and webinars**

Fleishman, E. January 2017. Reconciling rhetoric, statistical rigor, and ecological inference in the Great Basin. Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins.

Fleishman, E. March 2017. Measuring and interpreting faunal responses to climate in the Intermountain West. Department of Atmospheric Science, Colorado State University, Fort Collins.

Fleishman, E., D.S. Dobkin, M. Leu, B.R. Noon, and J.D.L. Yen. May 2017. Relations between environmental covariates and species richness and beta diversity of breeding birds at multiple spatial resolutions in the central and western Great Basin. Great Basin Bird Conference, Reno, Nevada.

Fogarty, F., E. Fleishman, and M. Wohlfeil. May 2017. Relations between riparian area in canyons and species richness of riparian breeding birds in the central Great Basin, Nevada, USA. Great Basin Bird Conference, Reno, Nevada.

Wohlfeil, M.E., and E. Fleishman. May 2017. Potential mechanisms responsible for within-season elevational movements of passerine species. Great Basin Bird Conference, Reno, Nevada.

Fleishman, E. September 2017. Science perspectives on responses of natural resources to climate change. Southwestern Tribal Climate Change Summit, San Diego, California.

Fleishman, E. October 2017. Relations among cheatgrass-driven fire, climate, and sensitive-status birds across the Great Basin. Great Basin Landscape Conservation Cooperative (webinar).

Fleishman, E. November 2017. Reconciling rhetoric, statistical rigor, and ecological inference. School of BioSciences, University of Melbourne, Australia.

Fogarty, F.A. February 2018. Relations between riparian area in canyons and species richness of riparian breeding birds in the central Great Basin. 10th Annual Graduate Student Symposium in Ecology. University of California, Davis, California.

Wohlfeil, M.E. February 2018. Potential mechanism responsible for within-season movements of birds in the Great Basin. 10th Annual Graduate Student Symposium in Ecology. University of California, Davis, California.

Fleishman, E. March 2018. Management of public lands in the Intermountain West. College of William and Mary, Williamsburg, Virginia.

Wohlfeil, M.E. March 2019. Potential mechanism responsible for within-season movements of birds in the Great Basin. 2019 Wildlife Professional Development Conference. University of California, Davis, California.

Fogarty, F.A., and E. Fleishman. June 2019. Bias in estimated breeding bird abundance from individual movement. American Ornithological Society Meeting, Anchorage, Alaska.

Leu, M. R. Scherer, V. Jirinec, and E. Fleishman. June 2019. Estimation of occupancy parameters for breeding birds on the basis of single-visit and multiple-visits point-count designs. American Ornithological Society Annual Meeting, Anchorage, Alaska.

Fleishman, E. October 2019. Plastic, adaptive, and health responses to climate variability in the western United States. Oregon State University, Corvallis, Oregon.

Fleishman, E. October 2019. Plastic, adaptive, and health responses to environmental variability in the western United States. Utah State University, Logan, Utah.

Fogarty, F.A. October 2019. Dealing with imperfect detection in wildlife surveys. EcoSeries Seminar, Humboldt State University, Arcata, California.

**Data archived**

Fleishman, E. 2019. Detections of breeding birds in the Shoshone, Toiyabe, Toquima, and Monitor ranges, Nevada. 4th edition. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2011-0002-4

Fleishman, E. 2019. Incidental and long-distance bird observations in the Shoshone, Toiyabe, Toquima, and Monitor ranges, Nevada. 3rd edition. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2013-0012-3

Fleishman, E. 2019. Detections of breeding birds in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. 2nd edition. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2015-0031-2

Fleishman, E. 2019. Incidental and long-distance bird observations in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. 2nd edition. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2015-0033-2

Fleishman, E. 2019. Vegetation structure and composition in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. 2nd edition. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2015-0032-2

Fleishman, E. 2019. Detections of breeding birds in the Sheeprock and East Tintic Mountains, Utah. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2019-0017

Fleishman, E. 2019. Incidental and long-distance bird observations in the Sheeprock and East Tintic Mountains, Utah. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2019-0018

Fleishman, E. 2019. Vegetation structure and composition in the Sheeprock and East Tintic Mountains, Utah. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/doi.org/10.2737/RDS-2019-0019

Fleishman, E. 2019. Detections of breeding birds in the Owyhee Uplands, Idaho. Forest Service Research Data Archive, Fort Collins, Colorado. https://doi.org/10.2737/RDS-2019-0021

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# Appendix C. Covariates included in models of the abundance of breeding birds.

