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LANDSCAPE TO LOCAL: A MULTI-SCALE EVALUATION OF VOLUNTARY EFFORTS TO REDUCE FRAGMENTATION AND ENHANCE MANAGEMENT OF RANGELANDS FOR SAGE-GROUSE

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LANDSCAPE TO LOCAL: A MULTI-SCALE EVALUATION OF VOLUNTARY EFFORTS TO REDUCE FRAGMENTATION AND ENHANCE MANAGEMENT OF RANGELANDS FOR SAGE-GROUSE

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Landscape to local: a multi-scale evaluation of voluntary efforts to reduce fragmentation and enhance management of rangelands for sage-grouse.

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For imperiled species, the hierarchical nature of habitat selection suggests the need for a hierarchical approach to conservation: address threats to persistence operating at broad scales on populations before focusing on the quality of patches or availability of particular resources used by individuals. We apply this approach to conservation and management of habitat for greater sage-grouse (*Centrocercus urophasianus*) in the eastern portion of their range where cropland conversion continues to fragment sagebrush grasslands. Using locations of active leks in portions of Montana, Wyoming, North Dakota, and South Dakota as spatial indices of populations, we found sage-grouse distribution was highly sensitive to cropland fragmentation in a 12 mi^2 landscape. A single square-mile parcel broken out into cropland can thus reduce population persistence within an area twelve times that size, emphasizing the need to conserve large, intact sagebrush landscapes. Simulated cropland buildout scenarios indicate 5-7% of the northern Great Plains population remains vulnerable to future cropland conversion. We demonstrate, however, that with a targeting scheme incorporating biological value, risk, and cost, a $100M investment in conservation easements could reduce potential losses by 80%. Next, using radio-marked birds to locate and monitor nests in a large-scale, replicated, natural grazing experiment in central Montana, we tested hypothesized relationships between livestock grazing and sage-grouse nest site selection and survival and evaluated effects of rest-rotation grazing systems on vegetation structure and nest survival. Surprisingly, we found no evidence that herbaceous vegetation structure affected choice of nest site or nest survival. Instead, females selected nest sites based on relatively static features such as sagebrush cover, terrain roughness, landscape fragmentation, and distance to major roads, while nest survival was affected primarily by severe weather. Rotational grazing systems had negligible effects on upland vegetation structure and no effect on sage-grouse nest survival. Finally, in light of recent research which demonstrated how commonly-used field methods can produce inflated or spurious inference on the relationship between vegetative concealment and nest survival, we re-analyze four independently collected sage-grouse nest datasets to test for relationships between grass height and nest survival. All four datasets indicated strong, positive effects of grass height on nest survival prior to correction for biased timing of vegetation measurement. Once this bias was accounted for, however, none of the datasets supported a positive effect, confirming that plant phenology is largely responsible for previously-reported relationships between herbaceous hiding cover and nest success in sage-grouse.

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As I write this I have been ‘relieved’ of field work for about three years. However, I will never forget the many long, tired, cold, hot, dusty, muddy, shivering, sweaty days and nights on the prairie that comprise the collective efforts of more than twenty (and counting) seasonal field technicians that helped collect the data analyzed in these pages. I sincerely enjoyed watching them grow into better field biologists and naturalists, and I hope they got something out of it, too. In turn, I thank Andie Lueders for giving me my first field job and sparking a love for big, open landscapes.

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PREFACE

This dissertation is organized into three chapters, each formatted for submission as a peer-reviewed article. At the time of submission, Chapter 1, “Reducing cultivation risk for at-risk species: predicting outcomes of conservation easements for sage-grouse,” was published in *Biological Conservation*, Chapter 2, “Effects of livestock grazing, weather, and landscape on nesting greater sage-grouse,” was submitted to *Journal of Wildlife Management*, and Chapter 3, “Phenology, not concealment, explains taller grass at successful nests in greater sage-grouse,” was in preparation for *Ecology and Evolution*. Organization, headers, and references of each chapter therefore conform to the specific formatting guidelines of their respective journals, with slight modifications for consistency and readability. The pronoun “we” is used throughout to acknowledge that all chapters were collaborative efforts of several co-authors.

CHAPTER 1: REDUCING CULTIVATION RISK FOR AT-RISK SPECIES: PREDICTING OUTCOMES OF CONSERVATION EASEMENTS FOR SAGE-GROUSE

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Abstract

Conversion of native habitats to cropland is a leading cause of biodiversity loss. The northeastern extent of the sagebrush (*Artemisia* L.) ecosystem of western North America has experienced accelerated rates of cropland conversion resulting in many declining shrubland species including greater sage-grouse (*Centrocercus urophasianus*). Here we present point-process models to elucidate the magnitude and spatial scale of cropland effects on sage-grouse lek occurrence in eastern Montana, northeastern Wyoming, North Dakota and South Dakota. We also use a non-parametric, probabilistic crop suitability model to simulate future cropland expansion and estimate impacts to sage-grouse. We found cropland effects manifest at a spatial scale of 32.2 km^2 and a 10 percentage point increase in cropland is associated with a 51% reduction in lek density. Our crop suitability model and stochastic cropland build-outs indicate 5-7% of the remaining population in the US portion of sage-grouse Management Zone I is vulnerable to future cropland conversion under a severe scenario where cropland area expands by 50%. Using metrics of biological value, risk of conversion, and acquisition cost to rank parcels, we found that a US $100M investment in easements could reduce potential losses by about 80%, leaving just over 1% of the population in the study are vulnerable to cropland expansion. Clustering conservation easements into high-risk landscapes by incorporating landscape-scale vulnerability to conversion into the targeting scheme substantially improved conservation outcomes.

Keywords: Agriculture; *Centrocercus urophasianus*; cropland conversion; land-use change; Northern Great Plains; sagebrush.

1. Introduction

Expansion of agriculture has been implicated as a major driver of biodiversity loss at global and continental scales, having caused greater environmental change to the earth's surface than any other land use (Wilcove et al. 1998, Green et al. 2005). Increases in global population and living standards are expected to add around 1 billion new hectares of agricultural land by 2050 (Tilman et al. 2001, 2011). In addition to direct habitat loss, wildlife populations in habitat fragmented by cropland may suffer from increased abundance of predators or parasites (Andren 1992, Rand et al. 2006, Vander Haegen 2007, Tscharntke et al. 2012). These landscape-scale effects of cropland may vastly increase the scope of impacts of agriculture on sensitive species. Low elevation arable lands are underrepresented in existing protected areas, leaving the associated biota especially vulnerable (Pressey 1994, Scott et al. 2001). Preventing loss of species and their habitats to cropland expansion will require innovative and strategic implementation of limited conservation funds.

Semi-arid sagebrush (*Artemisia* L.) ecosystems of western North America exemplify the conservation challenges in landscapes increasingly transformed by agricultural production. Once covering some 63 Mha in 14 U.S. states and 3 Canadian provinces, sagebrush ecosystems are afforded little formal protection and have experienced substantial loss and fragmentation from a diversity of human activities (Knick et al. 2003, Knick and Connelly 2011). Associated declines in many sagebrush-dependent species have elicited growing concern for their long-term persistence (Suring et al. 2005). While much of the sagebrush ecosystem occurs on shallow soils unsuitable for cultivation, extensive conversion has occurred where sagebrush vegetation overlays deeper, more arable soils (e.g., Vander Haegen et al. 2000). Shrublands were the second most common source for new cropland in the US between 2008 and 2012, a period of accelerated conversion activity during which nearly 3 million hectares of previously uncultivated land was brought into crop production (data expressed in acres by Lark et al. 2015; 1 ha = 2.47 ac).

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse), a sagebrush obligate bird requiring large, intact shrub-dominated landscapes, was added to the Endangered Species Act (ESA) candidate list in 2010 following several petitions for their federal protection (US Department of Interior 2010). A US Department of Interior Fish and Wildlife Service (USFWS) determination in September 2015 found current efforts by state and federal agencies and other partners adequate to obviate the need for a listing, but significant conservation challenges remain and the species' status will again be reviewed in 2020 (US Department of Interior 2015). Cropland conversion ranks high on the list of threats to sage-grouse in portions of their range (USFWS 2013). Populations of sage-grouse experienced local extirpation and isolation when regions with deep, arable soil formerly dominated by sagebrush were farmed in the late 19th and early 20th century (Swenson et al. 1987, Schroeder et al. 2000, Vander Haegen et al. 2000). Sagebrush-dominated lands in the northern Great Plains, with their shallower soils and harsher growing conditions, remained relatively intact. Advancing agricultural technologies and periodically favorable commodities prices, however, facilitate ongoing conversion (Rashford et al. 2011, Sylvester et al. 2013, Lark et al. 2015) and replacement of native rangeland by cropland is thought to be a dominant threat to the species in the northeast portion of their range (USFWS 2013). The magnitude of this threat, however, is poorly understood.

Cropland has been implicated as a limiting factor for sage-grouse (e.g., Walker et al. 2007, Aldridge et al. 2008, Knick et al. 2013) but the spatial scale at which cropland affects sage-grouse distribution has received little attention. For example, Knick et al. (2013) found that approximately 25% cropland within 5 km constituted an upper threshold for sage-grouse breeding habitat in the western portion of their range, and Aldridge et al. (2008) found that extirpation was likely in counties comprised of >25% cropland. These investigations considered only a single scale at which to measure cropland surrounding leks and therefore may not adequately characterize how sage-grouse respond to cropland. Walker et al. (2007) used an information-theoretic approach to select from among three scales (0.8 km, 3.2 km, and 6.4 km) and found support for the largest of the scales they considered. Their study area, however, was geographically restricted to the Powder River Basin of northeast Wyoming and southeast Montana, where tilled land is a relatively minor component of the landscape and largely comprises irrigated hay and alfalfa, not the annual small grain crops common elsewhere in the northern Great Plains (USDA-NASS 2014a). A better understanding of the spatial scale at which cropland affects the distribution of sage-grouse populations is urgently needed to predict effects of future land-use change on the species' habitat and populations and to prioritize conservation.

Conservation easements—voluntary legal agreements wherein landowners retain title of their land but are compensated to relinquish certain uses of the land in order to foster conservation goals (Fishburn et al. 2009)—are the primary management tool available to prevent further loss of sagebrush ecosystems to cropland conversion. Easements have been shown to both improve conservation value of land in sagebrush ecosystems (Pocewicz et al. 2011) and contribute to sage-grouse conservation (Copeland et al. 2013). A program of targeted acquisition of easements preventing further loss and fragmentation of sage-grouse habitat is recognized as a necessary component of a successful conservation strategy (USFWS 2013, Montana Greater Sage-grouse Habitat Conservation Advisory Council 2014), yet the potential for such a program to mitigate cropland conversion has yet to be evaluated. Easements involve significant opportunity costs that must be compensated and are therefore expensive to implement over large areas. Efficient, science-based allocation of conservation easement funds is therefore critical.

Focusing on the northern Great Plains portion of the sage-grouse range in eastern Montana, northeast Wyoming, and western North Dakota and South Dakota, we address the following questions: 1) At what scale does cropland affect the use of an area by breeding sage-grouse? 2) What proportion of the known breeding population faces risk of local extirpation due to future cropland conversion, and where do at-risk populations occur? 3) How could a program of targeted conservation easement acquisition affect long-term outcomes for sage-grouse in this region?

2. Methods

2.1 Study area

Our study area included potential habitat in sage-grouse Management Zone 1 (hereafter MZ1; Stiver et al. 2006), encompassing portions of eastern Montana, northeast Wyoming, and western North Dakota and South Dakota (Figure 1). Sage-grouse habitat in this region differs from other management zones in the predominance of privately-owned lands and its widespread use for non-irrigated farming. Major landowners include private (70%), US Bureau of Land Management (11%), State (7%), USDA Forest Service (5%), and Bureau of Indian Affairs (5%) (BLM 2013). Priority Areas for Conservation (PACs) are areas of high sage-grouse abundance that are focal areas for conservation efforts across the range of sage-grouse. PACs make up approximately 15% of the study area (Figure 1). We excluded areas deemed naturally unsuitable for sage-grouse because of extreme topography, the predominance of forest landcover, or presence of surface water by masking out areas where topographic roughness within 800 m, proportion forest landcover within 1 km, or proportion surface water within 800 m (see Table 1) exceeded the values found at known active leks (defined below). Sage-grouse require sagebrush during all phases of their life and leks, the communal breeding grounds used by sage-grouse in the spring, occur in landscapes with abundant nesting habitat (Gibson 1996a, Doherty 2008). Studies in the northern Great Plains indicate females commonly nest >5 km from the lek at which they are bred (Walker et al. 2007, Herman-Brunson et al. 2009, Tack 2009, J. Smith, unpublished data); hence we excluded areas >6.4 km from the nearest sagebrush landcover.

2.2 Lek suitability modeling approach

Observed locations of leks represent the best data available on sage-grouse distribution. Lek locations are suitable geographical indices of sage-grouse populations because they are proximal to habitats used during life stages critically important to population growth such as nesting and brood-rearing (Taylor et al. 2012). We hypothesize that sage-grouse use of an area for lekking is negatively related to the amount of the surrounding landscape converted to cropland. We treat observations of active leks as an inhomogeneous Poisson point-process (hereafter IPP; Cressie 1993, Warton and Shepherd 2010) where the expected intensity of sightings of active leks (λ_s) is a function of environmental attributes measured at various spatial scales (Table 1). Our model is conceptually equivalent to a resource selection function with a used-available sampling design (Manly et al. 2002, Johnson et al. 2006) at the second order of habitat selection (Johnson 1980) where we use leks to identify areas used by breeding populations and sample background locations randomly from a portion of the species estimated former geographic range. We define an active lek as a location where >1 male was observed displaying during the breeding season in ≥1 year between 2008 and 2012 (n = 1064). Where >1 active lek occurred within 1 km we included only the lek with the greatest average high male count (i.e., the highest count of males on a lek within a breeding season) during this period.

We used the downweighted Poisson regression method recently proposed by Renner et al. (2015) to maximize the IPP likelihood while estimating an intercept that would yield predictions on a biologically meaningful scale. This technique uses the area of the study area (A) to assign different weights to presence points (active leks; $y_i = 1$) and quadrature or background points ($y_i = 0$) such that the predicted response, λ_s, is scaled to represent the expected number of sightings of active leks per-unit area (Renner et al. 2015). We chose the number of background points n by randomly sampling 20 replicate sets of background points for each of 8 different values of n ranging from 1000 to 250 000, fitting the global model to each set, and visually assessing convergence of model log likelihoods as n increased (Renner et al. 2015). We fit IPP models using the glm function in R version 3.0.1 (R Development Core Team 2014) with Poisson distributed errors and a log link, set weights (w_i) equal to 10^{-8} at presence points and A/n at background points, and used $z_i = y_i/w_i$ as the response (Renner et al. 2015). We first fit a global model without quadratic terms and used variance inflation factors (VIF) to screen for multicollinearity (Fox and Monette 1992, Dormann et al. 2013). After removing collinear variables (VIF $\geq$ 10) we proceeded with model selection and validation.

2.3 Model selection and validation

A primary goal was to identify the scale at which cropland influences use of an area by breeding sage-grouse. We used an information theoretic approach to select from among candidate models with proportion of the landscape in cropland measured within five progressively-larger neighborhoods where the previous scale was partialed out using a donut-hole approach (Ramsey et al. 1994, Meyer et al. 1998). Sizes of neighborhoods (inside diameter – outside diameter) were 0.0 – 0.8 km, 0.8 – 3.2 km, 3.2 – 6.4 km, 6.4 –

8.5 km, and 8.5 – 10 km. The smallest scale (0.8 km) represents effects of cropland at the lek site itself while accounting for error in recorded lek coordinates, and coincides with the resolution of our spatial data. The next largest scale (3.2 km) has been recommended as a buffer around leks of non-migratory populations in which vegetation should be left undisturbed (Connelly et al. 2000). The 6.4 km scale was chosen because other studies have found 3.2 km buffers insufficient to prevent population declines (Holloran 2005, Walker et al. 2007), and Walker et al. (2007) found support for cropland effects at this scale in the southern portion of our study area. We included the 8.5 km scale because it was identified by Holloran and Anderson (2005) as an appropriate "area of interest" around leks based on distribution of nests. Finally, we included the 10 km scale to consider effects on resources used outside of the breeding and nesting seasons when birds may be distributed farther from leks and because effects of oil and gas development on lek attendance have been detected at this distance (Gregory and Beck 2014). We fit candidate models (Table 2) and selected amongst them using the Akaike Information Criterion corrected for small sample size (AIC_c; Akaike 1973, Hurvich and Tsai 1989). The model that minimized AIC_c was selected as the top model and subsequently simplified by collapsing all included cropland buffers into a single circular buffer and re-fitting the model as described above.

We evaluated fit of the selected IPP model using k-folds cross-validation (Boyce et al. 2002). We divided the presence dataset into 5 test sets each containing an approximately equal number of active leks and for each test set, fit the model with the data not included in the test set (the training set) and used the fitted model to predict intensity at test data locations. After binning model predictions into 10 equal-area bins, we calculated the

Spearman rank correlation between bin numbers—an ordinal representation of increasing predicted lek habitat suitability—and frequencies of test leks with fitted values falling in those bins. Strong positive correlation is an indication of good model performance (Boyce et al. 2002).

2.4 Point-process model covariates

We used the USDA National Agricultural Statistics Service (USDA-NASS) Cropland Data Layer (hereafter CDL; USDA-NASS 2014a) to measure the proportion of the landscape in each buffer occupied by cropland. Cells classified as an annual crop, hay, or alfalfa (hay and alfalfa included classes 36 and 37) in ≥1 year during the period 2008—2012 were classified as cropland. The fallow or idle cropland class (class 61) was not included as we observed frequent instances of native rangeland misclassified into this category, a pattern initially detected due to scattered single pixels or small groups of pixels not resembling tilled fields and verified by inspecting aerial imagery. Using a five-year time series, the large majority of cropland in fallow rotation should appear in our dataset as cropland.

Other covariates included in all candidate models included proportion forest landcover, which is negatively associated with lek persistence within 1 km of leks (Baruch-Mordo et al. 2013); distance to mesic landcover, an important seasonal resource that affects sage-grouse population distribution and abundance (Donnelly et al. 2016); topographic roughness (Doherty et al. 2008, Baruch-Mordo et al. 2013); proportion sagebrush-dominated landcover, and non-cropland anthropogenic disturbance within 5 km (e.g., Knick et al. 2013). We also included 30-year normalized seasonal precipitation and annual minimum and maximum temperatures to account for other abiotic factors potentially limiting sage-grouse lek distribution. Quadratic terms were included where they seemed biologically appropriate: for Forest, Sagebrush, Mesic_dist, and all climate-related variables (see Table 1 for complete list of covariates and their abbreviations).

All data were represented using a common resolution of 800 m. Neighborhood and distance calculations were first performed at the data's native resolution before aggregating to a resolution approaching 800 m and resampling. All raster processing was performed with the R packages raster v. 2.4 (Hijmans 2014), rgdal v. 1.0 (Bivand et al. 2015), and gdalUtils v. 0.3.1 (Greenberg and Mattiuzzi 2014).

2.5 Linking build-outs to birds

To identify leks at risk of extirpation from crop expansion we applied a threshold on IPP model predictions to create binary habitat maps for each iteration of the cropland build-out (see section 2.7) delineating areas suitable for lek persistence from those unlikely to support leks (hereafter "habitat threshold"). During model validation, the 5 test datasets (~212 leks in each dataset) withheld during model fitting and 5 sets of randomly generated background points (*n* = 500) were used to calculate the intensity value that maximized the sum of sensitivity and specificity of the model (Liu et al. 2013). The five resulting threshold values were averaged to produce a habitat threshold used to evaluate the effect of crop build-out scenarios on the population.

At each iteration of the build-out we measured cropland covariates at all leks from the simulated cropland map, calculated predicted intensities at active leks with the fitted IPP model, and determined which leks occurred in areas below the habitat threshold. We recorded the proportion of the known male population falling below the habitat threshold under each scenario using the maximum high male count at active leks from 2008 – 2012.

2.6 Crop suitability model

We fit a crop probability model indicating suitability using the non-parametric weak learner model, random forests (Breiman 2001). Model covariates included derived topographic metrics indicating surface variability, solar intercept and water holding capacity; climate including 30-year normalization (1981-2011) of mean annual precipitation, mean annual temperature, number of degree days >5°C and duration of frost free period; and soil characteristics from the SSURGO database (Soil Survey Staff 2012). See Table 2 for a list of independent variables considered in model. For computational tractability and control of highly localized variation, we produced independent models for each county (n = 67) and merged county-level model predictions to produce a final, continuous coverage for the study area.

