



Reducing cultivation risk for at-risk species: Predicting outcomes of conservation easements for sage-grouse

J.T. Smith^{a,*}, J.S. Evans^{b,c}, B.H. Martin^d, S. Baruch-Mordo^b, J.M. Kiesecker^b, D.E. Naugle^a

^a Wildlife Biology Program, University of Montana, Missoula, MT 59812, United States

^b The Nature Conservancy, Fort Collins, CO 80524, United States

^c Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, United States

^d The Nature Conservancy, Helena, MT 59601, United States

ARTICLE INFO

Article history:

Received 16 December 2015

Received in revised form 1 June 2016

Accepted 10 June 2016

Available online xxxx

Keywords:

Agriculture

Centrocercus urophasianus

Cropland conversion

Land-use change

Northern Great Plains

Sagebrush

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 km² 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 \$100 M 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.

© 2016 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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, Tschardt 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 overlies deeper, more arable soils (e.g., Vander Haegen et al., 2000).

* Corresponding author at: College of Forestry and Conservation, 32 Campus Drive, Missoula, MT 59812, United States.

E-mail address: joseph3.smith@umontana.edu (J.T. Smith).

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 Mha 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 (Fig. 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 (Fig. 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

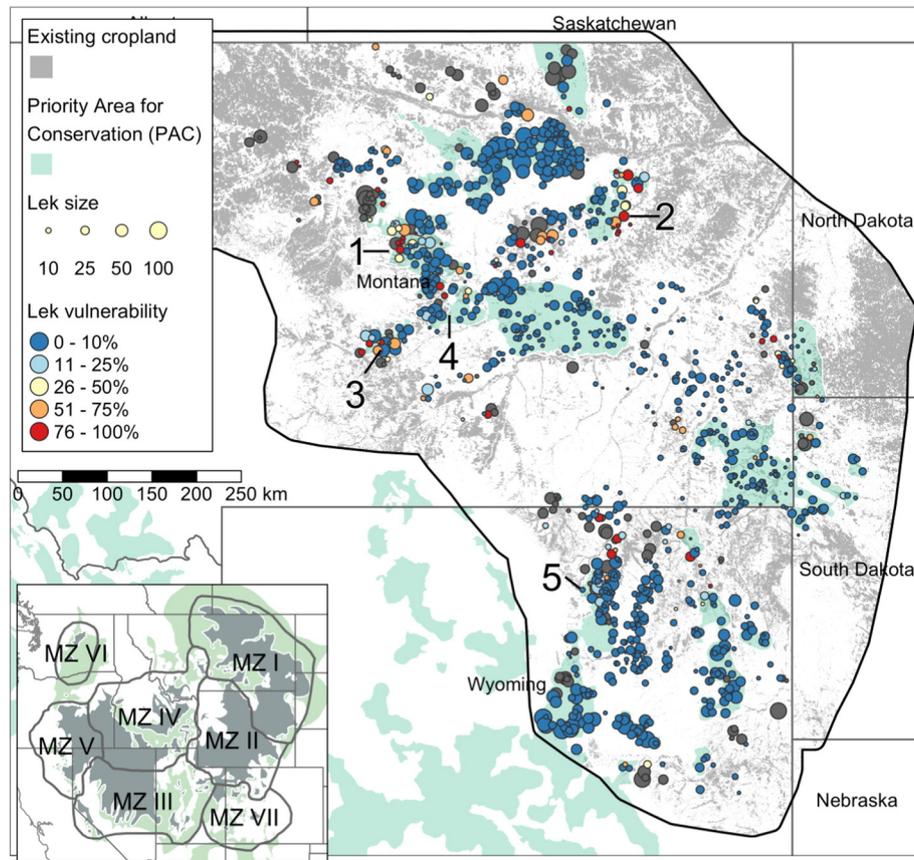


Fig. 1. Study area, sage-grouse Management Zone 1 (MZ1), showing active leks and areas currently occupied by cropland. Lek color indicates vulnerability to cropland expansion—i.e., the proportion of 1000 stochastic cropland build-outs in which the lek fell below the model-based habitat threshold (n = 122, see Section 3.3). Point size is proportional to maximum recorded male attendance from 2008 to 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. (For interpretation of the references to in this figure legend, the reader is referred to the web version of this article.)