Edges were measured as total length (m) within a 500-m buffer around the transect route. Aspen could not be differentiated in the central Great Basin. As a result, edge covariates that included aspen were not included in abundance models for that region. Covariates were removed from the final model if its variance inflation factor was > 4 or if its correlation with another covariate was > 0.75 and it had the higher variance inflation factor. We did not detect *Pinus* in the northern Great Basin, and therefore covariates that included *Pinus* were not included in abundance models for that region. All models included elevation and year (not noted in the table).

Bird data through 2018, and vegetation data and metadata, are archived with the Forest Service Research Data Archive (see Appendix B).

In the western Great Basin, montane conifers included *Abies* spp., *Pinus albicaulis*, *P. contorta*, *P. flexilis*, *P. jeffreyi*, and unidentified firs. Riparian trees included *Alnus*, *Cornus sericea*, *Elaeagnus angustifolia*, *Populus*, *Prunus emarginata*, *Salix*, *Sambucus nigra* ssp. *cerulea*, and *Shepherdia argentea*. Riparian shrubs and trees included *Alnus*, *Cornus sericea*, *Elaeagnus angustifolia*, *Populus*, *Prunus emarginata*, *P. virginiana*, *Rosa woodsii*, *Salix*, *Shepherdia argentea*, *Sambucus nigra,* and sedges and rushes. Xeric shrubs included *Artemisia*, *Chamaebatiaria millefolium*, *Chrysothamnus*, *Ephedra*, *Ericameria*, *Grayia*, *Prunus andersonii*, *P. tridentata*, *Rhamnus californica*, *Tetradymia*, and heathers.

In the central Great Basin, the montane conifer was *Pinus flexilis*. Riparian trees included *Betula occidentalis*, *Cornus sericea*, *Populus*, *Prunus virginiana*, *Salix*, and *Sambucus nigra* spp. *cerulea*. Riparian shrubs and trees included *Acer glabrum*, *Betula occidentalis*, *Cornus sericea*, *Populus*, *Prunus virginiana*, *Rosa woodsii*, *Salix*, and *Sambucus nigra*. Xeric shrubs included *Artemisia*, *Chrysothamnus*, *Ephedra*, *Ericameria*, *Grayia*, *Prunus andersonii*, *Purshia stansburiana*, *Purshia tridentata*, *Salsola*, and *Sarcobatus vermiculatus*.

In the eastern Great Basin montane conifers included *Abies concolor*, *Pseudotsuga menziesii*, and unidentified firs. Riparian trees included *Populus*, *Prunus virginiana*, and *Salix*. Riparian shrubs and trees included *Acer grandidentatum*, *Cornus sericea*, *Populus*, *Prunus virginiana*, *Rhus*, *Rosa woodsii*, *Salix*, and *Sambucus nigra*. Xeric shrubs included *Artemisia*, *Atriplex*, *Chrysothamnus*, *Ephedra*, *Ericameria*, *Purshia mexicana* var. *stansburyana*, *Purshia tridentata*, *Sarcobatus vermiculatus*, and *Tetradymia*.

In the northern Great Basin, the montane conifer was *Pseudotsuga menziesii*. Riparian trees included *Populus angustifolia* and *Salix*. Riparian shrubs and trees included *Populus*, *Prunus virginiana*, *Rosa woodsii*, *Salix*, and *Sambucus nigra*. Xeric shrubs included *Artemisia*, *Chrysothamnus*, *Ephedra*, *Ericameria*, *Purshia tridentata*, and *Tetradymia*.