To specify the dependent variable we used CDL maps from 2008 to 2011 to derive a binominal response. We first reclassified yearly CDL rasters to binary by reclassifying all crop related classes to 1 and all other classes to 0 and then summed across all years to produce a single crop frequency raster. We then classified all pixels with a crop frequency ≥1 as 1 and all others as 0. Since we had data representing both discrete, with highly variable spatial-area representation, and continuous processes we needed a sampling scheme that captured both spatial processes without introducing undue dependency and pseudo-replication issues in the models. Accordingly, we implemented an area-weighted variable random sample, using SSURGO polygons, capturing both the soil spatial aggregate and variability of the underlying continuous variables. For each random sample we assigned the associate soil attributes and continuous variables as well as the binary response variable.

We tested for multicolinearity and removed any independent variables exhibiting multivariate redundancy (Murphy et al. 2010). Using the resulting screened matrix we applied a random forest model selection (Murphy et al. 2010) with the randomForest (Liaw and Wiener 2002) and rfUtilities (Evans and Murphy 2014) packages in R. Each model was tested for zero-inflation or class imbalance (Evans and Cushman 2009). If a model exhibited zero-inflation, using the 1/3 rule, the Evans and Cushman (2009) variant of random forests was applied otherwise standard random forest was used. In exploratory analysis, global and class-level model error stabilized at ~500 bootstraps. Because interactions stabilize at a slower rate than error we doubled the number of bootstraps that stabilized error ($b = 1001$).

Using a Kappa statistic, we applied a model fit error criteria ($k > 0.7$) to accept or reject a model. For model validation, at each county-level model we calculated the Kappa (Cohen 1960) to chance correct the percent correctly classified, and the AUC/ROC (Fawcett 2006) to account for the balance between true and false positive agreement. Finally, we ran a permutated significance test (Evans et al. 2011, Evans and Murphy 2014) to calculate a p-value for each model.

2.7 Cropland build-out simulation

We used predictions from the crop suitability model at two scales—the mean suitability of units of land ownership derived from the cadastral boundaries of the Public Land

Survey System (mean 216.3 ha, SD 73.0 ha; hereafter "parcels") (US Bureau of Land Management 2013) and the suitability of individual cells (resampled to 56 m resolution, or 0.3 ha)—to develop build-out maps simulating possible future landscapes under continued cropland expansion. The two-scale approach was used to simulate land use decisions made hierarchically, first at the scale corresponding to units of ownership and second taking into account finer-scale edaphic and topographic variation. The following methods were used to create 1000 stochastic realizations of cropland maps at five levels of crop expansion—from 10 – 50% increases over 2008-2012 cropland area in 10% increments—to estimate effects on sage-grouse.

Privately-owned parcels were selected ("tilled") randomly using mean parcel-level crop suitability as probability weights until the desired increase in total crop area was achieved. Within selected parcels, cells with a suitability ≤ the 5th percentile of predicted suitability values underlying current cropland and cells presently classified as developed (i.e., roads, buildings, well pads, etc.) were exempted from classification as cropland. Parcels owned and managed by federal or state government were exempted from cropland conversion. In conservation easement scenarios, parcels selected for easement purchase were also exempted from cropland conversion.

2.8 Easement targeting strategies

We simulated cropland build-out under two conservation easement scenarios to quantify the potential reduction in the proportion of the population at risk that could be achieved with an investment similar to Wyoming's recent conservation easement acquisition efforts directed at subdivision threat (Copeland et al. 2013). Our US $100M easement scenarios included one in which benefit-loss-cost targeting (Newburn et al. 2005) was implemented using only parcel-level data, and one with a modification that allows landscape-scale conversion risk to be incorporated into the targeting scheme. Briefly, benefit-loss-cost targeting seeks to optimize allocation of resources for protecting land by preferentially selecting for protection those sites with the highest ratio of expected loss of biological "benefits" to cost (Newburn et al. 2005).

We quantified biological benefits associated with purchasing an easement on any given parcel of land as a function of the abundance of sage-grouse breeding on leks within the distance *D*, equal to the outer radius of the selected scale of cropland influence in the top IPP model, and the area of the parcel. We made the simplifying assumption that habitat value of lands surrounding leks is homogeneous within this distance. The benefit function is:

$$B = \left(\sum_{j=1}^{n} N_j \right) R$$

where n is the number of active leks within D of the parcel center, N_j is the maximum high male count from 2008 - 2012 at lek j, and R is the area of native rangeland in the parcel.

Probability of cropland conversion on a parcel (P) was represented by the mean predicted cropland suitability from the random forest model. Cropland suitability predictions range from 0 to 1; we calculate the parcel-level probability of loss as the mean suitability value of pixels classified as rangeland. The product BP represents the expected loss of benefits without conservation intervention (Newburn et al. 2005).

Sage-grouse respond to disturbance and landscape composition at spatial scales far exceeding the typical size of a parcel (Knick and Connelly 2011). The habitat value of a given parcel to sage-grouse thus depends on the state of surrounding parcels. Conservation intervention preventing conversion of a particular parcel selected by the benefit-loss-cost method may therefore fail to preserve the biological value of that parcel if lower-scoring, unprotected parcels in the surrounding landscape are subsequently converted. This issue was acknowledged by Newburn et al. (2005) but they did not provide a solution for incorporating landscape-dependency into the benefit-loss-cost prioritization method. We tested the efficacy of a potential solution to this issue by incorporating an additional term expressing risk of loss at the landscape scale surrounding a parcel. Multiplying parcel-scale probability of conversion by landscape-scale probability of conversion gives higher priority to parcels in vulnerable landscapes, effectively clustering easements into these regions and reducing the likelihood of inefficient outcomes.

A general approach might simply calculate the average risk among parcels within a moving window of a size relevant to the species or community of interest. In our case, we used the vulnerability of active leks calculated from our unconstrained cropland build-outs to represent landscape-scale risk of loss and thereby assign higher priority for easement acquisition to parcels surrounding leks in risky landscapes. These vulnerabilities—calculated as the proportion of 1000 simulated future cropland build-outs in which a lek falls below the habitat threshold—represent the probability that the landscape surrounding each lek will be converted to the extent that persistence of the local population is compromised. We multiplied the high male counts of leks by their vulnerability (*V*) to modify the benefits term:

$$B' = \left(\sum_{j=1}^{n} N_j V_j \right) R \, .$$

Costs of easement acquisition (*C*) was calculated using county-level and state-level data from USDA-NASS (2014b). Rangeland value is generally lower than cropland value and, because easements would only be purchased on rangelands, we wished to estimate average value of rangeland by county within the study area. Because these data are not tracked by USDA-NASS at the county scale, we used the ratio of rangeland value to cropland value at the state level to adjust county-level agricultural land values. We downloaded average 2015 agricultural land values for each county, which are an aggregate measure across agricultural land types (cropland and pastureland/rangeland). We then determined the proportion of each county's agricultural land area in cropland and rangeland, again using USDA-NASS statistics, and used this proportion and the statewide rangeland/cropland value ratio to adjust agricultural land value to reflect rangeland value. The cost of purchasing an easement on a given parcel was calculated by multiplying the parcel's area by the county-level rangeland value and multiplying again by an average diminution rate of 0.35, which reflects typical diminution rates for easements purchased by The Nature Conservancy in eastern Montana (B. Martin, personal communication).

In our parcel-scale benefit-loss-cost targeting scenario, parcels received a score, $S = BP / C$ and were selected in descending order until US $100M was exhausted. In our modified parcel+landscape benefit-loss-cost targeting scenario, parcels were selected in descending order of $S' = B'P / C$. We report mean per-area cost, mean crop suitability, and median sum of males counted on known leks within D for parcels selected under each scenario.

3. Results

3.1 Model selection

Model log likelihoods stabilized with 250 000 background points. Variance Inflation Factors for all variables were <5, so no covariates were screened from inclusion in candidate models. The IPP model with cropland measured at 0 – 0.8 km and 0.8 – 3.2 km was most supported (Table 3). In all cases confidence intervals for cropland coefficients at scales larger than 3.2 km substantially overlapped zero. We therefore collapsed the 0 – 0.8 km and 0.8 – 3.2 km scales into a single circular buffer (radius 3.2 km and area 32.2 km^2) and re-fit the model with this single cropland covariate to derive coefficient estimates and standard errors (Table 4). Model validation indicated good model fit; overall Spearman rank correlation between predicted intensity bin and test lek density was 0.97 and all test sets had correlations > 0.95.

The selected model indicates point intensity of active leks declines rapidly as the proportion of cropland within the 32.2 km^2 landscape (Crop_3.2) increases (Figure 2). The estimated coefficient indicates a 10 percentage point increase in Crop_3.2 is associated with a 51% decrease in expected density of active leks (95% CI from 46% to 56%). Manipulating cropland at all active leks from 0-1 in increments of 0.01, we found

10% of leks would fall below the threshold once cropland reached 0.08 and half the leks in our study area would fall below the habitat threshold once cropland reached 0.22.

3.2 Crop suitability model

Each county-level model met our error criteria (*k* > 0.7). All models were also significant from random at $p = 0.001$ with a Kappa (mean = 0.740, min = 0.707, max = 0.774) and AUC of (mean = 0.790, min = 0.670, max = 0.860). In addition to quantitative evaluation of models it should be noted that, once merged together, there was considerable consistency in the spatial predictions of county-level models.

3.3 Build-out Analysis

The sum of sensitivity and specificity of the IPP model was achieved with a threshold of $\lambda_s = 2.8 \times 10^{-3}$. Presently 122 of 1064 leks, comprising 7.6% of the MZ1 population, exist in places predicted to be below the habitat threshold (Figure 1). For the purposes of our build-out analysis we are concerned only with future impacts of cropland expansion; we therefore consider this 7.6% of the population at these 122 already-impacted leks the baseline to which scenarios are compared. Hereafter, reported percentages refer only to those males counted on leks that are predicted to be above the habitat threshold presently, and that fall below the threshold with simulated cropland expansion.

Under cropland build-out unconstrained by conservation easements, the percentage of the breeding population falling below the habitat threshold ranged from 0.8% (95% CI from 0.3 – 1.3%) with a 10% growth in cropland area to 5.7% (95% CI from 4.7 – 6.7%) with a 50% growth in cropland area (Figure 3 and Table 5). One hundred nineteen leks, representing 11.3% of the population, had vulnerabilities ≥ 0.1 (Figure 1). Fifty-one percent of males counted on these leks ("vulnerable males") were found in 5 PACs: Fergus (1), McCone-Garfield (2), Golden Valley (3), and Musselshell (4) in Montana and Buffalo (5) in Wyoming (see numbered PACs in Figure 1). Most of the remaining vulnerable males (40%) were outside PACs.

Benefit-loss-cost targeting using conversion risk only at the parcel scale reduced the percentage of the population falling below the habitat threshold to 0.4% (95% CI from 0.2 – 0.7%) with a 10% growth in cropland area and 2.6% (95% CI from 2.1 – 3.2%) with a 50% growth in cropland area. This represents a reduction of potential future losses of about 53%. Selected parcels (n = 1114, total area 207 200 ha) had a median of 45 males breeding on leks within 3.2 km, a mean crop suitability of 0.294, and cost US $482.38 per hectare (US $195.22 per acre) on average.

Incorporating the vulnerability of leks into the benefit-loss-cost score significantly improved the efficiency of easements, reducing the percentage of the population falling below the habitat threshold to 0.1% (95% CI from 0.0 – 0.3%) with a 10% growth in cropland area and 1.1% (95% CI from 0.7 – 1.6%) with a 50% growth in cropland area. The landscape + parcel scale benefit-loss-cost targeting scenario resulted in a reduction of potential future losses of about 80%. Selected parcels (n = 926, total area 190 300 ha) had a median of 27 males breeding on leks within 3.2 km, a mean crop suitability of 0.344, and cost US $525.44 per hectare (US $212.63 per acre) on average. Benefits of both easement targeting methods increased as the severity of crop expansion increased (Figure 3).

4. Discussion

Adding to evidence that sage-grouse respond negatively to a growing human footprint, we show that a 10 percentage point increase in cropland in a 32.2 km^2 (12.4 mi^2) landscape can reduce lek density by more than half. Ten percent of 32.2 km^2 equates to slightly more than one Public Land Survey System section (2.59 km^2 or 1 mi^2); a single landowner breaking out a new field can thus strongly reduce persistence of leks in a landscape ten times the size of the field itself. Our findings suggest that half of known active leks risk extirpation with ≤22% of the landscape in cropland, which generally agrees with results of previous investigations that found low tolerance for this disturbance (e.g., Aldridge et al. 2008, Knick et al. 2013). Importantly, our study builds upon previous work by clarifying the scale at which the cropland effect manifests. Approximately 96% of known active leks in MZ1 have <15% cropland within the 32.2 km^2 landscape (Figure 2), highlighting once again the importance of large, intact sagebrush landscapes to sage-grouse persistence. Conservation efforts to prevent future conversion should focus on protecting landscapes with little or no existing cropland.

Several mechanisms could be responsible for the strong negative effect of cropland fragmentation on lek density. Populations in crop-fragmented landscapes may be exposed to increased risk of nest predation or early brood failure due to altered predator abundance or their foraging efficiency—a phenomenon well documented in ground-nesting ducks (Greenwood et al. 1995, Phillips et al. 2003). Processes affecting the suitability of the breeding grounds more directly might include increased predation during lekking or while birds are concentrated near leks in spring. Avoidance of cropland may also play a role. Behavioral studies suggest lek location is driven at least in part by males positioning themselves to intercept females moving between wintering and nesting ranges (Bradbury et al. 1989, Gibson 1996b). Therefore, disruption of female movements during this period may reduce probability of lek formation or increase lek abandonment in landscapes fragmented by cropland. GPS-tracked sage-grouse in northeast Montana and southern Saskatchewan, which strongly avoided cropland in their migration between wintering and breeding ranges, lend preliminary support to this hypothesis (Smith 2013). Mortality of sage-grouse from exposure to organophosphate insecticides has been documented (Blus et al. 1989) and may periodically contribute to reduced survival, especially if grouse are attracted to field margins or alfalfa fields by abundant insect food sources during or immediately after insecticide application.

Without additional investment in conservation easements, our simulated cropland build-outs indicate around 5-7% of the population could be lost in a worst-case scenario of a 50% increase in total cropland area. Our conservation easement scenarios suggest, however, that most potential losses can be prevented with a strategically-implemented US $100M investment. The benefit-loss-cost targeting method, which reduced potential losses by over 50%, selected parcels with moderately high biological value and moderate probability of loss, while per-area cost was below the study area average (mean of all privately owned parcels: US $515.52 per hectare or US $208.58 per acre). Parcels selected by the parcel+landscape benefit-loss-cost targeting scheme, which resulted in an 80% reduction in potential losses, had lower biological value but higher risk compared to the parcel-only scheme, and slightly higher cost. Parcels of particularly high biological value were not often selected by either targeting scheme because biological value and risk were negatively correlated ($r = -0.13$, $p < 0.0001$). This highlights that ignoring risk could be highly detrimental, reducing efficiency by spending resources protecting habitat at very low risk of conversion. Cost and risk were weakly but significantly positively correlated ($r = 0.17$, $p < 0.0001$), indicating that accounting for cost improved efficiency (Newburn et al. 2005). Accounting for risk is of paramount importance in this system, however, because risk was much more variable (coefficient of variation [CV] = 0.96) than cost (CV = 0.32) and was similarly variable to biological value (CV = 1.0).

The recent mobilization of state and local governments, federal agencies, and non-governmental organizations to implement proactive conservation to prevent an ESA listing suggests the financial resources necessary to implement an easement program on this scale are within reach. For example, since 2005 Wyoming has drawn from a permanent trust established by the legislature to fund conservation easements, permanently protecting hundreds of thousands of hectares of sage-grouse habitat at risk of development. Montana recently established a Sage Grouse Stewardship Fund which made available US $10M for habitat protection and improvement projects on private lands over a two-year period (Executive Order No. 10-2014). USDA Natural Resources Conservation Service's Sage Grouse Initiative has channeled > US $200M from the conservation title of the Agriculture Act of 2014 (commonly known as the Farm Bill) toward voluntary, incentive-based conservation for sage-grouse, including a commitment to acquire ~24 300 ha (60 000 acres) in conservation easements in Montana, North Dakota, and South Dakota by 2018 to prevent cropland conversion (USDA NRCS 2015).

Because our envisioned easement program would likely take a decade or more to implement even with recently increased levels of funding and human capacity, the order with which properties are placed under easement is an important aspect of the conservation strategy. The conservation value of an easement depends on the intactness of the surrounding landscape, and a group of geographically clustered easements may more effectively conserve habitat than an equal area in easements isolated by great distances. The better performance of our parcel+landscape easement scenario (Figure 3) illustrates this point. We recommend a strategic approach amongst land trusts and funding entities that conserves entire vulnerable landscapes rather than scattered individual properties. Ultimately, while we strongly recommend a data-driven approach that uses biological value, risk, and cost to prioritize parcels, easements are a voluntary conservation tool that relies on landowner interest and relationships between communities and land trusts. Additionally, local practitioners may have access to auxiliary information regarding conversion risk or cost of particular properties. For example, areas where farming is a dominant feature of local residents' cultures and economies may face higher risk of conversion than predicted by biophysical factors. Successful implementation of a science-based easement acquisition program such as the one we describe relies on the expertise of competent, locally-based conservation practitioners (Neudecker et al. 2011).

We used a presence-only approach to model lek sighting rate as a function of environmental covariates because this approach allowed us to take advantage of the extensive available dataset of largely opportunistically-collected lek observations and incorporate information about disturbance in areas formerly suitable for sage-grouse. A shortcoming common to all presence-only analyses is the inability to estimate true occurrence rates (Aarts et al. 2012, Phillips and Elith 2013). Predicted sighting rates are, however, expected to be proportional to occurrence rates if covariates influencing occurrence do not also influence detection (Phillips et al. 2009, Fithian and Hastie 2013).

Our coefficient estimates likely provide reliable inference about effects of cropland on lek density, as cropland variables tested were not highly correlated with other human features, such as distance to roads and urban areas, potentially related to detection (all $|r| < 0.35$). We caution, however, against using our model to infer effects of anthropogenic disturbances other than cropland, which are likely to be correlated with features affecting detection; we instead point the reader to numerous studies focused specifically on these disturbances (e.g., Aldridge and Boyce 2007, Walker et al. 2007, Doherty et al. 2008, Doherty et al. 2010, Holloran et al. 2010, Naugle et al. 2011).

If sagebrush ecosystem conservation goals include private lands, then the high economic utility of cropland conversion must be counterbalanced by policies and programs that incentivize conservation of non-market benefits provided by native sagebrush grazing lands. The ‘Sodsaver’ provision in the 2014 Farm Bill (Title XI), which sharply reduces crop insurance premium subsidies crops grown on previously untilled land, may benefit sage-grouse by discouraging conversion in locations that are marginal for cultivation but provide sage-grouse habitat. In regions where sage-grouse habitat overlays more productive arable land, however, greater incentives are needed to prevent future habitat loss. Here, we have demonstrated that efficient allocation of US $100M in conservation easements can provide substantial coverage of sage-grouse habitat at risk of conversion.

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Tables

Table 1. Covariates used in IPP models of active sage-grouse lek sighting rate in sage-grouse Management Zone 1.