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 ≥ 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 partialled 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 among 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

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) ^a	1.0 km	1
Proportion sagebrush-dominated landcover (Sagebrush) ^a	6.4 km	1
Distance to mesic landcover (Dist_mesic) ^a	–	1
Topography		
Standard deviation of elevation (Roughness) ^a	0.8 km	2
Climate		
Average annual minimum temperature (Min_temp) ^a	0.8 km	3
Average annual maximum temperature (Max_temp) ^a	0.8 km	3
Average total precipitation March–May (Spring_precip) ^a	0.8 km	3
Average total precipitation June–August (Summer_precip) ^a	0.8 km	3
Average total precipitation September–November (Fall_precip) ^a	0.8 km	3
Anthropogenic features		
Proportion non-cropland anthropogenic disturbance (Disturb) ^a	5.0 km	4
Cropland		
Proportion cropland (Crop_0.8) ^a	0–0.8 km	5
Proportion cropland (Crop_3.2) ^a	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 (Fry 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).

^a In top IPP model.

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,

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

Covariate ^a	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 3 × 3 focal window	4
Roughness 27 × 27 focal window	4
Slope * COS(Aspect)	5
Slope * SIN(Aspect)	5
Slope in degrees	6
Slope position	7
Surface relief ratio 3 × 3 focal window	8
Surface relief ratio 27 × 27 focal window	8
Topographic Radiation Aspect Index	9
Available water storage 25 cm	10
Available water storage 50 cm	10
Available water storage 100 cm	10
Available water storage 150 cm	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

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:** Blaszczyński (1997); **8:** Pike (1971); **9:** Roberts and Cooper (1989); **10:** Soil Survey Staff (2012); **11:** USDA (2012).

^a 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.

Sagebrush, Dist_mesic, 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, 2015), 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 to 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 multicollinearity 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 permuted 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 to 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 \leq 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 \$100 M 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 to 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 \$100 M 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

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

Model	K	AICc	ΔAICc	wt _i
Crop_0.8 + Crop_3.2	23	12,257.78	0.00	0.59
Crop_0.8 + Crop_3.2 + Crop_6.4	24	12,259.54	1.76	0.24
Crop_0.8 + Crop_3.2 + Crop_6.4 + Crop_8.5	25	12,260.86	3.08	0.13
Crop_0.8 + Crop_3.2 + Crop_6.4 + Crop_8.5 + Crop_10.0	26	12,262.86	5.08	0.05
Crop_0.8	22	12,284.16	26.38	0.00
Null ^a	21	12,623.28	365.50	0.00

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

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 km²) 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 km² landscape (Crop_3.2) increases (Fig. 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 to 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 (Fig. 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

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
Dist_mesic	1.7E-01	4.0E-02	4.31	<0.0001
Dist_mesic 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

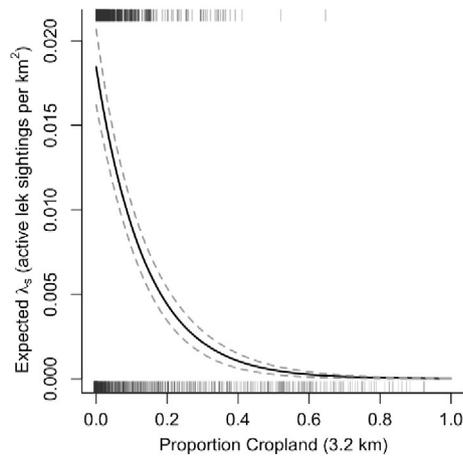


Fig. 2. Mean (black line) and 95% confidence intervals (dashed gray lines) of expected intensity of active lek sightings as a function of proportion cropland at the 32.2 km² scale. Rug plots indicates proportion cropland measured at active leks in Management Zone 1 ($n = 1064$, top) and an equal number of random locations in Management Zone 1 (bottom). 96% of active leks are found in landscapes with proportion cropland <0.15.