| Species | | | | | | |
|---|---|---|---|---|---|---|
| **Mourning Dove** | incidence of grasses | incidence of riparian trees and shrubs | incidence of xeric shrubs | percent cover of pinyon and juniper | percent cover of riparian trees | |
| **Broad-tailed Hummingbird** | hard edges between riparian meadow and shrubs | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | percent cover of pinyon and juniper | soft edges between riparian meadow and shrubs | soft edges between riparian woody and shrubs (removed from central) |
| **Northern Flicker** | hard edges between shrubs and conifers | incidence of riparian trees and shrubs | percent cover of montane conifers | percent cover of pinyon and juniper | percent cover of riparian trees (removed from central) | soft edges between shrubs and conifers | percent cover of Populus |
| **Gray Flycatcher** | hard edges between shrubs and conifers | incidence of xeric shrubs | percent cover of pinyon and juniper | soft edges between shrubs and conifers | | |
| **Dusky Flycatcher** | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | percent cover of mountain mahogany | percent cover of riparian trees (not included in central) | proportion of canyon area that is canyon bottom (100 m buffer around transect line) | soft edges between riparian woody and shrubs |
| **Plumbeous Vireo** | incidence of xeric shrubs | percent cover of mountain mahogany | percent cover of juniper | percent cover of pinyon | percent cover of pinyon and juniper (removed from eastern) | |
| **Warbling Vireo** | hard edges between riparian woody and conifers | incidence of riparian trees and shrubs | percent cover of Populus | soft edges between aspen and mixed conifers (not applicable to central) | soft edges between riparian woody and conifers | |
| **Pinyon Jay** | incidence of xeric shrubs | percent cover of juniper | percent cover of montane conifers | percent cover of pinyon | percent cover of pinyon and juniper | proportion of canyon area that is canyon bottom (500 m buffer around transect line) |
| **Woodhouse's Scrub-Jay** | incidence of riparian trees and shrubs | incidence of xeric shrubs | percent cover of juniper | percent cover of pinyon | percent cover of pinyon and juniper (removed from central) | |
| **Clark's Nutcracker** | percent cover of montane conifers | percent cover of pinyon (removed from central) | percent cover of pinyon and juniper | | | |

| Species | | | | | | |
|---|---|---|---|---|---|---|
| **Horned Lark** | incidence of grasses | incidence of xeric shrubs | percent cover of juniper | percent cover of pinyon | percent cover of pinyon and juniper (removed from eastern) | |
| **Mountain Chickadee** | incidence of xeric shrubs | percent cover of juniper | percent cover of montane conifers | percent cover of pinyon (removed from western) | percent cover of pinyon and juniper (not included in central) | |
| **Bushtit** | incidence of riparian trees and shrubs | incidence of xeric shrubs | percent cover of pinyon and juniper | percent cover of riparian trees | soft edges between shrubs and conifers | |
| **Rock Wren** | incidence of xeric shrubs | percent cover of pinyon and juniper | proportion of canyon area that is canyon bottom (500 m buffer around transect line) | | | |
| **House Wren** | hard edges between riparian woody and conifers | incidence of riparian trees and shrubs | percent cover of Populus | percent cover of riparian trees (removed from western and central) | soft edges between riparian woody and conifers | |
| **Blue-Gray Gnatcatcher** | incidence of riparian trees and shrubs | incidence of xeric shrubs | percent cover of pinyon and juniper | percent cover of riparian trees (not included in central) | | |
| **Mountain Bluebird** | incidence of grasses | incidence of riparian trees and shrubs | percent cover of pinyon and juniper | percent cover of Populus | | |
| **Hermit Thrush** | hard edges between riparian woody and conifers | incidence of riparian trees and shrubs | percent cover of mountain mahogany | percent cover of montane conifers | percent cover of riparian trees | soft edges between riparian woody and conifers |
| **American Robin** | hard edges between riparian meadows and conifers | hard edges between riparian meadows and riparian woody | hard edges between shrubs and conifers (removed from western) | incidence of riparian trees and shrubs | percent cover of riparian trees (not included in central) | soft edges between shrubs and conifers |
| **American Robin (western Great Basin only)** | hard edges between riparian woody and conifers | percent cover of pinyon and juniper | percent cover of Populus | soft edges between riparian woody and conifers | | |