Covariate (Abbreviation)	Scale	Source
Landcover		
Proportion forest landcover (Forest) ‡	1.0 km	1
Proportion sagebrush-dominated landcover (Sagebrush)‡	6.4 km	1
Distance to mesic landcover (Dist_mesic) ‡	—	1
Topography		
Standard deviation of elevation (Roughness) ‡	0.8 km	2
Climate		
Average annual minimum temperature (Min temp) ‡	0.8 km	3
Average annual maximum temperature (Max temp) ‡	0.8 km	3
Average total precipitation March-May (Spring precip) ‡	0.8 km	3
Average total precipitation June-August (Summer precip) ‡	0.8 km	3
Average total precipitation September-November (Fall precip) ‡	0.8 km	3
Anthropogenic features		
Proportion non-cropland anthropogenic disturbance (Disturb)‡	5.0 km	4
Cropland		
Proportion cropland (Crop_0.8)‡	0 - 0.8 km	5
Proportion cropland (Crop_3.2)‡	0.8 - 3.2 km	5
Proportion cropland (Crop_6.4)	3.2 - 6.4 km	5
Proportion cropland (Crop_8.5)	6.5 - 8.5 km	5
Proportion cropland (Crop_10.0)	8.5 - 10.0 km	5

Sources: **1**: LANDFIRE (2008) **2**: Standard deviation of elevation from 30 m DEM (Gesch et al. 2002, Gesch 2007) **3**: 30-year climate normals (1981-2010; PRISM Climate Group 2014); **4**: Proportion of area covered by disturbances after converting vector data sources to a single cumulative raster layer (30 m resolution). Vector data sources include: National Landcover Dataset (Frye et al. 2011), State oil & gas boards of Montana, North Dakota, South Dakota, and Wyoming, TIGER/Line vector data (US Census Bureau 2013), and Federal Communications Commission (wireless.fcc.gov); **5**: National Agricultural Statistics Service Cropland Data Layer (USDA-NASS 2014a)

‡ In top IPP model

Table 2. Covariates used to fit random forest model predicting cropland in sage-grouse Management Zone 1.

Covariate†	Source/Citation
Annual Drought Index	1
Degree Days <5C	1
Frost Free Period	1
Mean Annual Temperature	1
Mean Annual Precipitation	1
Compound Topographic Index (wetness)	2
Landform Index	3
Roughness 3x3 focal window	4
Roughness 27x27 focal window	4
Slope * COS(Aspect)	5
Slope * SIN(Aspect)	5
Slope in degrees	6
Slope Position	7
Surface Relief Ratio 3x3 focal window	8
Surface Relief Ratio 27x27 focal window	8
Topographic Radiation Aspect Index	9
Available water storage 25cm	10
Available water storage 50cm	10
Available water storage 100cm	10
Available water storage 150cm	10
Distance from the soil surface to top of a bedrock layer	10
Proportion of dominate drainage class	10
Proportion of wettest drainage class	10
Proportion of dominant flood frequency class	10

Proportion of highest probability class representing annual probability of a flood event	10
Proportion of hydric soils	10
Proportion of soils with high runoff potential	10
Proportion of soil unit exhibiting water being ponded on the soil surface	10
Slope gradient of soil map unit	10
Weighted average of slope gradient of soil map unit	10
Annual shallowest depth to a wet soil layer (water table)	10
Growing season shallowest depth to a wet soil layer (water table)	10
National Commodity Crop Productivity Index	11

[†] All data were resampled to a common resolution of 30 m for model fitting and prediction, then resampled to 56 m for cropland build-out to speed calculation.

Sources: **1:** Rehfeldt et al. (2006); **2:** Gessler et al. (1995); **3:** McNab (1993); **4:** Riley et al. (1999); **5:** Stage (1976); **6:** Horn (1981); **7:** Blaszczynski (1997); **8:** Pike (1971); **9:** Roberts and Cooper (1989); **10:** Soil Survey Staff (2012); **11:** USDA.

Table 3. Candidate models of active lek sighting rate ranked by Akaike Information Criterion corrected for small sample size (AIC_c).

Model	K	AIC_c	ΔAIC_c	wt_i
Crop_0.8 + Crop_3.2	23	12257.78	0.00	0.59
Crop_0.8 + Crop_3.2 + Crop_6.4	24	12259.54	1.76	0.24
Crop_0.8 + Crop_3.2 + Crop_6.4 + Crop_8.5	25	12260.86	3.08	0.13
Crop_0.8 + Crop_3.2 + Crop_6.4 + Crop_8.5 + Crop_10.0	26	12262.86	5.08	0.05
Crop_0.8	22	12284.16	26.38	0.00
Null[†]	21	12623.28	365.50	0.00

[†] The null model and all other candidate models include all topographic, landcover, climate, and non-cropland anthropogenic variables indicated in Table 1.

Table 4. Model coefficients of top-ranked IPP model.

Coefficient	Estimate	SE	z-value	p-value
Intercept	-3.6E+01	9.5E+00	-3.84	0.0001
Roughness	-1.2E-01	7.4E-03	-15.65	< 0.0001
Sagebrush	9.1E+00	8.2E-01	11.15	< 0.0001
Sagebrush^2	-1.5E+01	1.6E+00	-9.54	< 0.0001
Forest	-1.1E+01	2.0E+00	-5.15	< 0.0001
Forest^2	1.2E+01	1.1E+01	1.16	0.2469
Mesic_dist	1.7E-01	4.0E-02	4.31	< 0.0001
Mesic_dist^2	-1.6E-02	4.0E-03	-4.05	0.0001
Winter_precip	1.8E-01	4.8E-02	3.70	0.0002
Winter_precip^2	-2.2E-03	7.6E-04	-2.91	0.0037
Spring_precip	1.2E-01	3.5E-02	3.54	0.0004
Spring_precip^2	-5.5E-04	1.5E-04	-3.62	0.0003
Summer_precip	4.1E-02	2.6E-02	1.60	0.1105
Summer_precip^2	-1.4E-04	1.0E-04	-1.45	0.1473
Fall_precip	-2.6E-01	4.2E-02	-6.07	< 0.0001
Fall_precip^2	1.5E-03	2.9E-04	5.31	< 0.0001
Min_temp	1.6E-01	8.3E-02	1.95	0.0517
Min_temp^2	2.0E-02	7.2E-02	0.28	0.7819
Max_temp	4.3E+00	1.3E+00	3.42	0.0006
Max_temp^2	-1.6E-01	4.3E-02	-3.66	0.0003
Disturb	-4.3E+00	1.4E+00	-3.18	0.0015
Crop_3.2	-7.2E+00	5.3E-01	-13.42	< 0.0001

Table 5. Effects of simulated cropland expansion on proportion of sage-grouse population in sage-grouse Management Zone 1 occurring in areas falling below habitat threshold.

Scenario	Cropland Increase	Proportion of population occurring below habitat threshold†		
		Mean	Lower CL‡	Upper CL
No Conservation	10%	0.008	0.003	0.013
	20%	0.018	0.011	0.024
	30%	0.029	0.021	0.037
	40%	0.042	0.034	0.051
	50%	0.057	0.047	0.067
Benefit-Loss-Cost Targeting (Parcel)	10%	0.004	0.002	0.007
	20%	0.009	0.005	0.013
	30%	0.014	0.010	0.019
	40%	0.020	0.015	0.025
	50%	0.026	0.021	0.032
Benefit-Loss-Cost Targeting (Landscape + Parcel)	10%	0.001	0.000	0.003
	20%	0.003	0.001	0.005
	30%	0.005	0.003	0.008
	40%	0.008	0.004	0.011
	50%	0.011	0.007	0.016

† Habitat threshold is the value that maximizes the sum of sensitivity and specificity of the IPP model (see section 2.5).

‡ Confidence limits contain central 95% of 1000 iterations of cropland build-outs.

Figures

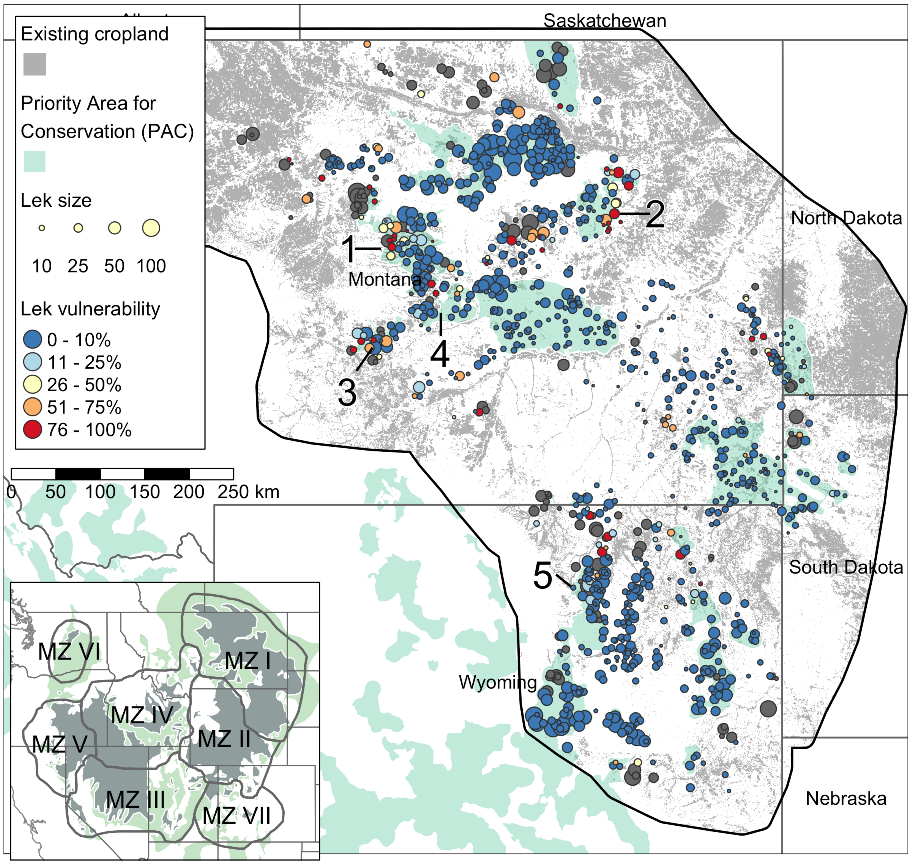

Figure 1. Study area, sage-grouse Management Zone 1 (MZ1), showing active leks and areas currently occupied by cropland. Lek color indicates vulnerability to cropland expansion—i.e., the proportion of 1000 stochastic cropland build-outs in which the lek fell below the model-based habitat threshold. Dark gray points indicate leks that currently fall below the habitat threshold (n = 122, see section 3.3). Point size is proportional to maximum recorded male attendance from 2008 – 2012. Numbered PACs contain more than half of the vulnerable males (section 3.3). Inset depicts the global range of sage-grouse (historical range in light green, current range in dark green) and boundaries of management zones.

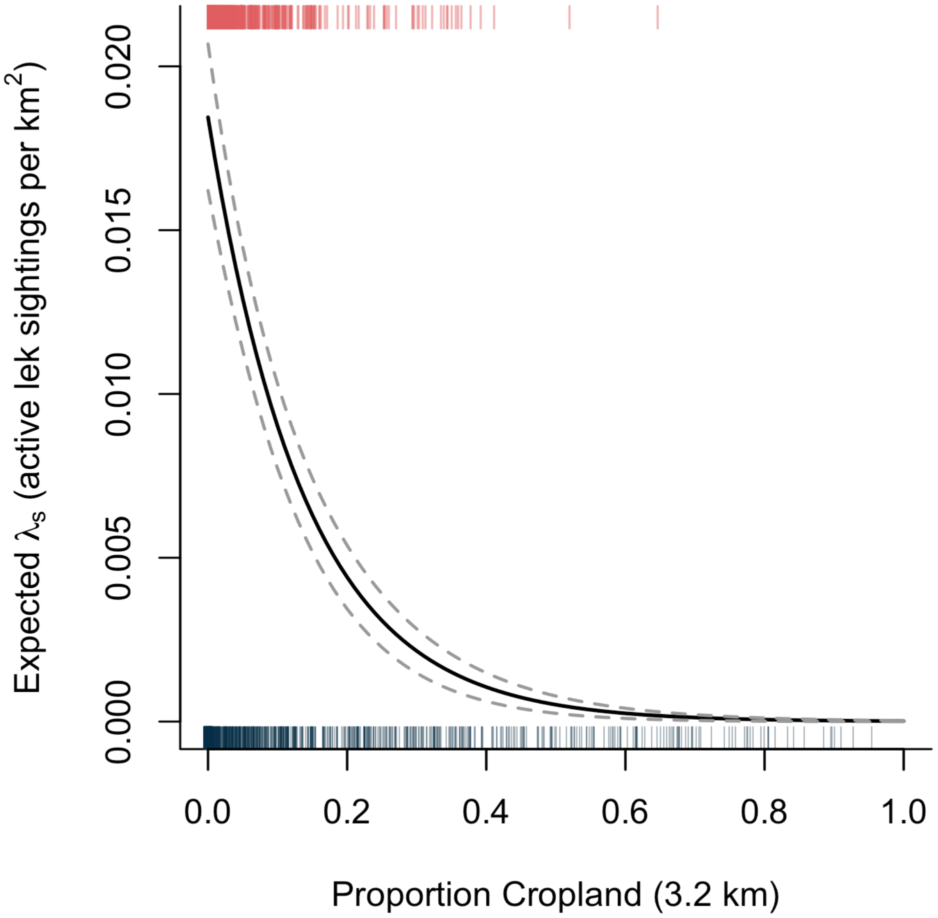

Figure 2. Mean (black line) and 95% confidence intervals (dashed gray lines) of expected intensity of active lek sightings as a function of proportion cropland at the 32.2 km^2 scale. Rug plots indicates proportion cropland measured at active leks in Management Zone 1 (*n* = 1064, top) and an equal number of random locations in Management Zone 1 (bottom). 96% of active leks are found in landscapes with proportion cropland <0.15.

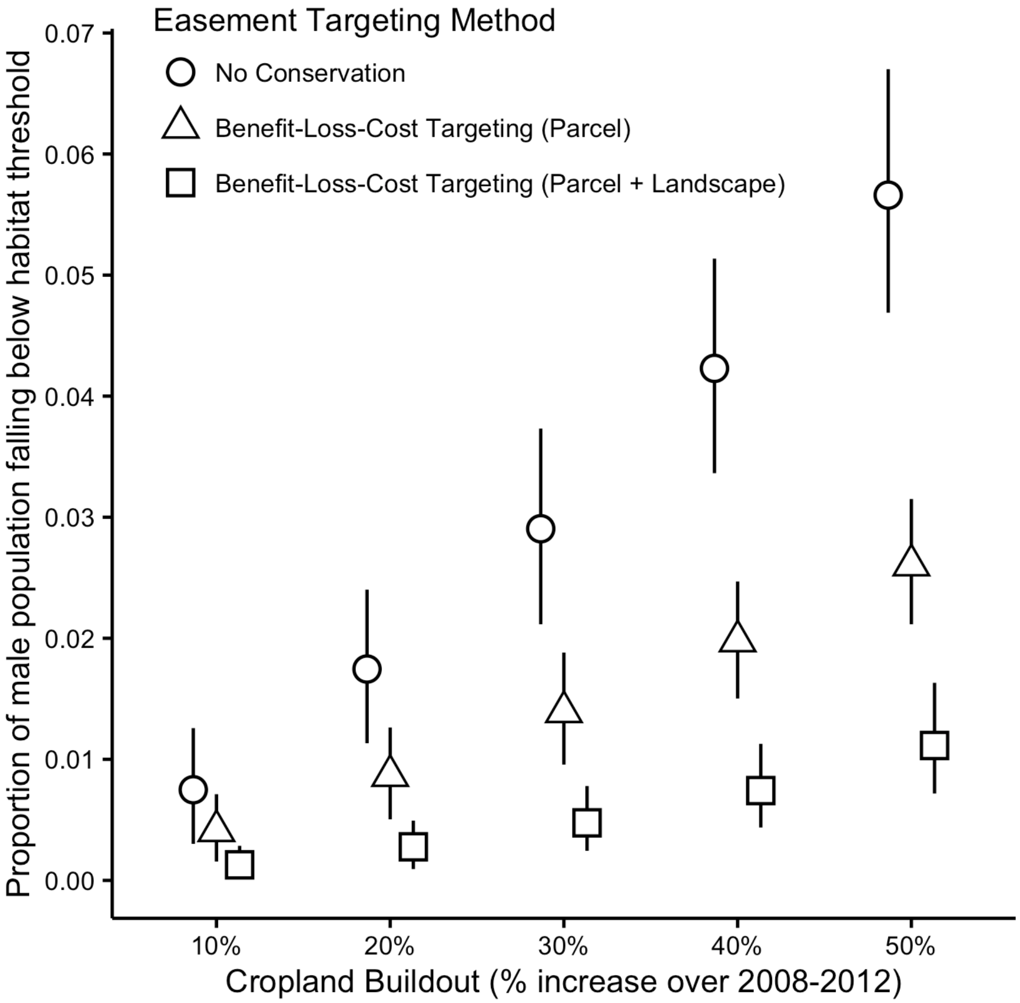

Figure 3. Proportion of male breeding population in sage-grouse Management Zone 1 falling below the habitat suitability threshold with simulated expansion of cropland area from 10 – 50% over 2012 extent. Error bars indicate lower and upper bounds of the central 95% of outcomes from 1000 stochastic cropland build-out iterations.

CHAPTER 2: EFFECTS OF LIVESTOCK GRAZING, WEATHER, AND LANDSCAPE ON NESTING GREATER SAGE-GROUSE

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ABSTRACT

Grazing by domestic livestock is a ubiquitous land use in the sagebrush (*Artemisia* L.) biome of western North America. Widespread, long-term population declines in greater sage-grouse (*Centrocercus urophasianus*) have elicited concern about potential negative effects of livestock management practices on sage-grouse populations. Hypothesized relationships, mostly untested, between livestock and sage-grouse nesting ecology have played a prominent role in shaping public land livestock grazing policy and broader conservation efforts aimed at bolstering struggling populations. We tested hypothesized relationships between livestock grazing and nest site selection and nest survival and evaluated whether recently-implemented rotational grazing systems positively affected nesting habitat quality as part of a large-scale, replicated, natural experiment in central Montana. Contrary to expectations, we found nest site selection and nest survival were unrelated to herbaceous vegetation structure, livestock presence, and indices of local grazing pressure. Rather, females selected nest sites based on relatively static features such as sagebrush cover, topography, density of anthropogenic features, and distance from roads, while nest failure was driven by extreme precipitation events. We discuss our findings in the context of recent literature on the relationship between vegetative concealment and nest predation, and emphasize the importance of considering the hierarchical nature of wildlife-habitat relationships when identifying threats to population persistence and crafting habitat management policies.

KEY WORDS *Centrocercus urophasianus*, Greater sage-grouse, grazing management, habitat selection, livestock, nest survival, Northern Great Plains

INTRODUCTION

Once occupying > 62 million ha (Kuchler 1970), nearly half the sagebrush (*Artemisia* L.) biome of western North America has been lost to sagebrush eradication, conversion to cropland, replacement by exotic annual grasslands, conifer encroachment, and expanding human settlements (Knick et al. 2003, Schroeder et al. 2004). Loss and fragmentation of sagebrush steppe has resulted in concomitant impacts to a broad array of sagebrush-dependent wildlife (Rich et al. 2005, Suring et al. 2005). Strategic, science-based management of land practices in remaining sagebrush grasslands is thus a top conservation priority (Davies et al. 2011). Grazing by domestic livestock is ubiquitous across sagebrush ecosystems (Anderson and Holte 1981, Knick et al. 2003). Management of livestock grazing therefore has potentially widespread implications for the integrity of the sagebrush ecosystem and its associated wildlife populations.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are a species of conservation concern that embody the challenges of conserving sagebrush ecosystems. Population declines since the mid 20th century are attributed to widespread habitat loss and degradation (Connelly and Braun 1997, Knick and Connelly 2011). Following several petitions for Endangered Species Act (ESA) protection, US Fish & Wildlife Service (USFWS) recently deemed ongoing public- and private-land conservation efforts sufficient to preclude the need for a listing. Livestock grazing, predominantly by cattle (*Bos taurus*) and sheep (*Ovis aries*), has been suggested as a contributing factor in historical population declines (Connelly and Braun 1997, Beck and Mitchell 2000, Wisdom et al. 2002, Crawford et al. 2004) and remains a contentious management issue.

Effects of livestock grazing on wildlife populations are thought to manifest primarily through the effects of herbivory on vegetation composition and structure—e.g., reduction in food abundance or hiding cover afforded by herbaceous plants (Fleischner 1994). Wildlife-habitat relationships are inherently hierarchical in scale (Johnson 1980), however, and variation at fine scales is properly treated within the context of broader-scale environmental attributes and processes affecting space use and fitness. Recent research, for example, has demonstrated the primacy of factors such as weather (Hovick et al. 2015) and landscape configuration (Jorgensen et al. 2014, Simonsen and Fontaine 2016) over local vegetation structure in driving nest survival in galliforms. Still, each of the eight petitions to list sage-grouse under the ESA received between 1999 and 2005 implicated livestock grazing among continued threats to population persistence. For the past 20 years there has been a recognized need for research on the relationship between livestock grazing and sage-grouse ecology (Dobkin 1995, Beck and Mitchell 2000, Crawford et al. 2004). However, no study to date has empirically linked sage-grouse behavior or demography to grazing management.