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 (Fig. 3 and Table 5). One hundred nineteen leks, representing 11.3% of the population, had vulnerabilities ≥ 0.1 (Fig. 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 Fig. 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

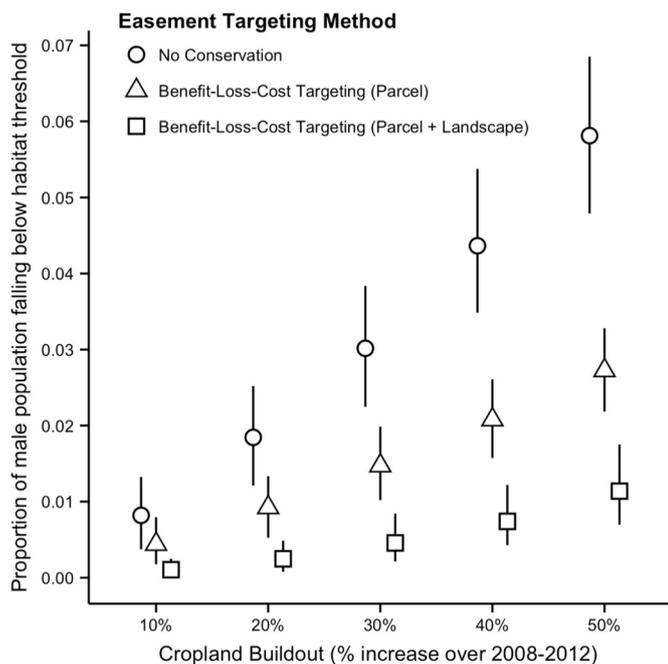


Fig. 3. Proportion of male breeding population in sage-grouse Management Zone 1 falling below the habitat suitability threshold with simulated expansion of cropland area from 10 to 50% over 2012 extent. Error bars indicate lower and upper bounds of the central 95% of outcomes from 1000 stochastic cropland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

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 ^a		
		Mean	Lower CL ^b	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

^a Habitat threshold is the value that maximizes the sum of sensitivity and specificity of the IPP model (see Section 2.5).

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

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 (Fig. 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 km² (12.4 mi²) landscape can reduce lek density by more than half. Ten percent of 32.2 km² equates to slightly more than one Public Land Survey System section (2.59 km² or 1 mi²); 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 $\leq 22\%$ 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 km² landscape (Fig. 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 cropland 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 \$100 M 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 \$10 M 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 \$200 M 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 (Fig. 3) illustrates this point. We recommend a strategic approach among 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 \$100 M in conservation easements can provide substantial coverage of sage-grouse habitat at risk of conversion.

Acknowledgements

Funding for this research was provided by USDA Natural Resources Conservation Service through their Sage Grouse Initiative and Conservation Effects Assessment Project (Grant #68-7482-9-10-525). We are grateful to Tim Griffiths, Jeremy Maestas, Hal Gordon, Josh Nowak, and Paul Lukacs for conceptual and/or analytical assistance. We thank Montana Department of Fish, Wildlife & Parks, Wyoming Game and Fish Department, North Dakota Game and Fish, and South Dakota Game, Fish, and Parks for sharing lek data. The 3 M Foundation and Anne Ray Charitable Trust also provided financial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.06.006>.