| Species | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Sage Thrasher** | hard edges between shrubs and conifers | incidence of xeric shrubs | soft edges between shrubs and conifers | | | | |
| **MacGillivray's Warbler** | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | percent cover of Populus | percent cover of riparian trees (removed from western, not included in central) | soft edges between riparian woody and shrubs | | |
| **Yellow Warbler** | hard edges between riparian meadow and shrubs (removed from western) | hard edges between riparian meadows and riparian woody | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | soft edges between riparian meadows and shrubs | soft edges between riparian woody and shrubs | |
| **Yellow-rumped Warbler** | hard edges between aspen and mixed shrubs (not applicable to central) | incidence of riparian trees and shrubs | percent cover of montane conifers | percent cover of pinyon and juniper | percent cover of Populus | soft edges between aspen and mixed conifers (not applicable to central) | soft edges between aspen and mixed shrubs (removed from western, not applicable to central) |
| **Black-throated Gray Warbler** | incidence of xeric shrubs | percent cover of pinyon and juniper | percent cover of riparian trees | | | | |
| **Wilson's Warbler** | hard edges between riparian meadows and conifers (removed from western) | hard edges between riparian meadows and riparian woody | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | percent cover of montane conifers | soft edges between riparian meadows and conifers | soft edges between riparian woody and shrubs |
| **Green-tailed Towhee** | incidence of grasses | incidence of xeric shrubs | percent cover of juniper (removed from western) | percent cover of pinyon (removed from western) | percent cover of pinyon and juniper (removed from eastern) | | |
| **Spotted Towhee** | hard edges between shrubs and conifers (removed from western) | incidence of riparian trees and shrubs | incidence of xeric shrubs | percent cover of pinyon and juniper | soft edges between shrubs and conifers | | |
| **Chipping Sparrow** | hard edges between shrubs and conifers | incidence of grasses | incidence of riparian trees or shrubs | incidence of xeric shrubs | percent cover of montane conifers | percent cover of pinyon and juniper | soft edges between shrubs and conifers |

| Species | | | | | |
|---|---|---|---|---|---|
| **Brewer's Sparrow** | hard edges between shrubs and conifers (removed from western) | incidence of xeric shrubs | percent cover of pinyon and juniper | soft edges between shrubs and conifers | |
| **Vesper Sparrow** | incidence of grasses | incidence of xeric shrubs | percent cover of juniper | | |
| **Lark Sparrow** | incidence of grasses | incidence of xeric shrubs | percent cover of juniper | percent cover of pinyon | percent cover of pinyon and juniper (removed from eastern) |
| **Fox Sparrow** | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | percent cover of riparian trees (central: removed) | soft edges between riparian woody and shrubs | |
| **Song Sparrow** | hard edges between riparian meadow and shrubs | hard edges between riparian meadows and riparian woody | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | soft edges between riparian woody and shrubs |
| **Dark-eyed Junco** | incidence of riparian trees and shrubs | percent cover of montane conifers | percent cover of pinyon and juniper | percent cover of riparian trees (not included in central) | |
| **Western Tanager** | hard edges between shrubs and conifers (removed from western) | incidence of riparian trees and shrubs | percent cover of montane conifers | percent cover of pinyon and juniper | soft edges between shrubs and conifers |
| **Black-headed Grosbeak** | hard edges between riparian woody and conifers | incidence of riparian trees and shrubs | percent cover of pinyon and juniper | percent cover of riparian trees | soft edges between riparian woody and conifers |
| **Lazuli Bunting** | hard edges between riparian woody and shrubs | incidence of riparian trees and shrubs | incidence of xeric shrubs | percen cover of Populus | percent cover of mountain mahogany | soft edges between riparian woody and shrubs |
| **Western Meadowlark** | incidence of grasses | incidence of xeric shrubs | percent cover of juniper | percent cover of pinyon | percent cover of pinyon and juniper (removed from eastern) |
| **Brewer's Blackbird** | hard edges between riparian meadow and shrubs | incidence of grasses | incidence of xeric shrubs | percent cover of pinyon and juniper | soft edges between riparian meadow and shrubs |

| Species | | | | |
|---|---|---|---|---|
| Cassin's Finch | hard edges between shrubs and conifers | percent cover of montane conifers | percent cover of pinyon and juniper | soft edges between shrubs and conifers |