Numerous relationships between livestock grazing and sage-grouse have been hypothesized (see Beck and Mitchell 2000), with a consensus that nest success, one of the most influential vital rates affecting sage-grouse population growth (Taylor et al. 2012, Dahlgren et al. 2016), is likely impacted by grazing. The primary mechanisms through which grazing is thought to impact nest success include increased nest abandonment from direct disturbance by livestock and reduced concealment by herbaceous understory vegetation facilitating nest detection by predators. There is anecdotal evidence of cattle (Rasmussen and Griner 1938, Coates et al. 2008) and sheep (Patterson 1952) causing nest abandonment, but to our knowledge no published studies have quantified the effect of livestock presence on sage-grouse nest survival. The latter, indirect mechanism is supported by studies reporting a positive relationship between cover or height of herbaceous vegetation—primarily grasses—and nest success (Gregg et al. 1994, Delong et al. 1995, Holloran et al. 2005, Doherty et al. 2014) coupled with the fact that livestock consume herbaceous vegetation. However, the importance of grass height was recently questioned by Gibson et al. (2016) who highlighted an inherent bias in commonly-used field methods that produces inflated or even spurious effects of vegetation height on nest survival. Nevertheless, it is widely believed that livestock grazing has played a role in contemporary population declines (Connelly and Braun 1997) and that increasing herbaceous cover and height through altered or reduced grazing may help bolster populations (Wisdom et al. 2002, Taylor et al. 2012, Doherty et al. 2014). Moreover, the relationship between herbaceous understory and sage-grouse nest survival has played a prominent role in shaping public lands grazing policy, with 11 of 15 completed BLM Resource Management Plan Amendments within the range of sage-grouse containing minimum grass height recommendations among habitat objectives for sage-grouse.

The scarcity of reliable knowledge (Romesburg 1981) about relationships between sage-grouse and livestock grazing reflects, in part, the challenges of conducting grazing-related research at relevant scales. Sage-grouse often occupy patchworks of private and public ownership and individuals may frequently cross boundaries delimiting differing management strategies. Females, for example, may travel 10 km or more between breeding grounds and their eventual nest site (Holloran and Anderson 2005). Implementing—let alone replicating—experimental treatments over areas sufficiently large to measure a response is therefore both logistically challenging and costly. Replicated natural experiments may, however, provide the necessary conditions for testing many scientific hypotheses (Sinclair 1991), including those regarding effects of livestock grazing management on sage-grouse.

In 2010, the US Department of Agriculture Natural Resources Conservation Service (NRCS) began a coordinated range-wide conservation effort called the Sage Grouse Initiative (SGI). Rotational grazing systems are among the primary tools NRCS employs to improve sage-grouse habitat on private lands. Briefly, rotational grazing systems involve moving livestock herds through a number of pastures or paddocks throughout the grazing season, shortening the duration of use, and often altering the timing of use of each pasture from year to year (Hormay 1956;1970). Additionally, one or more pastures may be rested (i.e., no livestock grazing for ≥ 12 months) on a rotating basis to allow for plant recovery and accumulation of residual plant matter and litter. Though frequently recommended to foster a number of conservation goals, evidence for benefits of rotational grazing systems over alternative grazing management strategies is mixed at best (Briske et al. 2008), though few studies have explicitly measured outcomes of rotational grazing systems on species of conservation concern.

We present findings from the first five years of a 10-year grazing experiment in central Montana where SGI rotational grazing systems were simultaneously implemented on several ranches. NRCS began enrolling landowners in SGI rotational grazing systems (*hereafter* SGI-RGS) in 2010, targeting ranches in state-designated "core areas" of high sage-grouse abundance. From 2010 to 2012, 10 landowners in one such core area in central Montana elected to participate in SGI-RGS contracts, with enrolled acreage peaking in 2012 at approximately 50,585 ha (125,000 ac), 67% of which were inside core area boundaries.

Our objectives were twofold. First, we sought to test the aforementioned hypothesized direct and indirect effects of livestock grazing on nest survival. If livestock grazing reduces nest survival by inducing abandonment, we predict that the presence of livestock in the pasture during incubation and/or increased evidence of livestock use surrounding the nest will be associated with lower nest survival. If livestock grazing indirectly affects nest survival through consumption of herbaceous hiding cover around the nest, we predict that greater height and/or cover of herbaceous vegetation surrounding the nest will be associated with increased nest survival. Second, we compared vegetation structure and nest survival on SGI-RGS ranches to neighboring, non-participating ranches (*hereafter* non-SGI) to test the hypothesis that rotational grazing systems implemented through SGI increase the attractiveness or quality of nesting habitat. We predicted that herbaceous vegetation metrics related to nest site selection and/or nest survival would be positively affected by SGI-RGS and pasture rest and that nests on SGI-RGS ranches or rested pastures would be more successful.

STUDY AREA

Our study area, near the town of Roundup, Montana (46.448° N, 108.543° W, Figure 1), is characterized by rolling topography ranging in elevation from 975 to 1250 m. Vegetation is typical of inter-mountain big sagebrush steppe (NatureServe 2015), with Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and silver sagebrush (*Artemisia cana*) both common and co-dominant with a mix of rhizomatous and caespitose perennial grasses. Mean annual precipitation at Roundup (1981 – 2010) is 359 mm and annual precipitation during the study ranged from 265 mm in 2012 to 485 mm in 2014. Approximately 40% of annual precipitation falls between June and August (Figure 1). The study area encompasses 30 sage-grouse leks with >1 displaying male recorded in ≥ 1 year between 2011 and 2015. Area lek counts suggest the study was initiated just before the bottom of a trough in the population cycle, with recovery evidently beginning during 2015 and continuing through 2016 (Figure 2). Median high male counts on these leks ranged from 7 in 2014 to 25 in 2016.

Rotational Grazing Systems

Ranches enrolled in SGI-RGS comprised a variety of configurations (i.e., ranch size, number of herds, stocking rate, existing infrastructure), therefore grazing plans were individually customized to accommodate ranch configuration and landowner needs. However, all plans adhered to the NRCS Montana Prescribed Grazing conservation practice standards (NRCS 2012) and implemented a consistent set of minimum criteria designed to positively influence features of sage-grouse habitat. These criteria included: 1) utilization rates of 50% or less of current year's growth of key forage species, 2) duration of grazing ≤ 45 days, 3) timing of grazing changed by at least 20 days each year, and 4) a contingency plan for exceptional circumstances such as drought or fire. Infrastructure such as cross fencing and supplemental water were added where necessary, and NRCS cost-shared to cover these expenses. In return for higher rates of compensation, landowners could optionally elect to rest 20% of the identified sage-grouse nesting habitat (areas with ≥5% sagebrush cover) on their ranches from grazing on an annually rotating basis. Nine of the 10 landowners enrolled during the study elected to incorporate rest. Rest period was intended to provide rested pastures two full sage-grouse nesting seasons without livestock use and was generally ≥15 months in duration. Enrollment in an SGI-RGS contract is entirely voluntary but incentive payments are contingent upon contract compliance, which is monitored annually. SGI-RGS contracted ranches ranged in size from approximately 1,660 to 7,690 ha (4,100 to 18,990 ac) and covered approximately 40% of the Golden Valley core area (Figure 1). We secured permission to access all 10 ranches enrolled in SGI-RGS, which constituted our treatment group.

We also received permission to access land owned by >40 area landowners with non-enrolled lands, which constituted our control group. Management of non-SGI lands encompassed a variety of grazing systems, but most were managed less intensively, i.e., with a season-long grazing strategy or slower rotations through larger pastures, usually without annual changes in season of use. Non-SGI ranches were distributed throughout the remainder of the Golden Valley core area as well as in the Musselshell and Petroleum core areas (Figure 1).

METHODS

Sage-Grouse Capture and Nest Monitoring

We captured female sage-grouse during the early breeding season (March-April) in 2011-2015, and during late summer (August-September) in 2012-2015 using spotlights and hoop netting techniques from all-terrain vehicles (Wakkinen et al. 1992). We aged sage-grouse as juveniles (1^{st} year after hatch) or adults, and affixed 25 g necklace-style VHF transmitters (Advanced Telemetry Systems, Isanti, MN). Females were tracked at least twice weekly until they began to make localized movements indicative of nesting behavior, at which point we reduced our monitoring interval to daily if possible. When a female was detected in the same location on successive relocations, we attempted to identify the female on a nest while maintaining a distance of at least 10 m to avoid flushing. Nests were marked from a distance of ~ 10 m with natural materials, and listening points were established ≥ 100 m from the nest for monitoring nest status remotely via telemetry. We monitored nests from the listening point every 2-3 days until the female moved from the nest, at which point we confirmed nest fate as successful (at least one hatched egg with membrane detached) or failed. Predation is the primary cause of nest failure in sage-grouse, but we recorded failed nests without evidence of predation (i.e., without broken or missing eggs) as abandoned. All animal handling was approved under University of Montana's IACUC Animal Use Protocol 011-14DNWB-031914.

Modeling Framework and Model Selection

We used Bayesian methods to fit nest site selection and nest survival models to facilitate simultaneous variable selection and parameter estimation. We began nest site selection and nest survival analyses with an initial screening of candidate variables to consider for multi-variable models by fitting univariate models to each variable and rejecting those with 85% credible intervals of coefficient estimates overlapping zero. For univariate model fitting we placed vague N(0, 100) priors on regression coefficients, and ran 10,000 iterations following 50,000 samples for burn-in. Remaining candidate variables were screened for multicollinearity using pairwise Pearson correlation coefficients. When pairs of variables were highly correlated ($|r| > 0.5$), we retained the variable that we reasoned to have the simplest biological interpretation.

We used a Bayesian variable selection technique to identify supported variables and produce model-averaged coefficient estimates (O'Hara and Sillanpaa 2009). The screened set of K candidate variables entered into the final model, in which each coefficient β_k was multiplied by a binary indicator variable I_k (Kuo and Mallick 1997, O'Hara and Sillanpaa 2009), and inference was based on the posterior distributions of $\beta_k I_k$, providing model-averaged parameter estimates and 95% credible intervals. In model fitting, coefficient priors were scaled according to the number of parameters in the model at each MCMC iteration such that total model uncertainty was held constant across candidate models. Thus, priors for all β_k were distributed N(0, $(V/M)^{-1}$) where M was the number of non-zero indicator variables and $V \sim$ Gamma(3.29,7.8) such that the marginal prior distributions on nest-site selection probability or daily nest survival probability were approximately U[0,1] (Link and Barker 2006, Smith et al. 2011). We placed

Bernoulli(0.5) prior distributions on all indicator variables, representing no prior information about individual variable importance (O'Hara and Sillanpaa 2009). We calculated Bayes factors (BF) to determine support for inclusion of each variable in a final model, where BF for each indicator variable was calculated using prior ($I_{prior} = 0.5$) and posterior mean ($I_{posterior}$) estimates (Smith et al. 2011) as

$$BF = \frac{I_{posterior}/(1 - I_{posterior})}{I_{prior}/(1 - I_{prior})}$$

A BF ≥ 3 is indicative of a coefficient with strong support, so we used this threshold to determine which coefficients to use for inference - analogous to a top model as identified by other forms of model selection (e.g., Akaike's Information Criterion; Converse et al. 2013). For final model fitting we ran 100,000 iterations following 100,000 samples for burn-in. We visually assessed convergence and mixing and calculated the Gelman-Rubin statistic (Gelman and Rubin 1992, Brooks and Gelman 1997) for all coefficients using 3 chains with different initial values. Models were fit using JAGS (version 4.2.0, mcmc-jags.sourceforge.net, accessed 19 February 2016) via the runjags package (Denwood *in press*) in program R (version 3.3.0, www.r-project.org, accessed 3 May 2016).

Nest Site Selection Modeling

Used-Available Design.— Following cessation of nesting, we returned to nests to measure vegetation and other covariates. We made identical measurements at a random sample of available locations to quantify resources available to nesting females. We imposed several criteria to develop a sample of available locations relevant to the behavior of female sage-grouse selecting a nest site (3rd and 4th order; Johnson 1980).

Specifically, available points were constrained to areas with ≥ 5% visually estimated sagebrush canopy cover at the plot scale (15 m) and within 6.4 km of leks from which females were captured (Holloran and Anderson 2005, Coates et al. 2013). At points meeting these criteria we selected the nearest sagebrush shrub ≥ 30 cm in height to designate the nest shrub, as sage-grouse are known to select shrubs of at least this height for nesting (Connelly et al. 2000).

Nest-Site Selection Model.— We fit used-available resource selection function (RSF; Manly et al. 2002, Johnson et al. 2006) models using a logit-link to relate measured covariates to used ($y = 1$) or available sites ($y = 0$). Only first nests were included, as birds may alter nest site selection following nest predation (Marzluff 1988, Chalfoun and Martin 2010). We enforced a separate intercept β_0 for each breeding season j to account for varying prevalence of used nests across years because prevalence was a design parameter rather than a random variable. For each site, *i*:

$$y_i \sim Bern(\pi_i)$$

and π_i was modeled as a function of K covariates x_i:

$$logit(\pi_i) = \beta_{0j} + \sum_{k=1}^{K} I_k \beta_k x_{i,k}$$

Daily Nest Survival Modeling

Nest encounter histories consisted of observed nest states Y for each day *t* of observation, where $Y_{i,t} = 1$ if nest *i* was observed alive on day *t*, $Y_{i,t} = 0$ if nest *i* was observed to have failed (female absent and some or all eggs destroyed), and $Y_{i,t} =$ NA on days when nest state was not observed. Beginning on the first day after the nest was detected,

$$Y_{i,t+1} \sim \begin{cases} 0 & if\ Y_{i,t} = 0 \\ Bern(\phi_{i,t}) & if\ Y_{i,t} = 1 \end{cases}$$

Daily survival probability $\phi_{i,t}$ was modeled as a function of nest- and time-varying covariates $x_{i,t}$ using a logit link. We estimated a global intercept and included a random effect for each year *j*:

$$\text{logit}(\phi_{i,t}) = \beta_0 + \sum_{k=1}^{K} I_k \beta_k x_{i,t,k} + +\alpha_j$$

$$\alpha \sim \text{N}(0, \sigma^{\alpha})$$

The standard deviation for the random year effect, σ^{α}, was given a vague half-Normal prior with mean 0 and standard deviation 100 (Gelman 2006). Prior to testing habitat covariates, we tested for effects of hen age (juvenile or adult), nest attempt, date, and nest age. A random effect for ranch was included in models with a categorical grazing system variable to acknowledge non-independence of repeat observations within a ranch. All variables were scaled and centered before model fitting. We derived an estimate of annual nest success by exponentiating estimated daily survival rate from the full model by the 27-day incubation period typical in our study area.

Vegetation Response to RGS and Rest

In addition to directly testing for effects of SGI-RGS on nest survival, we sought to quantify the response of vegetation attributes suspected to influence sage-grouse nesting ecology to SGI-RGS. We hypothesized that SGI-RGS would increase herbaceous vegetation structure, particularly live and residual grass height and cover. Metrics considered indicators of rangeland health, such as litter cover and bare ground, were also of interest. We sampled vegetation attributes on enrolled and non-enrolled ranches in 2012 – 2015. In addition to differences among grazing systems we wanted to quantify effects of rest from grazing. Pastures rested from grazing were rotated on an annual basis, and we were unable to get reliable long-term grazing schedules for most ranches. Additionally, some ranches began or ended their enrollment during the study. We were therefore unable to use permanent vegetation plots, and instead generated random samples each year. We did not sample SGI-RGS treatments during the first year of implementation to reduce the chance of lag effects affecting our inferences. We conducted a pilot study in 2012, sampling 100 plots (50 SGI-RGS and 50 non-SGI) to determine necessary sample sizes in following years. Based on earlier studies (e.g., Gregg et al. 1994, Holloran et al. 2005, Doherty et al. 2014) reporting a positive effect of grass height on nest survival, we chose target sample sizes to achieve 80% power to detect a 10% difference in grass height (i.e., approximately 2 cm) associated with treatment at $\alpha = 0.05$. From our pilot samples we found variation in topographic position (i.e., hilltops, flats, valley bottoms or drainages) and soil type accounted for much of the observed variation in grass height. We therefore stratified the study area by topographic position, soil type, and distance from water and restricted our samples in 2013 – 2015 to a range of conditions we felt were representative of sage-grouse nesting habitat (see Appendix A for details). Statistical tests were conducted only on plots sampled from 2013 – 2015.

At vegetation response plots, we measured a subset of the variables measured at nests that were likely to be affected by grazing management. We measured areal cover of herbaceous plants, litter, and bare ground using 12 20x60 cm frames (Daubenmire 1959) per plot, placed at 3, 6, and 9 m from plot center in each of the cardinal directions. At the same points, we measured the tallest droop height of the nearest live and residual herbaceous plant, excluding inflorescences. We also measured visual obstruction with a Robel pole, taking readings from 1 m above the ground 4 m from the pole with the pole placed 1, 3, 5, and 7 m from the plot center in each cardinal direction. We did not measure shrub density or cover, nor require a minimum shrub cover at sampled locations, as we did not anticipate differences in the shrub component due to grazing management. Plots were, however, restricted to sites dominated by native rather than invasive or planted vegetation. All vegetation response plots were measured during July to minimize variation due to plant phenology.

We used linear mixed-effects models to test for grazing system and pasture rest effects (fixed effects) on vegetation metrics while accounting for variation among years and ranches (random effects). Models were fit using the lme4 package (Bates et al. 2015) in R. Significance of fixed effects was assessed with likelihood ratio tests comparing models with and without fixed effects for SGI-RGS and pasture rest.

Factors Influencing Sage-Grouse Nesting Ecology

Sage-grouse nest-site selection and survival are influenced by environmental factors at multiple spatial scales (Aldridge and Boyce 2007, Doherty et al. 2010). We therefore considered variables measured at several spatial scales, including attributes of 1) the landscape within 1.61 km (1 mi) of the nest (landscape scale), 2) sagebrush cover and topography within 100 m of the nest (patch scale), 3) vegetation within 15 m of the nest site (plot scale), and 4) the nest shrub and vegetation immediately beneath its canopy (nest shrub scale).

Landscape-scale Variables.—Landscape composition has demonstrated effects on nest survival in birds (Chalfoun et al. 2002, Stephens et al. 2004), which should exert selective pressures shaping behavior. We quantified the proportion of the landscape in sagebrush dominated vegetation using a geographic information system (GIS) coverage developed specifically for our study area. This product uses field-collected high-resolution vertical digital photographs in conjunction with aerial and satellite imagery to map cover of functional components of rangeland vegetation (e.g., herbaceous vegetation cover, bare ground, shrub cover) at 1 m resolution (Sant et al. 2014). We aggregated the 1 m product to 10 m resolution and determined the proportion of the landscape with ≥5% sagebrush cover. We tested for a cumulative effect of disturbance using an anthropogenic disturbance layer which included the footprint of roads, urban areas and other impervious surfaces, wind turbines, and oil & gas well pads (J.S. Evans, The Nature Conservancy, unpublished data). Finally, we quantified the proportion of the landscape in cropland using the annually-updated Cropland Data Layer from the USDA National Agricultural Statistics Service (Johnson and Mueller 2010, USDA-NASS 2015).

Landscape-scale variables also included distances from features potentially facilitating nest predators such as roads (Webb et al. 2012, Coates et al. 2014), including county roads and highways and lesser-traveled two-track service roads; mesic areas (Webb et al. 2012); and cropland (Greenwood et al. 1995, Phillips et al. 2003, Manzer and Hannon

2005). We log-transformed all distance metrics to impose a decaying influence as locations are farther from features, except in the case of mesic vegetation, which was included as a quadratic term for nest site selection. We hypothesized females would select nest sites at an intermediate distance from mesic areas, which represent poor habitat for nesting but contain critical resources for brood rearing (Schreiber et al. 2015, Donnelly et al. 2016).

Patch-scale Variables.— We characterized sagebrush cover at the patch scale (100 m grain) by first aggregating the 1 m sagebrush canopy cover layer to 10 m resolution using the mean value then calculating the mean and standard deviation within a 100 m buffer around each point to characterize average cover and cover heterogeneity of sagebrush. To characterize patch-scale topography we calculated terrain roughness as the standard deviation of elevation estimates from a 10 m digital elevation model in a 100 m buffer around each point (U.S. Geological Survey 2015).

Nest- and Plot-scale Variables.— The influence of nesting shrub and plot-scale variables on sage-grouse nesting ecology has received disproportionate attention in past research, with studies variously reporting evidence for the importance of live or residual herbaceous vegetation height (Aldridge and Brigham 2001, Holloran et al. 2005) and cover (Gregg et al. 1994, Sveum et al. 1998), bare ground (Dzialak et al. 2011), shrub height (Popham and Gutierrez 2003) and cover (Gregg et al. 1994, Kolada et al. 2009a, Webb et al. 2012), visual obstruction, and litter (Kaczor et al. 2011). We measured canopy cover of shrub species using the line intercept method with two perpendicular 30 m tapes centered at the nest shrub (Wambolt et al. 2006), and parsed measurements between all shrubs and sagebrush-only species. We also measured shrub height as the tallest live portion, excluding inflorescences, of the nearest shrub 3 and 6 m from the center of the nest in each cardinal direction. We measured nest shrub height, maximum width, and greatest width perpendicular to the axis of the maximum width to calculate nest shrub volume using the formula for the volume of an ellipse. When the nest was located beneath >1 shrub with a contiguous canopy, the shrubs were treated as a single shrub for measurement purposes.

We visually estimated percent cover of all herbaceous plants, grasses (classified as native and nonnative), litter, forbs, and mosses and lichens, and bare ground using 20x60 cm frames (Daubenmire 1959) at 3 and 6 m from the center of the transect in each cardinal direction. All technicians were trained to estimate cover by a single lead observer each year and periodically checked throughout the season for consistency (i.e., +/- 5% for all cover classes). Cover estimates by category were made beneath the shrub canopy, and were therefore constrained to sum to 100%. We estimated the height of live and residual herbaceous vegetation by measuring the maximum droop height (i.e., the vertical height of the undisturbed plant), excluding inflorescences, of the grass or forb plant nearest to points 3 and 6 m from the center of the nest in each cardinal direction. We also measured the maximum droop height of the tallest live and residual grass rooted beneath the canopy of the shrub(s) concealing the nest.

Visual obstruction at the nest was measured using a Robel pole (Robel et al. 1970) centered at the nest shrub, with measurements read from 4 m in each cardinal direction at a height of 1 m above the ground. Measurements at 1, 3, and 5m from the shrub in each cardinal direction were averaged for a plot-level visual obstruction estimate. We hypothesized that preference for herbaceous hiding cover might be more pronounced at nest sites with little shrub cover, and therefore considered interaction terms between shrub cover and residual grass height or total herbaceous cover. It remains unclear whether herbaceous vegetation or shrubs are more important in concealing sage-grouse nests (France et al. 2008, Gibson et al. 2016), so we considered support for size of the nest shrub, visual obstruction at the nest shrub, and height of herbaceous plants rooted beneath the nest shrub for survival analyses.

To quantify past and current seasons' livestock use in the immediate vicinity of nests, we counted cattle dung pats and measured the proportion of herbaceous plants grazed within 15 m of the nest. Density of dung pats is an index of intensity of use of an area by grazing animals that has been shown to be indicative of forage utilization and vegetation structure (Bailey and Welling 1999). We recorded both current year's and previous year's dung pats, distinguished by the level of degradation and oxidation. We also recorded the number of plants showing evidence of grazing during the current year from a sample of 100 randomly selected herbaceous plants. We then scaled and centered measurements of current year's dung pats and proportion of plants grazed and added them to produce an index of current year's livestock use intensity at the plot scale. Dung pats from previous years were used as an index of previous year's livestock use intensity. Cattle dung may persist in arid ecosystems for up to 6 years (Lussenhop et al. 1982), therefore the historical livestock use index represents a relative index of use integrated over the past several grazing seasons (Milchunas et al. 1989).

Detailed grazing records were obtained from most landowners to determine whether livestock had been present in the pasture at any time during nesting, and observers recorded livestock presence or absence at each visit to the nest. Finally, we recorded whether nests were located in an SGI-RGS pasture and if the pasture was rested from grazing for use as treatment factors in nest survival analyses. A pasture was considered rested only if it had not been grazed for at least 12 months prior to the onset of the nesting season.

Accounting for bias in herbaceous vegetation measurements.— Measurements of nest- and plot-scale variables were made following the fate (hatched or failed) of nests, which can produce misleading inference for the effect of concealment on nest survival (Gibson et al. 2016). Briefly, Gibson et al. (2016) showed that measuring vegetation at nests following nest fate induces a bias in timing of measurement such that successful nests are measured later, on average, than failed nests. Successful nests may therefore have greater vegetative concealment due to plant phenology alone, as nesting corresponds with a season of rapid aboveground plant growth. We used concepts from Gibson et al. (2016) to correct for temporal bias between failed and hatched nests when testing herbaceous variables affected by plant phenology. We first tested all herbaceous cover and height metrics for temporal trends using univariate linear regression on date of measurement, fitting separate models for each year to account for annual variation in phenology. If a metric displayed a temporal trend in any year, we applied the following correction to that metric prior to nest survival model fitting. The estimated slope from the linear regression of the variable on date of measurement was multiplied by the days elapsed between estimated hatch date and date of measurement, and this adjustment was subtracted from the value measured in the field. The resulting predicted hatch-date value was treated as data in the nest survival model. For nest site selection models we made a similar correction, with measurements at nest and available plots corrected to the median incubation initiation date of their corresponding year.

Weather Variables.—Precipitation can positively affect productivity of galliforms (Heffelfinger et al. 1999, Lusk et al. 2001, Hernandez et al. 2005) including sage-grouse (Dusek et al. 2002, Holloran et al. 2005, Blomberg et al. 2012, Blomberg et al. 2014). Individual precipitation events, however, can cause nest or brood failure (Flanders-Wanner et al. 2004, Herman-Brunson et al. 2009, Kaczor et al. 2011, Webb et al. 2012). We observed high nest mortality in 2011 during a spring of record high precipitation and many days-long rain events during the nesting season. To account for this potential source of variation in survival, we tested several daily rainfall variables derived from DAYMET interpolated weather data (1 km resolution; Thornton et al. 2014). Specifically, we considered variables for the current day's precipitation, the previous day's precipitation (Moynahan et al. 2007), or total precipitation falling over a 3, 4, or 5 day period prior to and including the nest-day. We conducted variable selection as described above to select the single most supported precipitation variable independently of and prior to building the full nest survival model.

RESULTS

We captured 298 female sage-grouse between 2011 and 2015 and located and determined the fate of 419 nests (SGI-RGS: 80, Non-SGI: 339) from 230 females. We measured vegetation at 705 available nest shrubs (SGI-RGS: 130, Non-SGI: 575). Nest and random plots from 2011 (n = 97 and 107, respectively) were omitted from nest site selection analyses because vegetation was sampled at available plots after nearly all nest plots were completed, resulting in a significant temporally-induced bias among measurements (J. T.

Smith, unpublished data). Three nests were removed from the survival analysis because of early observer-induced abandonment. Among the remaining 416 nests, 199 (47.7%) hatched at least one egg, predators destroyed 205 nests (49.3%), 10 nests (2.4%) were abandoned for unknown reasons, and 2 nests (0.5%) were abandoned due to predation of the female while off the nest. Three more nests were omitted from analyses because technicians were unable to access nests to measure nest- and plot-scale covariates. Average annual nest success was 49.2% (95% CI from 34.1 – 58.4%). Median clutch size was 8 eggs for first nest attempts and 7 for second and third nest attempts.

Nest Site Selection

After omitting nests from 2011 and renests within a season, our sample included 286 used sites and 597 available sites. Of the variables considered in the nest site selection model (Table 1), 18 passed initial variable screening with 85% credible intervals that did not overlap zero. Sagebrush cover and total shrub cover at the plot scale were highly correlated ($r = 0.93$) and we chose to include sagebrush cover because of its demonstrated importance to sage-grouse nest site selection in previous studies. Patch-scale roughness and plot-scale slope were also highly correlated ($r = 0.69$); we chose patch-scale roughness because we reasoned topographic structure would be perceived at a larger spatial scale. Finally, visual obstruction at the plot- and nest shrub scales were highly correlated ($r = 0.74$), and visual obstruction at the nest shrub scale was chosen because it’s relationship to nest concealment seemed more plausible. Of the 14 variables included in the final model, seven were supported with Bayes factors ≥ 3 (Table 2; Figure 3). Females preferred to locate nests farther from county roads and highways but closer to two-track roads, and avoided landscapes with greater amounts of non-cropland anthropogenic disturbance. At the patch scale, females selected gentler terrain. At the plot scale, females selected greater sagebrush cover. Finally, at the scale of the nest substrate, females selected shrubs of greater volume. We found no evidence of selection with respect to herbaceous vegetation metrics or indices of livestock use.

Nest Survival

Effects of hen age, nest attempt, date, and nest age were not supported (85% credible intervals overlapped zero). Of the five candidate precipitation variables examined, the total amount of precipitation falling over a 4-day period received the greatest support with a Bayes factor of 4.26 and was passed on to the final model. Of the variables considered in the nest survival model (Table 1), 15 passed initial variable screening. Three pairs of variables were highly correlated: visual obstruction at the nest shrub and plot scales ($r = 0.79$), live grass height at the nest shrub and plot scales ($r = 0.60$), and residual grass height at the nest shrub and plot scales ($r = 0.54$). We chose to include all three variables at the nest shrub scale because we assumed a stronger link with predators' ability to detect the nest at this scale. Of the 12 variables passed to the final model, only precipitation and distance to county roads and highways were supported by Bayes factors ≥ 3, with greater amounts of rainfall over a 4-day period and greater proximity to roads associated with lower daily nest survival (Table 3; Figure 4). Herbaceous vegetation height and cover, grazing system, pasture rest, presence or absence of livestock in the pasture during nesting, and indices of livestock use were all unrelated to daily nest survival.

Vegetation Response to SGI-RGS

We sampled 325 vegetation plots on non-SGI ranches and 472 vegetation plots on SGI-RGS ranches, including 218 plots in rested pastures, from 2013-2015 (Figure 6). Likelihood ratio tests indicated that live grass height ($\chi^2 = 5.84$, $df = 1$, $p = 0.016$) was greater on SGI-RGS ranches than non-SGI ranches. Residual grass height ($\chi^2 = 3.40$, $df = 1$, $p = 0.065$), bare ground ($\chi^2 = 1.28$, $df = 1$, $p = 0.259$), litter ($\chi^2 = 2.33$, $df = 1$, $p = 0.127$), herbaceous vegetation cover ($\chi^2 = 0.01$, $df = 1$, $p = 0.929$), and visual obstruction ($\chi^2 = 0.66$, $df = 1$, $p = 0.417$) did not differ between grazing systems. After accounting for grazing systems, only visual obstruction ($\chi^2 = 7.03$, $df = 1$, $p = 0.008$) and litter ($\chi^2 = 5.44$, $df = 1$, $p = 0.019$) differed between rested and grazed pastures, with greater visual obstruction but less litter associated with rested pastures.

Grazing system and rest effect sizes were modest relative to annual variation (Figure 6). Live grass height was 1.35 cm (SE 0.49 cm) greater on SGI-RGS ranches, while the estimated standard deviation among years was 0.86 cm. Rest was associated with a 1.26 cm (SE 0.47 cm) increase in visual obstruction, while the estimated standard error among years was 1.23 cm.

DISCUSSION

We found no evidence that variation in livestock grazing influenced the nesting ecology of sage-grouse, contrary to oft-cited literature relating nest site selection and survival to herbaceous vegetation influenced by livestock herbivory. Rather, female selection for nest sites was best explained by more temporally static features including topography, sagebrush cover, shrub size, and human footprint, whereas precipitation, distance to major roads, and year effects explained variation in nest survival. Our findings suggest the importance of good grazing management may lie in maintaining the functioning components of intact native sagebrush ecosystems on which grouse rely rather than managing for microhabitat conditions found at nests.

Sage-grouse nest site selection for less rugged areas with greater sagebrush canopy cover is consistent with the bulk of previous research (*reviewed in* Hagen et al. 2007). We also found that females generally selected less fragmented landscapes and avoided county roads and highways. Selecting sites farther from major roads may reflect selective pressure exerted by nest predation. Raised grades, culverts, and power lines associated with these roads may provide resources for nest predators (Coates et al. 2014, Hovick et al. 2014), and nest survival was positively related to distance from major roads (Figure 4). Curiously, females demonstrated selection nearer unpaved two-track roads. While this finding is contrary to avoidance of anthropogenic features, we suspect this relationship may be more reflective of road placement than sage-grouse behavior. Two-track roads in this landscape are infrequently used service roads, generally traversing gentle topography and used to access areas far from main roads, similar to areas selected by sage-grouse for nest sites. Furthermore, two-track roads are not associated with the aforementioned features supporting potential nest predators, and may therefore be less likely to exert selective pressure leading to avoidance.

Contrary to expectations, herbaceous vegetation structure did not influence nest site selection. This contradicts previous findings of preference for greater cover (Holloran et al. 2005, Kirol et al. 2012) and height of herbaceous material (Hagen et al. 2007, Davis et al. 2014, Stonehouse et al. 2015) at nests. However, evidence for these relationships is mixed, with many studies reporting no evidence of selection for herbaceous vegetation structure at nest sites (Aldridge and Brigham 2002, Popham and Gutierrez 2003, Kolada et al. 2009b, Doherty et al. 2010, Kaczor et al. 2011, Kirol et al. 2015, Lockyer et al. 2015). Similarly, herbaceous vegetation structure failed to explain variation in nest survival. While initial models fit using measurements taken following nest fate indicated a strong positive effect of live grass height on daily nest survival, correction of grass heights to account for growth through the season revealed a lack of association, replicating findings of Gibson et al. (2016). Height and cover of residual herbaceous material, which did not change appreciably throughout the season, were also unrelated to nest survival. In light of these results, it was unsurprising that we found no support for positive effects of either rotational grazing systems or rest from grazing on nest survival.

Evidence for grass height's association with nest success in sage-grouse—a relationship considered sufficiently established to have directly influenced public land management policy and private land conservation efforts across the West—should be critically reexamined considering the methodological flaws now known to pervade this body of literature. Among 12 studies reviewed by Gibson et al. (2016) reporting positive effects of grass height or cover on nest survival in greater sage-grouse, only two (Gregg et al. 1994, Sveum et al. 1998) controlled for plant phenology by measuring vegetation at predicted hatch date. Re-analysis of previously published datasets using methods that account for phenology could provide useful inferences without additional data collection.

Support for the "nest-concealment hypothesis," (Martin and Roper 1988, Martin 1992) which posits that females should select nests among dense foliage and experience lower predation compared to less concealed areas, is mixed. In a comprehensive review, Borgman and Conway (2015) reported that 74% of studies testing the nest concealment hypothesis in open-cup nesting songbirds failed to find an association between nest concealment and nest success. In their examination of the methodological and biological drivers of this ambiguity, they found studies that reported measuring concealment within one week of nest hatch or failure were about twice as likely to support the nest concealment hypothesis (Borgmann and Conway 2015). This may, however, simply reflect that the timing of measurement of concealment is most systematically biased when measurements are restricted to within one week of hatch or failure. Measurement later in the season, on the other hand, may obscure real relationships because concealment at the time of measurement is vastly different than what the active nest experienced. Acquiring representative measurements of concealment at nests while accounting for phenological changes is challenging but fundamental to drawing unbiased inference on the effect of concealment on nest survival (Burhans and Thompson 1998, Borgmann and Conway 2015, Gibson et al. 2016).

An alternative hypothesis regarding vegetation structure and nest predation is based on predator foraging efficiency and posits that the abundance of other potential nesting sites surrounding a nest that must be searched by a predator, rather than the obstructing effect of vegetation *per se*, determines vulnerability to predation (Martin and Roper 1988, Chalfoun and Martin 2009). If this were the case for sage-grouse, the density of sagebrush plants of a suitable dimension surrounding the nest (i.e., at the plot or patch scale) should determine susceptibility to predation and, thus, nest site preference. We are unaware of studies that have specifically tested for effects of density of alternative nesting sites on selection or survival in sage-grouse, but Gregg et al. (1994) found that cover of medium-height shrubs (40 – 80 cm, the class most typical of nest shrubs) was greater at successful nests than at failed nests in Oregon. In future studies, we suggest investigators collect the necessary data to assess support for this alternative hypothesis.

The lack of association between herbaceous hiding cover and nest survival may, alternatively, indicate that herbaceous understory vegetation simply contributes little to nest concealment when compared to cover afforded from sagebrush and other shrubs. In replicated, experimental grazing trials in southeast Oregon, France et al. (2008) reported that 75% utilization of the herbaceous understory in a Wyoming big sagebrush plant community resulted in only a 5% decrease in visual obstruction at simulated sage-grouse nests. That such heavy herbaceous vegetation utilization had such a minor effect on concealment supports the hypothesis that shrubs, not grasses or forbs, provide the majority of concealing cover for sage-grouse nests. Thus, nesting females may use shrub structure as a primary cue of quality when selecting a nest site, which is supported by our finding that sagebrush cover at the plot scale had the largest impact on selection (Figure 3). Given such strong selection, we may have failed to detect concealment effects on nest survival because female selection has canalized natural variation in sagebrush cover at nests, with most nests occurring in "adaptive peaks" providing sufficient concealment from predators (Remeš 2005, Latif et al. 2012).

Ultimately, extended precipitation events had the greatest impact on sage-grouse nest survival. The most supported precipitation variable was total rainfall over a 4-day period, indicating that nest survival is particularly sensitive to precipitation events lasting several days (Figure 5). Nesting females may be able to "sit out" shorter storms, foregoing off-bouts until after the rain subsides, while longer storms force females to leave the nest exposed to cold and wet conditions. Expectations of greater frequency of heavy precipitation events under most climate change scenarios (Walsh et al. 2014) may therefore be cause for concern, especially in sage-grouse populations east of the continental divide. Precipitation is often thought to positively contribute to reproduction in galliforms (but see Flanders-Wanner et al. 2004), including sage-grouse, through greater availability of forb and insect food, and has been positively linked to population-level response among sage-grouse in the Great Basin (Blomberg et al. 2012). However, this apparent contradiction may simply be an issue of scale and timing. Studies reporting a positive effect of precipitation have measured rainfall at coarse scales (e.g. annual regional climatic variables) to explain population-level responses whereas we used 1 km-resolution daily rainfall data to assess impacts to survival of individual nests. Furthermore, our study area is east of the Rocky Mountains in a region characterized by a more continental climate (i.e., a greater portion of annual precipitation falling in the summer) than studies that have found positive effects of precipitation on sage-grouse populations (Figure 1). In this climate, major rainfall events are more likely to coincide with incubation and brood rearing when grouse may be most sensitive to exposure.

While we did not find that variation in livestock grazing influenced the nesting ecology of sage-grouse, it is important to note that nest survival is only one among several influential vital rates driving population growth. Estimated annual nest success rates—approximately 49% across all years—were typical of sage-grouse populations range-wide (Connelly et al. 2000, Taylor et al. 2012), suggesting that nest success is unlikely to be limiting growth of this population. Fitness benefits may still accrue if SGI-RGS positively affects resources needed during other life stages. Although we detected negligible differences in upland vegetation associated with SGI-RGS, the scope of this analysis precluded an evaluation of several resources thought to be important for chick survival such as forb diversity and abundance, arthropod abundance, and vegetation structure in mesic areas used intensively by brood-rearing hens in late summer. Data collection will continue in this study system for an additional 5 years (2016 – 2020) to assess factors associated with adult female and individually-marked chick survival (n = 342 from 184 broods to date). Furthermore, our results should be extrapolated with caution, as our study area is characterized by a different precipitation regime than much of the range (Figure 1). For example, extreme precipitation events during the nesting season, which drove much of the variation in nest survival in our study, may be more common in our region than west of the continental divide.

MANAGEMENT IMPLICATIONS

Our findings reinforce the importance of intact, sagebrush dominated landscapes to nesting sage-grouse. Livestock grazing, within the parameters observed in our study area, did not appear to affect sage-grouse nesting habitat quality through mechanisms widely hypothesized in management literature. Grazing strategies and policy focused on fundamental rangeland health principles such as promoting diverse native plant communities resistant to exotic plant invasion and resilient to natural disturbances such as drought and fire (Davies et al. 2011, Chambers et al. 2016) may be sufficient to conserve resources needed by nesting sage-grouse. While further research is needed to address potential relationships between livestock grazing and other influential vital rates (e.g., chick and adult female survival), the foremost management priority should be preventing further loss and fragmentation of sagebrush-dominated vegetation communities from land-uses and activities known to affect sage-grouse populations, such as infrastructure and activities related to energy development (Green et al. 2016, Naugle et al. 2011) and conversion of sagebrush-dominated rangelands to cropland (Smith et al. 2016).