# Appendix D. Results of models of the abundance of breeding birds.

Results of single-species abundance models for breeding birds in four regions of the Great Basin. Models for a given species could not be run for all regions; in some cases a given species was not detected in all regions, and in some cases abundances in a given region were insufficient for rigorous modeling. covar, covariate; SD, standard deviation. The sign of the covariate mean value indicates the direction of association with abundance. Overlaps zero, values of the covariate overlap zero (and therefore are not considered highly statistically significant); 1, yes, 0, no. p, Bayesian p-values for the detection and abundance submodels. These values are associated with the full model rather than with a given covariate. A Bayesian p-value ~0.5 is considered ideal, and values 0.1–0.9 are considered acceptable. Gray shading indicates that on the basis of extremely large standard deviations of the covariate, covariate values that overlap zero, or Bayesian p-values that are < 0.1 or > 0.9, inference from the model is uncertain.

| Species | Covariates in final model, western Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, central Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mourning Dove | | | | | | | | | | | | |
| Broad-tailed Hummingbird | | | | | | | Did not pass goodness of fit tests | | | | | |
| Northern Flicker | | | | | | | percent cover of Populus | 0.26 | 0.09 | 0 | 0.91 | 0.46 |
| | | | | | | | year | 0.24 | 0.07 | 0 | | |
| Gray Flycatcher | | | | | | | percent cover of pinyon and juniper | 0.40 | 0.10 | 0 | 0.56 | 0.42 |
| Dusky Flycatcher | Did not pass goodness of fit tests | | | | | | Did not pass goodness of fit tests | | | | | |
| Plumbeous Vireo | | | | | | | | | | | | |
| Warbling Vireo | Did not pass goodness of fit tests | | | | | | Did not pass goodness of fit tests | | | | | |
| Pinyon Jay | | | | | | | Did not pass goodness of fit tests | | | | | |

| Species | Covariates in final model, western Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, central Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Woodhouse's Scrub-Jay | | | | | | | Did not pass goodness of fit tests | | | | | |
| Clark's Nutcracker | | | | | | | Did not pass goodness of fit tests | | | | | |
| Horned Lark | | | | | | | | | | | | |
| Mountain Chickadee | percent cover of pinyon and juniper | 0.41 | 0.10 | 0 | 0.99 | 0.55 | Did not pass goodness of fit tests | | | | | |
| Bushtit | Did not pass goodness of fit tests | | | | | | Did not pass goodness of fit tests | | | | | |
| Rock Wren | | | | | | | year | 0.39 | 0.05 | 0 | 0.58 | 0.53 |
| House Wren | percent cover of Populus | 0.60 | 0.12 | 0 | 0.02 | 0.44 | percent cover of Populus | 0.59 | 0.10 | 0 | 0.20 | 0.27 |
| Blue-Gray Gnatcatcher | elevation | -1.15 | 0.22 | 0 | 0.01 | 0.28 | incidence of xeric shrubs | 0.39 | 0.57 | 0 | 0.11 | 0.54 |
| | year | 0.24 | 1.07 | 0 | | | elevation | -0.93 | 0.15 | 0 | | |
| Mountain Bluebird | | | | | | | Did not pass goodness of fit tests | | | | | |

| Species | Covariates in final model, western Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, central Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **American Robin** | No covariates retained | | | | | | incidence of riparian trees and shrubs | 0.21 | 2.38 | 1 | 0.82 | 0.52 |
| | | | | | | | year | 0.27 | 0.04 | 0 | | |
| **MacGillivray's Warbler** | incidence of riparian trees and shrubs | 0.41 | 0.11 | 0 | 0.15 | 0.37 | incidence of riparian trees and shrubs | 0.54 | 0.87 | 0 | 0.73 | 0.51 |
| | | | | | | | hard edges between riparian woody and shrubs | 0.68 | 0.39 | 1 | | |
| | | | | | | | year | 0.21 | 0.04 | 0 | | |
| **Yellow Warbler** | Did not pass goodness of fit tests | | | | | | Did not pass goodness of fit tests | | | | | |
| **Yellow-rumped Warbler** | Did not pass goodness of fit tests | | | | | | elevation | 0.40 | 0.13 | 0 | 0.94 | 0.50 |
| **Black-throated Gray Warbler** | percent cover of pinyon and juniper | 0.54 | 0.16 | 0 | 0.58 | 0.44 | percent cover of pinyon and juniper | 0.52 | 0.08 | 0 | 0.37 | 0.12 |
| | year | 0.36 | 0.06 | 0 | | | elevation | -0.33 | 0.23 | 0 | | |
| | | | | | | | year | 0.25 | 0.03 | 0 | | |