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FIGURES

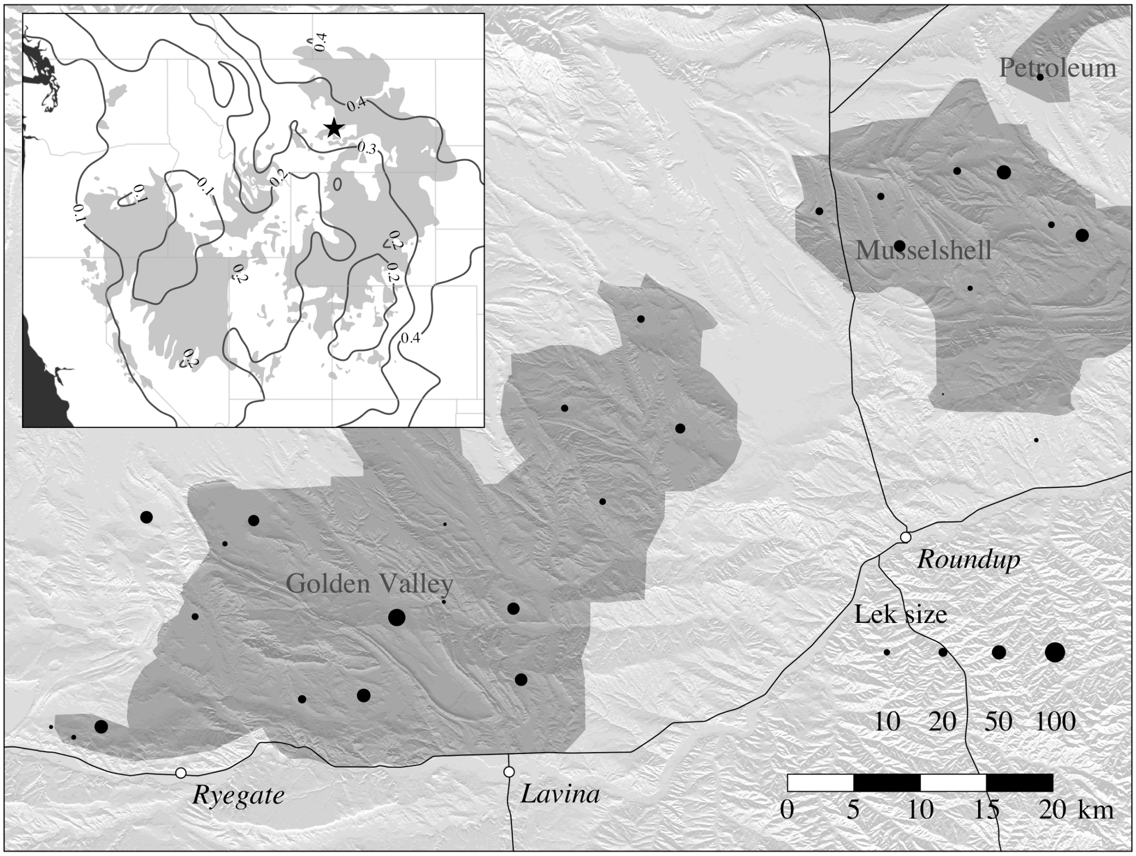

Figure 1. Study area in central Montana. Sage-grouse core areas are indicated by gray polygons and leks are indicated by black circles, with size of circles proportional to the highest male count recorded from 2011 – 2015. Inset map shows location of study area (star) within the current range of sage-grouse (gray shading), and isopleths indicate the proportion of annual rainfall occurring between June 1 and August 31. In the study area, approximately 39% of annual rainfall occurred during these months on average from 1981 – 2010.

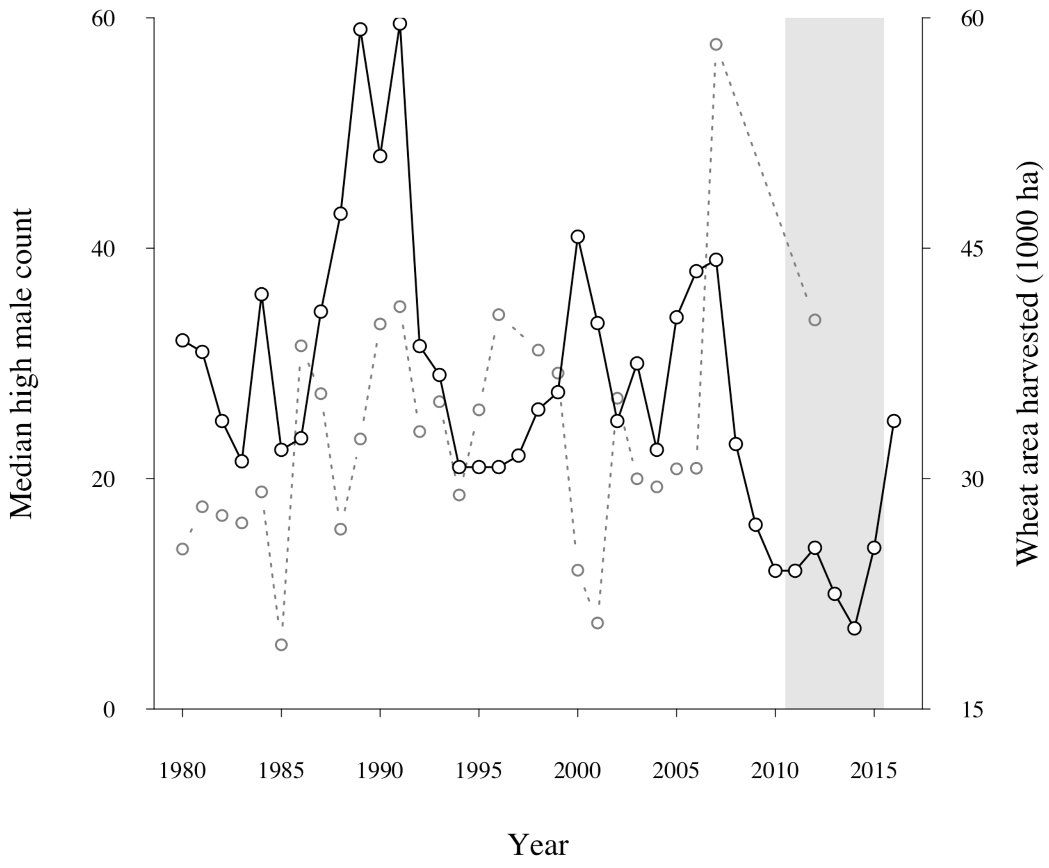

Figure 2. Historical trend in median high male count at sage-grouse leks active between 2011 and 2015 (n = 30; solid black line) within the study area in central Montana. Total area of wheat harvested in these three counties over the same period is shown by the dashed gray line (source: U.S. Department of Agriculture, National Agricultural Statistics Service; data not available for all years). Annual fluctuation in harvested area reflects fallow rotations and short-term responses to grain prices, but the long-term trend in peaks and troughs indicate a steady increase in crop area over the past several decades. Shaded area depicts the years during which the study was conducted.

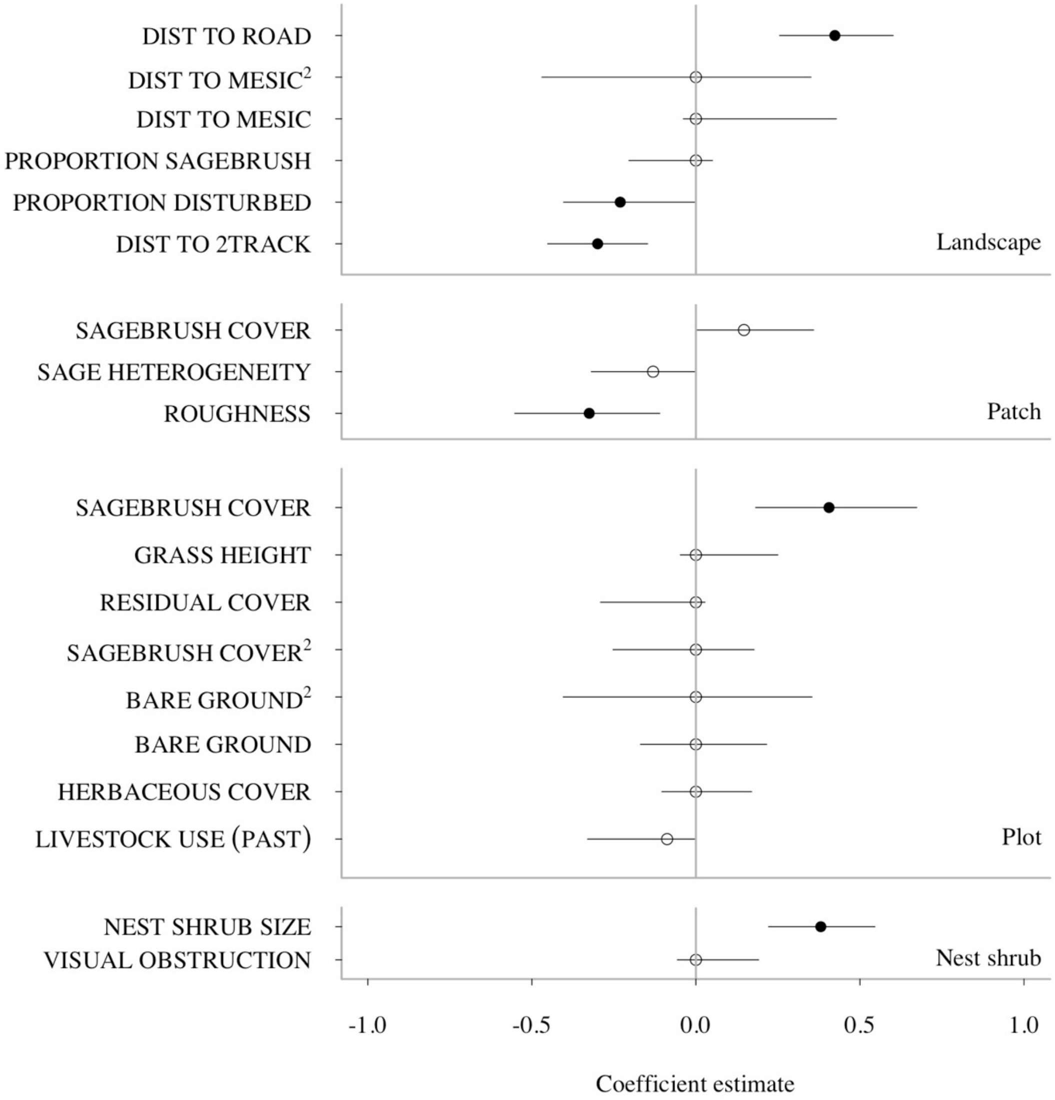

Figure 3. Coefficient estimates from logistic regression model of variables influencing selection of nest sites (n = 286 used sites, n = 597 available sites) by sage-grouse in central Montana from 2012 to 2015. Circles indicate medians of coefficient posterior distributions and error bars represent 95% credible intervals. Filled circles identify important variables supported by Bayes factors ≥3. Selection of nest sites was driven not by herbaceous vegetation characteristics at or around the nest but by preference for greater shrub cover and nest shrub size, gentle topography, avoidance of county roads

and highways, and avoidance of fragmented landscapes. Nest sites were also associated with greater proximity to two-track roads, which does not have a clear biological interpretation but may reflect tendency for these roads to traverse terrain preferred by sage-grouse for nesting, e.g., areas of gentle topography.

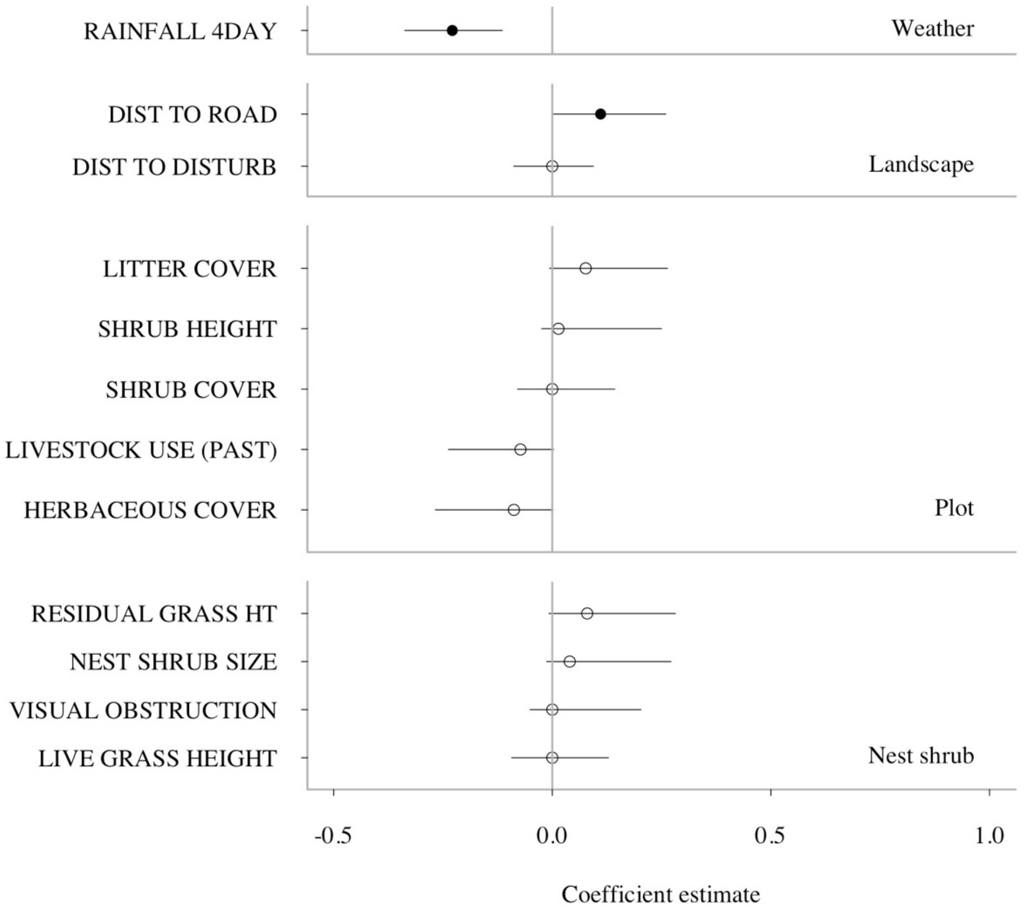

Figure 4. Coefficient estimates from logistic regression model of variables influencing daily nest survival of sage-grouse nests (n = 413) in central Montana from 2011 to 2015. Circles indicate medians of coefficient posterior distributions and error bars represent 95% credible intervals. Filled circles identify important variables supported by Bayes factors ≥3. Greater amounts of rainfall over a four-day period was associated with reduced daily nest survival, and greater distance from county roads and highways was associated with increased daily nest survival.

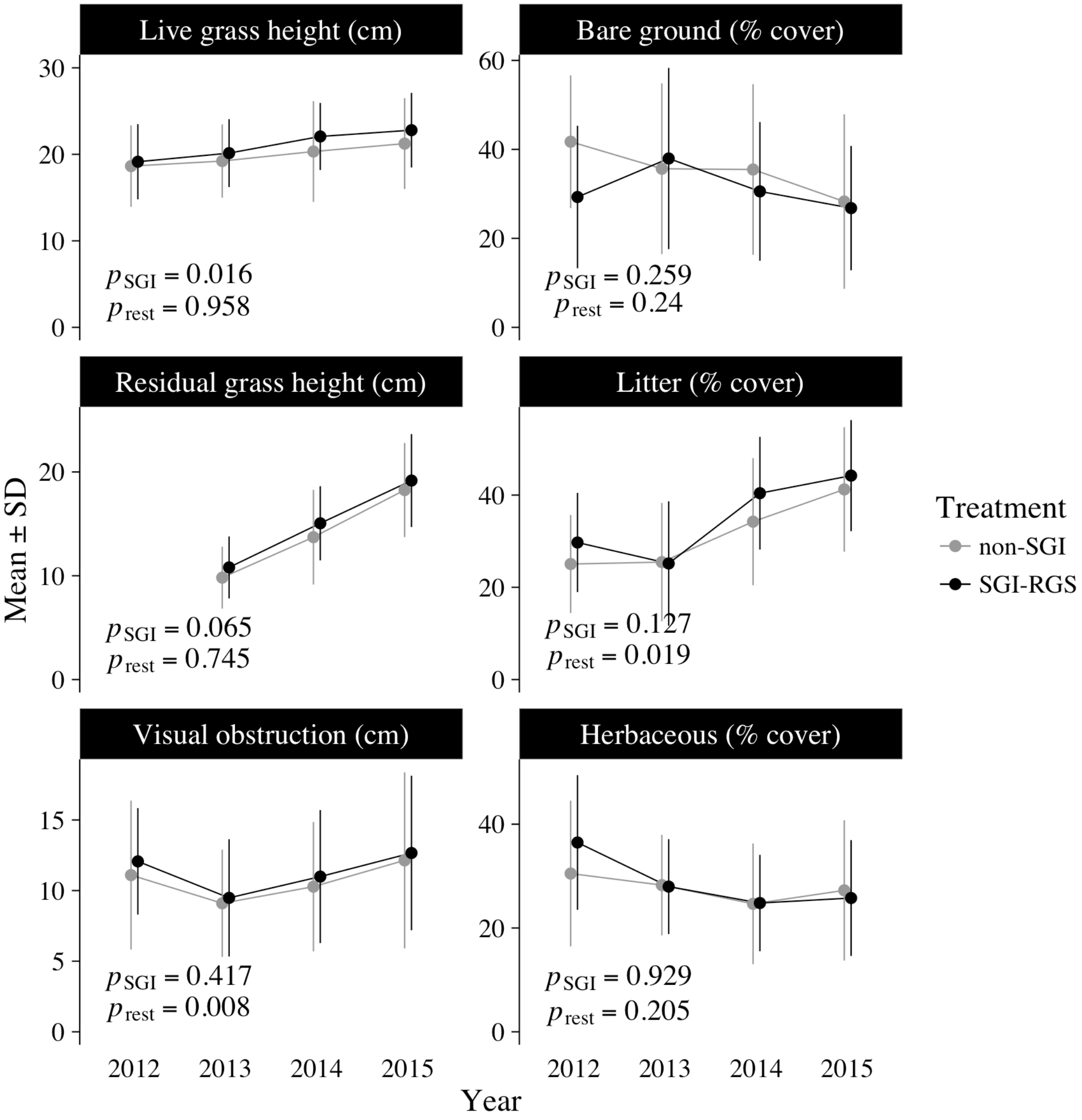

Figure 5. Means and standard deviations of vegetation metrics measured at vegetation response plots on central Montana ranches enrolled in Sage Grouse Initiative rotational grazing systems (SGI-RGS) and on non-enrolled (non-SGI) ranches, 2012 – 2015. Linear mixed effects models revealed that only live grass height differed significantly between non-enrolled and SGI-RGS ranches. Visual obstruction measured with a Robel pole was significantly higher in rested pastures. Estimated effect sizes were small, however, relative to annual variation.