| Species | Covariates in final model, western Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, central Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Wilson's Warbler | incidence of riparian trees and shrubs | 0.83 | 86.90 | 1 | 0.88 | 0.58 | No covariates retained | | | | | |
| | year | 0.55 | 0.08 | 0 | | | | | | | | |
| Green-tailed Towhee | Did not pass goodness of fit tests | | | | | | Did not pass goodness of fit tests | | | | | |
| Spotted Towhee | Did not pass goodness of fit tests | | | | | | Did not pass goodness of fit tests | | | | | |
| Chipping Sparrow | | | | | | | No covariates retained | | | | | |
| Brewer's Sparrow | incidence of xeric shrubs | 1.16 | 0.15 | 0 | 0.13 | 0.67 | incidence of xeric shrubs | 0.49 | 0.10 | 0 | 0.98 | 0.79 |
| | percent cover of pinyon and juniper | -0.74 | 0.16 | 0 | | | percent cover of pinyon and juniper | -0.58 | 0.13 | 0 | | |
| | year | 0.19 | 0.04 | 0 | | | elevation | 0.80 | 0.12 | 0 | | |
| | | | | | | | year | 0.23 | 0.03 | 0 | | |
| Vesper Sparrow | | | | | | | percent cover of pinyon and juniper | -1.74 | 0.39 | 0 | 0.82 | 0.63 |

| Species | Covariates in final model, western Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, central Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Lark Sparrow** | | | | | | | elevation | 1.34 | 0.23 | 0 | | |
| **Fox Sparrow** | Did not pass goodness of fit tests | | | | | | incidence of riparian trees and shrubs | 0.43 | 24.40 | 1 | 0.68 | 0.54 |
| | | | | | | | hard edges between riparian woody and shrubs | 1.96 | 0.41 | 0 | | |
| **Song Sparrow** | Did not pass goodness of fit tests | | | | | | No covariates retained | | | | | |
| **Dark-eyed Junco** | percent cover of montane conifers | 0.50 | 0.12 | 0 | 0.25 | 0.45 | elevation | 0.61 | 0.13 | 0 | 0.83 | 0.61 |
| | elevation | 0.51 | 0.20 | 0 | | | year | 0.25 | 0.82 | 0 | | |
| | year | 0.18 | 0.03 | 0 | | | | | | | | |
| **Western Tanager** | percent cover of montane conifers | 0.71 | 0.14 | 0 | 0.31 | 0.46 | year | 0.47 | 0.07 | 0 | 0.79 | 0.48 |
| | percent cover of pinyon and juniper | 0.48 | 0.12 | 0 | | | | | | | | |
| **Black-headed Grosbeak** | No covariates retained | | | | | | elevation | -0.62 | 1.04 | 0 | 0.66 | 0.47 |
| | | | | | | | year | 0.27 | 2.57 | 0 | | |

| Species | Covariates in final model, western Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, central Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Lazuli Bunting** | elevation | -1.11 | 0.18 | 0 | 0.91 | 0.91 | incidence of riparian trees and shrubs | 0.50 | 0.13 | 0 | 0.93 | 0.56 |
| | year | 0.44 | 0.07 | 0 | | | elevation | -0.55 | 0.15 | 0 | | |
| | | | | | | | year | 0.97 | 0.09 | 0 | | |
| **Western Meadowlark** | | | | | | | | | | | | |
| **Brewer's Blackbird** | | | | | | | Did not pass goodness of fit tests | | | | | |
| **Cassin's Finch** | No covariates retained | | | | | | Did not pass goodness of fit tests | | | | | |

| Species | Covariates in final model, eastern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, northern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mourning Dove | | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |
| Broad-tailed Hummingbird | | | | | | | | | | | | |
| Northern Flicker | | | | | | | | | | | | |
| Gray Flycatcher | percent cover of pinyon and juniper | 0.62 | 0.16 | 0 | 0.24 | 0.34 | No covariates retained, did not pass goodness of fit tests | | | | | |
| Dusky Flycatcher | elevation | 1.38 | 0.25 | 0 | 0.22 | 0.40 | year | -0.28 | 0.06 | 0 | 0.93 | 0.36 |
| | year | -0.26 | 2.83 | 1 | | | | | | | | |
| Plumbeous Vireo | No covariates retained | | | | | | | | | | | |
| Warbling Vireo | | | | | | | | | | | | |
| Pinyon Jay | | | | | | | | | | | | |

| Species | Covariates in final model, eastern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, northern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Woodhouse's Scrub-Jay | | | | | | | | | | | | |
| Clark's Nutcracker | | | | | | | | | | | | |
| Horned Lark | elevation | -2.49 | 0.48 | 0 | 0.49 | 0.50 | | | | | | |
| Mountain Chickadee | | | | | | | | | | | | |
| Bushtit | | | | | | | | | | | | |
| Rock Wren | | | | | | | | | | | | |
| House Wren | | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |
| Blue-Gray Gnatcatcher | No covariates retained | | | | | | | | | | | |
| Mountain Bluebird | No covariates retained | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |

| Species | Covariates in final model, eastern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, northern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| American Robin | | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |
| MacGillivray's Warbler | | | | | | | | | | | | |
| Yellow Warbler | | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |
| Yellow-rumped Warbler | | | | | | | | | | | | |
| Black-throated Gray Warbler | percent cover of pinyon and juniper | 0.45 | 0.14 | 0 | 0.03 | 0.28 | | | | | | |

| Species | Covariates in final model, eastern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, northern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Wilson's Warbler | | | | | | | | | | | | |
| Green-tailed Towhee | incidence of grasses | 0.66 | 1.99 | 0 | 0.03 | 0.34 | No covariates retained, did not pass goodness of fit tests | | | | | |
| | elevation | 1.05 | 0.23 | 0 | | | | | | | | |
| Spotted Towhee | No covariates retained | | | | | | | | | | | |
| Chipping Sparrow | No covariates retained | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |
| Brewer's Sparrow | percent cover of pinyon and juniper | -1.54 | 0.37 | 0 | 0.44 | 0.35 | percent cover of juniper | -0.07 | 0.16 | 0 | 0.58 | 0.50 |
| | elevation | -1.11 | 0.28 | 0 | | | year | 0.36 | 0.04 | 0 | | |
| Vesper Sparrow | | | | | | | percent cover of juniper | -0.76 | 0.22 | 0 | 0.83 | 0.41 |

| Species | Covariates in final model, eastern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, northern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | year | 0.08 | 49.13 | 1 | | |
| Lark Sparrow | percent cover of pinyon | -1.12 | 25.33 | 1 | 0.79 | 0.64 | | | | | | |
| | elevation | -1.70 | 1.06 | 0 | | | | | | | | |
| Fox Sparrow | | | | | | | | | | | | |
| Song Sparrow | | | | | | | | | | | | |
| Dark-eyed Junco | | | | | | | | | | | | |
| Western Tanager | | | | | | | | | | | | |
| Black-headed Grosbeak | | | | | | | | | | | | |

| Species | Covariates in final model, eastern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance | Covariates in final model, northern Great Basin | covar mean | covar SD | overlaps zero | p, detection | p, abundance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lazuli Bunting | | | | | | | | | | | | |
| Western Meadowlark | percent cover of pinyon | -2.02 | 1.44 | 0 | 0.97 | 0.49 | | | | | | |
| | elevation | -1.97 | 0.39 | 0 | | | | | | | | |
| | year | 0.54 | 0.09 | 0 | | | | | | | | |
| Brewer's Blackbird | | | | | | | | | | | | |
| Cassin's Finch | | | | | | | No covariates retained, did not pass goodness of fit tests | | | | | |