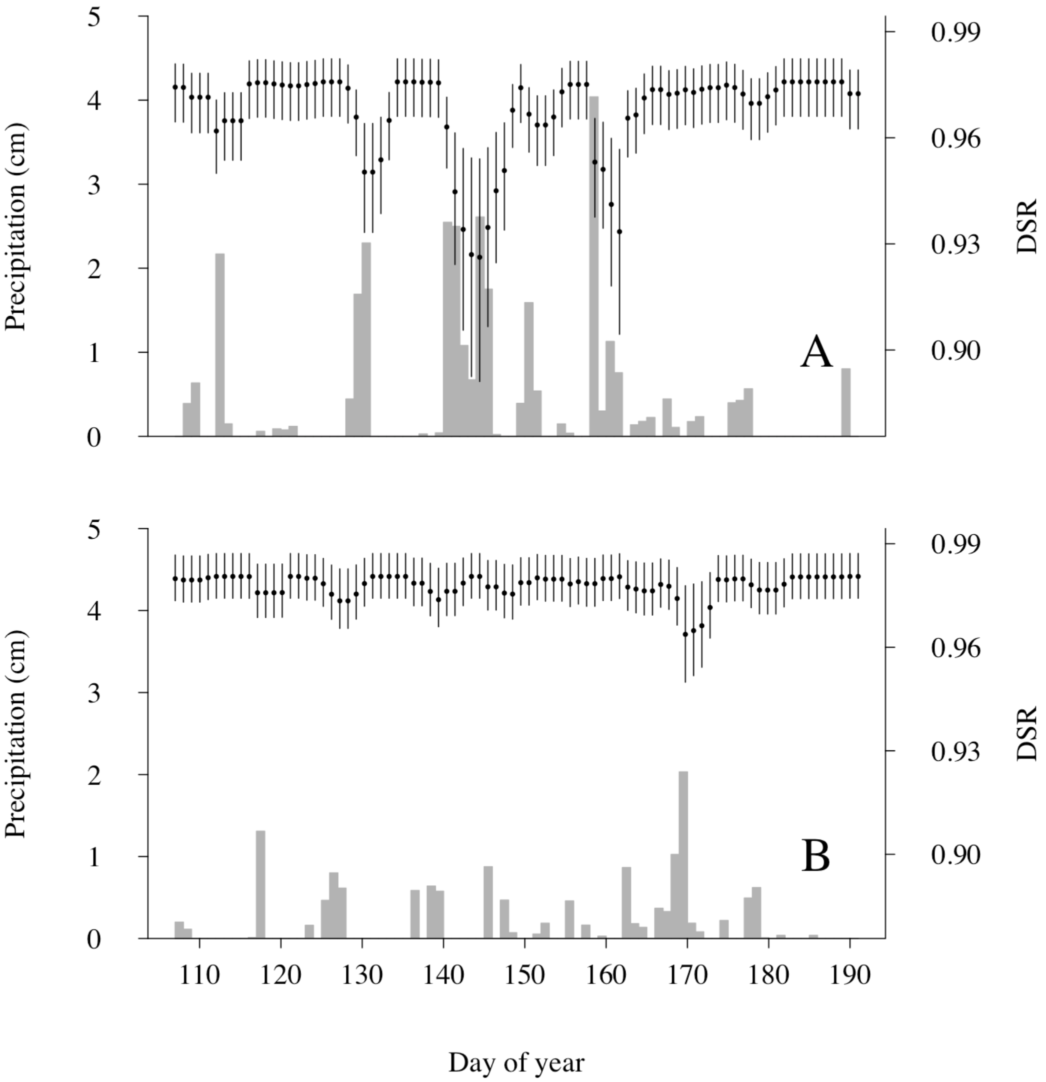

Figure 6. Estimated daily survival rate (DSR; black dots) of greater sage-grouse nests and 95% credible intervals (vertical black lines) and daily rainfall (grey bars) during the year of lowest apparent nest survival (A; 2011), and the year of highest apparent nest survival (B; 2014). Total precipitation over a 4-day period was one of only two supported variables in our nest survival model, with greater amounts of rainfall associated with lower nest survival.

TABLES

Table 1. Variables considered in models of nest site selection and daily nest survival for greater sage-grouse in central Montana, 2011 – 2015.

Variable	Abbreviated variable name	Transformation
Landscape covariates (0 - 1.61 km from nest)		
Distance to major road (county, highway)	DIST TO ROAD[a,b]	Logarithmic[a,b]
Distance to two-track road	DIST TO 2TRACK[a,b]	Logarithmic[a,b]
Distance to cropland	DIST TO CROPLAND[a,b]	Logarithmic[a,b]
Distance to mesic vegetation	DIST TO MESIC[a,b]	Quadratic[a]; Logarithmic[b]
Proportion of landscape disturbed (non-cropland)	PROPORTION DISTURBED[a,b]	
Proportion of landscape in cropland	PROPORTION CROPLAND[a,b]	
Proportion of landscape in sagebrush landcover (≥5%)	PROPORTION SAGE[a,b]	
Patch (0 - 100 m from nest) covariates		
Topographic roughness	ROUGHNESS[a]	
Sagebrush cover	SAGEBRUSH COVER[a,b]	
Standard deviation of sagebrush cover	SAGE HETEROGENEITY[a,b]	
Plot (0-15 m from nest) covariates		
Live grass height	GRASS HEIGHT[a,b]	
Residual grass height	RESIDUAL HEIGHT[a,b]	
Total herbaceous cover	HERBACEOUS COVER[a,b]	Quadratic[a]
Bare ground	BARE GROUND[a,b]	Quadratic[a]
Residual herbaceous cover	RESIDUAL COVER[a,b]	Quadratic[a]
Litter cover	LITTER COVER[a,b]	
Visual obstruction (Robel pole)	VISUAL OBSTRUCTION[a,b]	
Shrub height	SHRUB HEIGHT[a,b]	
Sagebrush cover	SAGEBRUSH COVER[a,b]	Quadratic[a]
Total shrub cover	SHRUB COVER[a,b]	Quadratic[a]
Slope	SLOPE[a]	
Shrub cover × residual grass height	[INTERACTION][a,b]	
Shrub cover × total herbaceous cover	[INTERACTION][a,b]	
Nest shrub covariates		
Maximum live grass height at nest	GRASS HEIGHT[a,b]	
Maximum residual grass height at nest	RESIDUAL HEIGHT[a,b]	
Visual obstruction (Robel pole)	VISUAL OBSTRUCTION[a,b]	
Nest shrub volume	NEST SHRUB SIZE[a,b]	
Nest substrate (other = 0, sagebrush = 1)	NEST SUBSTRATE[b]	
Grazing covariates		

Pasture grazed during nesting	GRAZED DURING[b]
Livestock use index, current year	LIVESTOCK INDEX (CURRENT)[a,b]
Livestock use index, historical	LIVESTOCK INDEX (PAST)[a,b]
Grazing system (Other = 0, SGI RGS = 1)	SGI-RGS[b]
Pasture rest (no = 0, yes = 1)	REST[b]
Weather (daily covariate)	
Predicted total rainfall in last 4 days	RAINFALL 4DAY[b]
Other covariates	
Date	DATE[b]
Nest age (days since estimated initiation)	NEST AGE[b]
Hen age (juvenile = 0, adult = 1)	HEN AGE[b]
Nest attempt (1st = 0, 2nd or 3rd = 1)	NEST ATTEMPT[b]

[a] Variable or transformation was considered as a candidate in nest site selection model

[b] Variable or transformation was considered as a candidate in nest survival model

Table 2. Variables selected for final model fitting for nest site selection of greater sage-grouse in central Montana, 2012 – 2015.

Variable	Bayes Factor[1]	Coefficient Estimate	95% Credible Interval	
			Lower	Upper
Landscape				
DIST TO ROAD	>1000	0.42	0.25	0.60
DIST TO MESIC	0.42	0.00	-0.04	0.43
DIST TO MESIC^2	0.99	0.00	-0.47	0.35
PROPORTION DISTURBED	16.08	-0.23	-0.40	0.00
PROPORTION SAGEBRUSH	0.43	0.00	-0.20	0.05
DIST TO 2TRACK	467.75	-0.30	-0.45	-0.15
Patch				
SAGEBRUSH COVER	2.71	0.15	0.00	0.36
SAGE HETEROGENEITY	2.54	-0.13	-0.32	0.00
ROUGHNESS	104.71	-0.33	-0.55	-0.11
Plot				
SAGEBRUSH COVER	>1000	0.41	0.18	0.67
SAGEBRUSH COVER^2	0.49	0.00	-0.25	0.18
BARE GROUND	0.38	0.00	-0.17	0.22
BARE GROUND^2	0.82	0.00	-0.40	0.35
HERBACEOUS COVER	0.35	0.00	-0.10	0.17
RESIDUAL COVER	0.71	0.00	-0.29	0.03
GRASS HEIGHT	0.54	0.00	-0.05	0.25
LIVESTOCK USE (PAST)	1.61	-0.09	-0.33	0.00
VISUAL OBSTRUCTION	0.40	0.000	-0.057	0.191
Nest shrub				
NEST SHRUB SIZE	>1000	0.381	0.221	0.546

[1] Bayes factors ≥ 3 indicate support for variable inclusion.

Table 3. Variables selected for final model fitting for daily nest survival of greater sage-grouse in central Montana, 2011 – 2015.

Variable	Bayes Factor[1]	Coefficient Estimate	95% Credible Interval	
			Lower	Upper
Intercept		3.62	3.20	3.91
σ^{α} (SD of random year effect)		0.17	0.01	0.90
Weather				
RAINFALL 4DAY	853.70	-0.23	-0.34	-0.11
Landscape				
DIST TO ROAD	3.28	0.11	0.00	0.26
DIST TO DISTURB	0.41	0.00	-0.09	0.09
Plot				
HERBACEOUS COVER	2.24	-0.09	-0.27	0.00
LITTER COVER	1.97	0.08	-0.01	0.26
SHRUB HEIGHT	1.29	0.01	-0.02	0.25
SHRUB COVER	0.51	0.00	-0.08	0.14
LIVESTOCK USE (PAST)	1.96	-0.07	-0.24	0.00
Nest shrub				
LIVE GRASS HEIGHT	0.48	0.00	-0.09	0.13
RESIDUAL GRASS HT	2.00	0.08	-0.01	0.28
NEST SHRUB SIZE	1.46	0.04	-0.01	0.27
VISUAL OBSTRUCTION	0.78	0.00	-0.05	0.20

[1] Bayes factors ≥ 3 indicate support for variable inclusion.

Appendix 1: Criteria for selecting plots to measure vegetation response to Sage Grouse Initiative rotational grazing systems (SGI-RGS) and pasture rest in central Montana, 2013 – 2015.

Variable	Acceptable Range	Source
Slope	0 – 5 degrees	10 m-resolution digital elevation model[1]
Soil Type[2]	60C, 60D, 64A, 64B, 68C	NRCS SSURGO Database[3]
Distance to Water	200 – 1500 m	Local NRCS records, National Hydrography Dataset[4]

[1] USGS 2015

[2] Soil map units chosen for inclusion are silty clay loams that typically support sagebrush in the study area.

[3] http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx

[4] http://nhd.usgs.gov; verified in the field.

CHAPTER 3: PHENOLOGY, NOT CONCEALMENT, EXPLAINS TALLER GRASS AT SUCCESSFUL NESTS IN GREATER SAGE-GROUSE

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ABSTRACT

Much interest lies in the identification of manageable habitat variables that affect key vital rates for species of concern. For birds, vegetation surrounding the nest may play an important role in mediating nest success by providing concealment from predators. Height of grasses surrounding the nest is thought to be a driver of nest survival in greater sage-grouse (*Centrocercus urophasianus*), a ground-nesting species that has experienced

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widespread population declines throughout their range. Recent research, however, found that widely-used field methods in past studies of nest survival can produce spurious inference on the relationship between grass height and nest success. In that study, authors demonstrated how measurement of vegetative concealment following nest fate (failure or hatch) introduces a bias in timing of measurement such that successful nests are measured later in the season, on average, than failed nests. Though tests revealed positive effects of grass height on nest survival, grass was taller at successful nests due to the confounding effect of plant phenology, not an effect on predation risk. To test the generality of this result for sage-grouse we re-analyzed existing datasets comprising nearly 900 sage-grouse nests from four independent studies across the range, and confirmed that the positive relationship between grass height and sage-grouse nest survival previously found in each of these datasets was solely explained by a methodological bias. Overall, evidence for a biological effect of grass height on nest success in sage-grouse is weak, and re-evaluation of land management guidelines emphasizing the importance of tall grasses in nesting habitat may be warranted.

INTRODUCTION

Environmental factors affecting influential demographic parameters are appropriate targets of management to promote habitat quality for species of conservation concern (Mills 2007). For many birds, characteristics of nest sites that mediate nest predation are of interest, as nest success is often a key driver of population growth and predation is the primary cause of nest failure (Martin 1993; Ricklefs 1969). According to the nest concealment hypothesis, nests surrounded by dense vegetation should be more successful because they are more difficult for predators to detect or access (Martin & Roper 1988;

Martin 1992). Furthermore, vegetative concealment may represent an attractive target for conservation action because it can often be managed, e.g., through silvicultural practices or manipulation of livestock grazing.

Support for the nest concealment hypothesis is, however, mixed. In a recent review and comparative analysis, only 26% of 114 reviewed studies in open-cup-nesting songbirds supported an effect (Borgmann & Conway 2015). Effects of concealment on nest survival may be difficult to detect if strong selection for concealed nest sites canalizes variation among nests such that most occur in ‘adaptive peaks’ providing adequate concealment (Latif et al. 2012; Remeš 2005). However, even studies employing experimental removal of vegetation have returned mixed support for the nest concealment hypothesis (e.g., Bengtson 1972; Peak 2003; Howlett & Stutchbury 1996; Latif et al. 2012). Numerous intrinsic and extrinsic factors may influence the effect of concealment on nest success; for example, birds with more brightly-colored plumage appear more dependent on vegetation to conceal the nest from predators (Borgmann & Conway 2015) and the benefits of visual concealment may depend on the composition of the local predator community (Dion et al. 2000; Colombelli-Negrel & Kleindorfer 2009; Clark & Nudds 1991). More problematic, however, are methodological aspects of studies that produce biased inference regarding effects of concealment on nest survival (Borgmann & Conway 2015; Gibson, Blomberg & Sedinger 2016; Burhans & Thompson 1998). Here, we focus on a recently discovered methodological bias pervasive in research regarding habitat-fitness relationships in greater sage-grouse (Centrocercus urophasianus).

Greater sage-grouse (herein, sage-grouse) is a species of conservation concern inhabiting sagebrush ecosystems of western North America. Though sage-grouse nest beneath shrubs—primarily sagebrush—the perennial grasses and forbs in the interspaces between shrubs have long been thought to provide critical visual concealment of nests from potential predators (Connelly et al. 2000). This idea is supported by studies reporting positive relationships between height and/or cover of herbaceous vegetation surrounding nest sites and nest survival (Gregg et al. 1994; DeLong et al. 1995; Doherty et al. 2014; Sveum et al. 1998; Coates & Delehanty 2008). Consequently, sage-grouse conservation efforts have focused on increasing herbaceous hiding cover in suitable nesting habitat throughout the range of the species. Although direct links between livestock grazing and sage-grouse demography are lacking, studies indicating positive effects of herbaceous vegetation height and/or cover on nest survival provide a plausible mechanism linking livestock grazing and nest success (Connelly et al. 2000)—a key demographic rate for sage-grouse (Taylor et al. 2012). The validity of inference about the importance of herbaceous hiding cover for sage-grouse nest success thus has major implications for management of sagebrush ecosystems, where livestock grazing is a ubiquitous land use.

Recently, Gibson et al. (2016) demonstrated that the positive association between grass height—a commonly-used metric of herbaceous concealing cover—and nest survival may be indicative of biased methods rather than causation. Using both real and simulated data, they found that measuring grass height at nests following nest fate (i.e., hatch or failure) produced inflated or even spurious statistical relationships between grass height and nest survival. Because successful nests persist and are therefore measured later in the season than failed nests, measured vegetative concealment is greater at successful nests due to concurrent plant growth rather than the presumed reduction in predation. Despite knowledge of this sampling issue dating back decades (e.g., Burhans & Thompson 1998), the pervasiveness of this sampling bias is widespread in sage-grouse literature, with >70% of studies sampling vegetation following nest fate (Gibson, Blomberg & Sedinger 2016). Given the far-reaching implications derived from inference about grass height and sage-grouse demography, a post-hoc analysis of previous research was warranted.

METHODS

We employ the model-based methods presented in Gibson et al. (2016) to correct for phenology in a re-analysis of four datasets from Montana, Utah, and Wyoming (Figure 1). In the dataset from Eureka County, Nevada analyzed by Gibson et al. (2016), vegetation measurements were made at predicted hatch date and a linear model relating vegetation height to the date of measurement was used to predict vegetation height at fate date, thereby demonstrating the potential bias arising from such a sampling scheme. In our re-analysis, we employ this concept in reverse fashion; that is, we regress vegetation height on date of measurement to predict grass height at hatch date, as though it had been sampled using unbiased methods.

Datasets

Re-analyzed datasets included a previously published study that found a significant positive influence of live grass height on sage-grouse nest survival across two study areas in the Powder River Basin (PRB) in southeast Montana (hereafter PRB North, n=217) and northeast Wyoming (hereafter PRB South, n=164); the first 5 years of an ongoing evaluation of grazing treatments on sage-grouse ecology in central Montana (Chapter 2, n=413); and the first 4 years of a study comparing sage-grouse demography across two study areas in northern Utah (Seth Dettenmaier, Utah State University, Unpublished

Data, n=105). Including findings from Gibson et al. (2016), these studies encompassed 1295 sage-grouse nests over a total 28 study-site years from across the range of sage-grouse (Table 1). Each study used similar methodologies to sample herbaceous vegetation surrounding nest sites by taking multiple measurements of grass height along intersecting transects centered on the nesting shrub, and using the mean of replicated measurements to represent grass height surrounding nests (Table 1).

Statistical Analyses

For datasets in which grass height was measured following nest fate, we estimated hatch date as 28 days after the estimated nest initiation date, and applied a correction to measured grass height covariates following Gibson et al. (2016):

$$GrassHeight_{Hatch} = GrassHeight_{Fate} - (SurveyDate_{Fate} - SurveyDate_{Hatch}) * \beta_{grass}$$

where, for each study site, we fit a linear regression of measured grass height ($GrassHeight_{Fate}$) on day of nesting season ($SurveyDate_{Fate}$) to estimate β_{grass}. This simple correction provided a standardized measurement for grass height across nests regardless of fate.

We estimated the effect of grass height on nest success using both corrected and uncorrected covariate measurements by fitting Bayesian daily nest survival models to each dataset (Schmidt et al. 2010) with the exception of data from Gibson et al. (2016), whom provided estimates from their published analysis. In this approach we estimated nest survival (φ) for each nest (i) on each day of the nesting season (t) via a logit-linear model, which at minimum included an intercept (β_0)and coefficient for grass height, while also including coefficients respective authors deemed supportive in top models. Nest encounter histories consisted of observed nest states y for each day t of observation, where $y_{i,t} = 1$ if nest i was observed alive on day t, $y_{i,t} = 0$ if nest i was observed to have failed (female absent and some or all eggs destroyed), and $y_{i,t} = \text{NA}$ on days when nest state was not observed. Beginning on the first day after the nest was detected,

$$y_{i,t} \sim Bern(y_{i,t-1}\phi_{i,t})$$

and

$$logit(\phi_{i,t}) = \beta_0 + \boldsymbol{x_i}'\beta$$

Specifically, Doherty et al. (2014) modeled nest survival using covariates including a main and quadratic effect for nest age, and categorical variables for a particularly harsh spring nesting season with major snow events (2003) and the two study regions (PRB North and PRB South). The model fit to data from central Montana included covariates for the log of distance to major roads and a measure of 4-day cumulative rainfall (see Chapter 2), whereas data from Gibson et al. (2016), and models fit to Utah data include only an intercept and coefficient for measurements of grass height.

We fit daily nest survival models in JAGS 4.0 (Plummer 2003) with the package rjags (Plummer 2016) in R 3.3.0 (R Core Team 2016), estimating posterior distributions of coefficients using 3 MCMC chains, each with 30,000 samples following 20,000 burn-in iterations, while placing vague normal prior distributions on coefficients (μ=0; σ=1000). Using coefficient posterior distributions, we generated predictions for the mean influence of grass height on nest success, the product of daily nest survival over a 28 d incubation period, and 95% credible intervals over the range of grass height values observed within each respective dataset. We held additional covariates at their mean value where applicable.

We performed an additional analysis on the four re-analyzed datasets to test whether grass surrounding successful nests was taller than grass surrounding failed nests after accounting for date of measurement. The null hypothesis states that grass heights (GH) measured at nests are a linear function of date of measurement (TIME; days since January 1), with normally distributed errors. The alternative hypothesis states that grass heights are a linear function of date of measurement, but that successful nests have, on average, taller grass than failed nests. We first used AIC to determine the best structure for the null model—random intercepts or random intercepts and slopes. The random intercepts null model had a fixed effect for TIME and random intercepts for each study area-year (STUDY:YEAR) combination to allow for variation in grass height inherent among geographically distant study areas. The random intercepts and slopes null model consisted of random intercepts and slopes of GH on TIME for each study area-year combination to account for different rates of grass growth among years, reflecting differences in available soil moisture and timing and quantity of precipitation through the nesting season. The independent variable TIME was centered by subtracting the median day of measurement from all observations and fit a model. The alternative hypothesis was represented by a model where we added a categorical fixed effect for nest fate (FATE; failed=0, hatched=1) to the most supported null model. We used a likelihood ratio test to assess whether accounting for nest fate improved model fit. Linear mixed models were fit using the lme4 package (Bates et al. 2015) in R.

RESULTS

Uncorrected, each of the four re-analyzed datasets revealed a strong, positive association between grass height and daily nest survival (Figure 2; dotted lines). Estimated coefficients for grass height using uncorrected grass heights were 0.055 (95% CI from 0.029 - 0.084) for PRB North and PRB South, 0.044 (95% CI from 0.020 - 0.070) for Roundup, and 0.058 (95% CI from 0.002 - 0.118) for NE Utah. Following adjustment of measured grass heights to remove temporal bias, we found no association between grass height and nest survival in any of the four datasets (Figure 2; solid lines). Estimated coefficients for grass height using grass heights corrected to hatch date were 0.006 (95% CI from -0.019 - 0.032) for PRB North and PRB South, 0.003 (95% CI from -0.015 - 0.024) for Roundup, and -0.015 (95% CI from -0.060 - 0.032) for NE Utah.

The random intercept-only model of grass height received the most support, and was used as the null model (Table 2). The alternative hypothesis, that grass height surrounding successful nests was greater than that surrounding failed nests after accounting for date of measurement, was not supported ($\chi2 = 1.54$, df = 1, p = 0.21).

DISCUSSION

The analysis presented by Gibson et al. (2016) and confirmed by our reanalysis demonstrates that relationships between herbaceous vegetation structure and sage-grouse nest success are largely unsupported when phenology is taken into account. The nest data we examined were sampled from a broad geographic extent and a variety of ecological contexts, including study areas in the Great Basin and northern Great Plains. Given these results, the long-held view that the height of herbaceous understory vegetation at the nest site is a crucial determinant of sage-grouse nest success is equivocal at best. While taller grass may provide effective concealment from predators under some conditions (e.g., particular predator communities), it does not appear that this relationship is universally applicable to sage-grouse populations throughout their range.

Although two studies using unbiased methods reported a positive effect of grass height on nest survival (Sveum et al. 1998; Figure 1; Gregg et al. 1994), the preponderance of evidence fails to support this relationship. Together, the two studies that support an effect of grass height comprise 212 nests monitored across 5 study area-years, while our re-analyzed datasets in conjunction with Gibson et al.'s (2016) dataset encompass 1295 nests monitored over 25 study area-years. Moreover, the data presented by Sveum et al. (1998; Table 2) merely indicate that cover of short grasses (<18 cm) was lower at successful nests than failed nests in 1 out of 2 years (n = 32 nests), while cover of tall grasses (>18 cm) did not differ between successful and failed nests in any year, even using a liberal α level of 0.1. Nonetheless, the results of this study have generally been interpreted to support the hypothesis that taller grass produces greater nest survival (Crawford et al. 2004; Connelly et al. 2000).

The absence of support for an effect of grass height does not necessarily imply nest concealment is unrelated to nest survival in sage-grouse. Selection for larger, taller sagebrush for nest substrates and preference for nesting in areas with greater areal cover of shrubs are well-documented (reviewed in Hagen et al. 2007). In preferred nesting sites, grasses and forbs may simply provide little additional cover beyond that provided by shrubs (see France et al. 2008). Furthermore, while grasses and forbs afford mostly lateral cover, shrubs may provide more effective cover from aerial visual predators such as common ravens (*Corvus corax*), a primary nest predator for sage-grouse (Coates & Delehanty 2008; Coates et al. 2008). Previous research indicates nest site selection in sage-grouse is driven by avian predators at broad scales (Dinkins et al. 2012) and characteristics of nest sites at small scales are more consistent with avoidance of visual (i.e., avian) predators than olfactory (i.e., mammalian) predators (Conover et al. 2010).

Further research is needed to address whether cover and height of grasses and forbs is an important driver of other vital rates in sage-grouse. Selection of sites with greater visual concealment and higher arthropod abundance by brood-rearing sage-grouse has been documented (Schreiber et al. 2015; Kaczor et al. 2011), but studies directly examining effects of herbaceous vegetation structure on either arthropod abundance or sage-grouse chick survival in sagebrush ecosystems are few and have produced mixed results (Gregg & Crawford 2009; Aldridge 2005). Recently, Gibson et al. (2016) found survival of sage-grouse chicks to 2 weeks of age was positively associated with height of grass at the nest, presumably because height of grass at the nest site is correlated with conditions encountered by the precocial chicks during the first weeks of life. A causal relationship between grass height and chick survival, however, cannot be inferred from this study. Positive effects of herbaceous plant height on chick survival could result from concealment from predators or from effects on abundance or community composition of arthropods, a critical food source for chicks (Drut et al. 1994; Dahlgren et al. 2010; Gregg & Crawford 2009), but it is also plausible that taller grass at the nest is associated with some unmeasured factor—e.g., site productivity, precipitation, soil moisture—which in turn influences factors causally related to chick survival.

While the herbaceous understory is clearly a key component of sagebrush ecosystems and sage-grouse habitat (e.g., Chambers et al. 2014), its role in concealing nests from predators has been overstated in management guidelines and land management documents built on inference now known to be biased. For example, the Habitat Assessment Framework (HAF; Stiver et al. 2015), a tool used by the US Bureau of Land Management and US Forest Service to evaluate whether public lands are meeting habitat requirements of sage-grouse, includes specific guidelines for maintaining adequate height of perennial grasses and forbs (>18 cm) based largely on studies indicating positive effects on nest success. While it appears these ‘fourth order’ guidelines may place unwarranted emphasis on the importance of maintaining herbaceous hiding cover for nesting, it should be noted that the HAF appropriately lays out a hierarchical management approach which suggests policies be set at the rangewide and regional scales to limit habitat loss and fragmentation—known causes of sage-grouse population declines—but emphasizes that significant flexibility should be granted to local managers applying finer scale guidelines (see Chapter 1, Stiver et al. 2015). Maintenance of tall grasses and forbs for nesting cover clearly should not preclude the use of management tools that could otherwise help mitigate threats to sage-grouse habitat.

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TABLES

Table 1. We used predictions from five studies across the range of greater sage-grouse, representing n=1295 nests over a total of 25 study years. Each study sampled grass height similarly, using measurements of the nearest grass height to various points along two intersecting transects centered at the nesting shrub. However, total transect length and the number of samples per nest varied by study.

Study Area	n	Years	Transect Length (m)	Samples Per Nest	Data Source
Eureka County	396	2004-2012	10	10	Gibson et al. 2016
PRB North	217	2003-2006	30	20	Doherty et al. 2014
PRB South	164	2004-2006	30	20	Doherty et al. 2014
Roundup	413	2011-2015	24	8	J. Smith, Chapter 2
NE Utah	105	2012-2015	30	20	S. Dettenmaier, Unpublished Data

Table 2. Candidate linear mixed models of grass height (GH) as a function of day of year measured (TIME), study area (STUDY), year of measurement (YEAR), and nest fate (failed or hatched; FATE). A model containing a fixed effect of TIME and random intercepts for each study area-year combination (STUDY:YEAR) was used as the null model. After accounting for phenology among study sites and years, the additional information of nest fate provided no improvement to model fit.

Model	log(Likelihood)	K	AIC_c	ΔAIC_c
GH ~ TIME + (1 | STUDY:YEAR)	-2848.66	4	5705.37	0.00
GH ~ 1 + (TIME | STUDY:YEAR)	-2852.42	5	5714.90	9.53

FIGURES

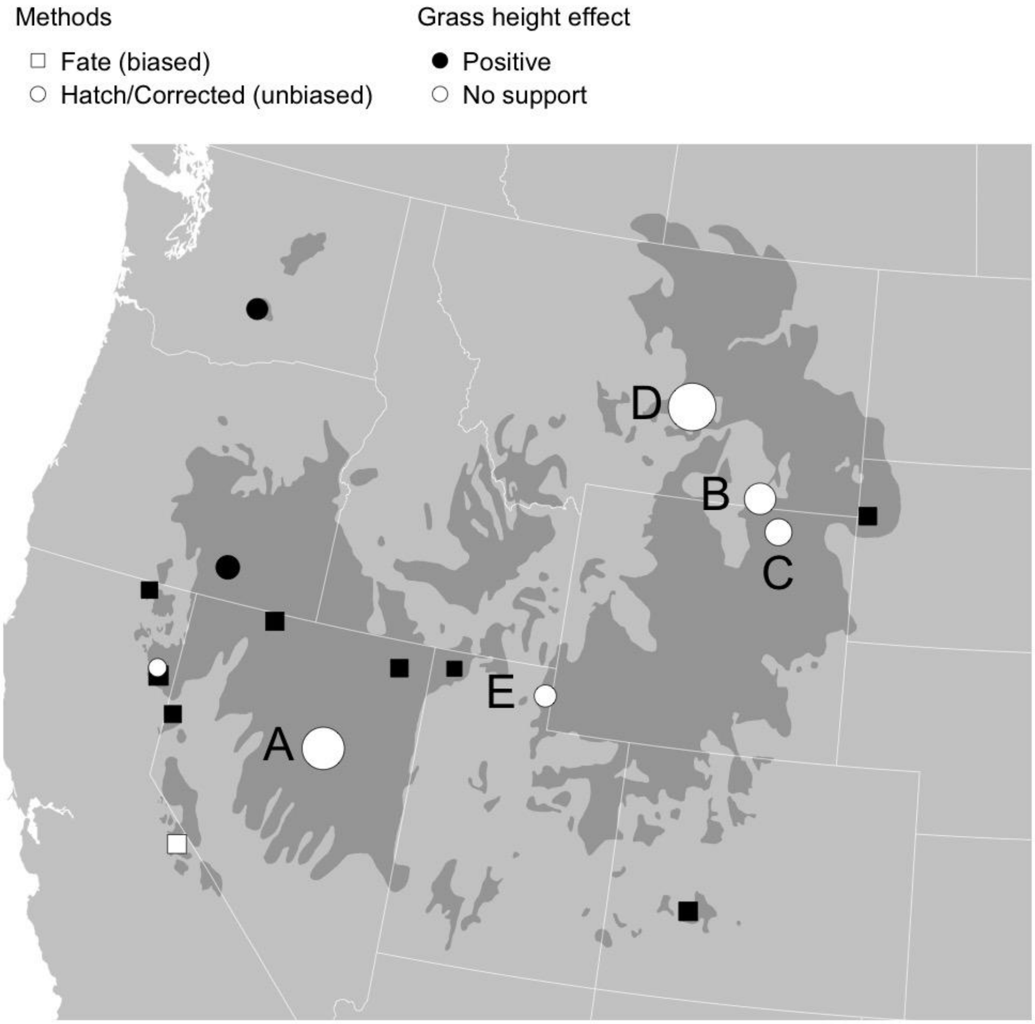

Figure 1. Studies testing relationship between sage-grouse nest survival and grass height surrounding the nest (data from Table 1 in Gibson et al. [2016]). Only studies reporting timing of vegetation measurement relative to the nesting cycle are shown. Size of points is proportional to sample size. Gibson et al. (2016; A) found studies using grass cover or height measured following nest fate (squares) are susceptible to producing inflated or spurious effects of vegetative concealment on nest survival, while those using measurements taken following the predicted hatch date regardless of nest fate (circles)

are unbiased. Our re-analysis of two previously published datasets from Montana and Wyoming (B and C) and two unpublished datasets from long-term grazing studies in Montana and Utah (D and E) revealed no support for an effect of grass height on nest survival after accounting for phenology.

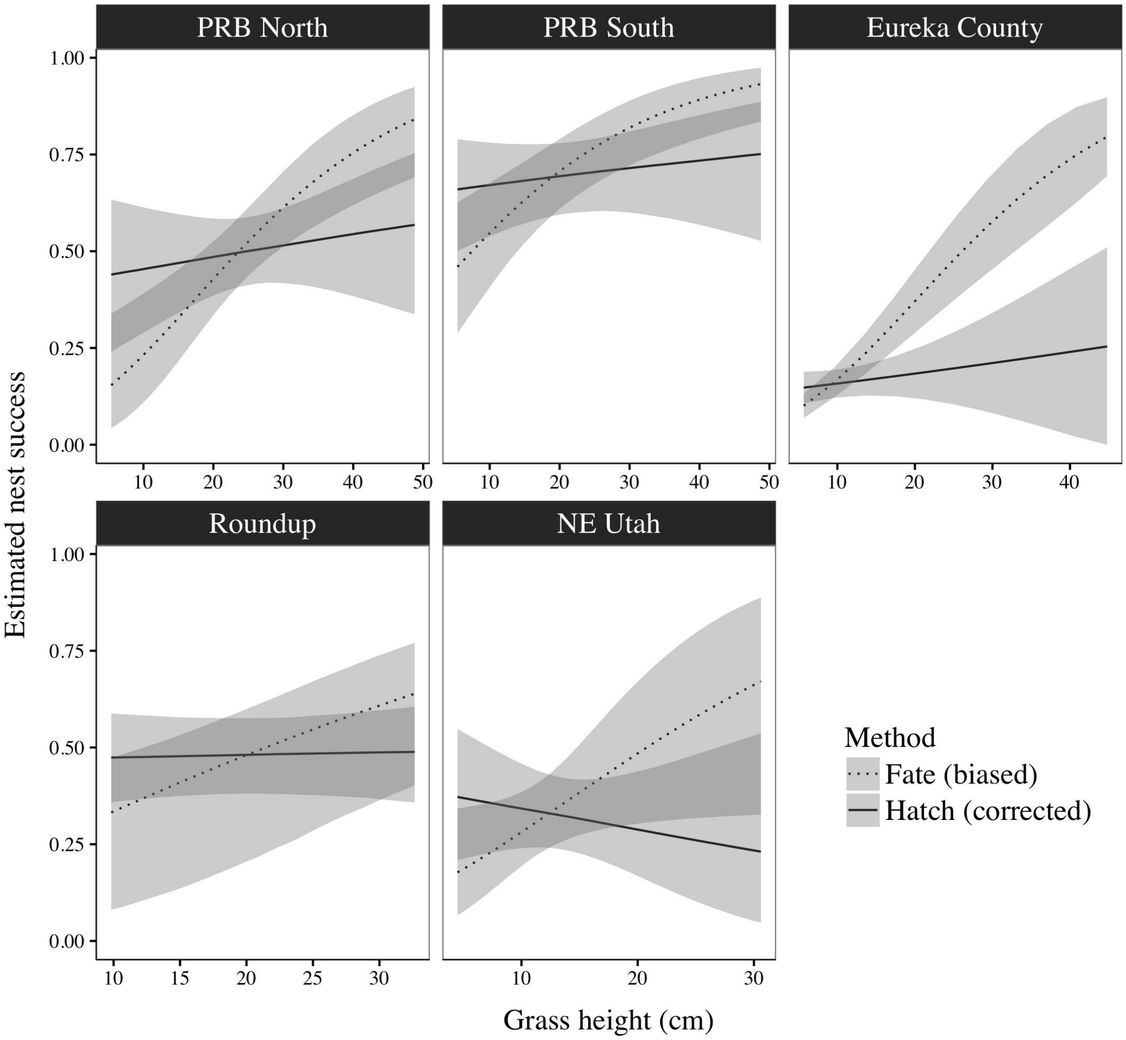

Figure 2. Predicted response of sage-grouse nest success (and 95% CI [Eureka County] or CRI [other studies]) to live grass height using measurements using a biased method following determination of nest fate (dotted lines), and those measured or corrected to the predicted hatch date of nests (solid lines). Nest data includes studies from the Powder River Basin (PRB) in southeastern Montana (PRB North, Doherty et al. 2014, n=217, 2003-2007) and northeast Wyoming (PRB South, Doherty et al. 2014, n=164, 2003-2007); Eureka County, Nevada (Gibson et al. 2016, n=396, 2004-2012); central Montana near the town of Roundup (Chapter 2, n=413, 2011-2015), and northeast Utah

(Dettenmaier, Utah State University, unpublished data; n=105, 2012-2015). Note that limits of x-axes change to reflect the range of grass heights observed within respective studies.

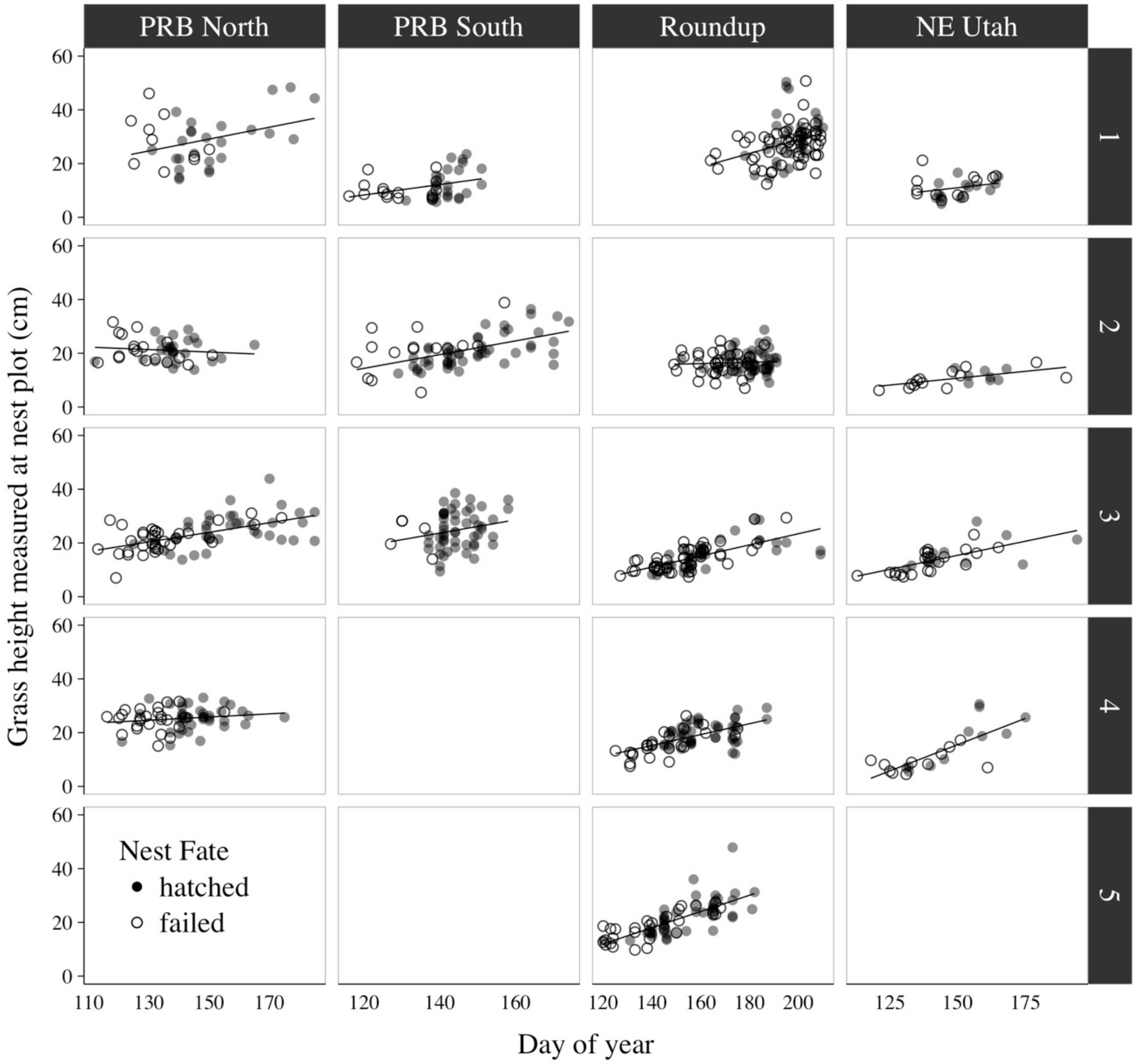

Figure 3. Average grass height measurements surrounding successful and failed sage-grouse nests by day of year in each year (rows) in four independent study areas (columns). After accounting for phenology, a difference in grass height between successful and failed nests was not supported.