References

- Aarts, G., Fieberg, J., Matthiopoulos, J., 2012. Comparative interpretation of count, presence-absence and point methods for species distribution models. *Methods Ecol. Evol.* 3, 177–187.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, B.F. (Eds.), *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, Hungary, pp. 267–281.
- Aldridge, C.L., Boyce, M.S., 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. *Ecol. Appl.* 17, 508–526.
- Aldridge, C.L., Nielsen, S.E., Beyer, H.L., Boyce, M.S., Connelly, J.W., Knick, S.T., Schroeder, M.A., 2008. Range-wide patterns of greater sage-grouse persistence. *Divers. Distrib.* 14, 983–994.
- Andren, H., 1992. Corvid density and nest predation in relation to forest fragmentation – a landscape perspective. *Ecology* 73, 794–804.
- Baruch-Mordo, S., Evans, J.S., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falkowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biol. Conserv.* 167, 233–241.
- Bivand, R., Keitt, T., Rowlingson, B., 2015. Rgdal: Bindings for the Geospatial Data Abstraction Library. R Package Version Vol. 1 pp. 0–4 (<https://CRAN.R-project.org/package=rgdal>).
- Blaszczynski, J.S., 1997. Landform characterization with geographic information systems. *Photogramm. Eng. Remote. Sens.* 63, 183–191.
- Blus, L.J., Staley, C.S., Henny, C.J., Pendleton, G.W., Craig, T.H., Craig, E.H., Halford, D.K., 1989. Effects of organo-phosphorus insecticides on sage grouse in Southeastern Idaho. *J. Wildl. Manag.* 53, 1139–1146.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecol. Model.* 157, 281–300.
- Bradbury, J.W., Gibson, R.M., McCarthy, C.E., Vehrencamp, S.L., 1989. Dispersion of displaying male sage grouse 0.2. The role of female dispersion. *Behav. Ecol. Sociobiol.* 24, 15–24.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32.
- Bureau of Land Management, 2013. GeoCommunicator website. http://www.geocommunicator.gov/GeoComm/isis_home/home/index.htm.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* 20, 37–46.
- Connelly, J.W., Schroeder, M.A., Sands, A.R., Braun, C.E., 2000. Guidelines to manage sage grouse populations and their habitats. *Wildl. Soc. Bull.* 28, 967–985.
- Copeland, H.E., Pocewicz, A., Naugle, D.E., Griffiths, T., Keinath, D., Evans, J., Platt, J., 2013. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. *PLoS One* 8.
- Cressie, N.A.C., 1993. *Statistics for Spatial Data*. Wiley, New York, New York, USA.
- R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Doherty, K.E., 2008. Sage-Grouse and Energy Development: Integrating Science with Conservation Planning to Reduce Impacts. The University of Montana, Missoula, Montana, USA.
- Doherty, K.E., Naugle, D.E., Walker, B.L., Graham, J.M., 2008. Greater sage-grouse winter habitat selection and energy development. *J. Wildl. Manag.* 72, 187–195.
- Doherty, K.E., Naugle, D.E., Evans, J.S., 2010. A currency for offsetting energy development impacts: horse-trading sage-grouse on the open market. *PLoS One* 5.
- Donnelly, J.P., Naugle, D.E., Hagen, C.A., Maestas, J.D., 2016. Public lands and private waters: scarce Mesic resources structure land tenure and sage-grouse distributions. *Ecosphere* 7 (Article e01208).
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Laffourcade, B., Leitao, P.J., Munkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schroeder, B., Skidmore, A.K., Zurell, R., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Evans, J.S., Cushman, S.A., 2009. Gradient modeling of conifer species using random forests. *Landsc. Ecol.* 24, 673–683.
- Evans, J.S., Murphy, M.A., 2014. rUtilities: An R Package for Model Selection and Validation of Random Forests.
- Evans, J.S., Murphy, M.A., Holden, Z.A., Cushman, S.A., 2011. Modeling species distribution and change using random forests. In: Drew, C.A., Wiersma, Y.F., Huettmann, F. (Eds.), *Landscape Ecology: Concepts and Applications*. Springer, New York, New York, USA.
- Fawcett, T., 2006. An introduction to ROC analysis. *Pattern Recogn. Lett.* 27, 861–874.
- Fishburn, I.S., Kareiva, P., Gaston, K.J., Armsworth, P.R., 2009. The growth of easements as a conservation tool. *PLoS One* 4.
- Fithian, W., Hastie, T., 2013. Finite-sample equivalence in statistical models for presence-only data. *Ann. Appl. Stat.* 7, 1917–1939.
- Fox, J., Monette, G., 1992. Generalized collinearity diagnostics. *J. Am. Stat. Assoc.* 87, 178–183.
- Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogramm. Eng. Remote. Sens.* 77, 858–864.
- Gesch, D.B., 2007. The National Elevation Dataset in Maune, D., Editor. *Digital Elevation Model Technologies and Applications: The DEM Users Manual*. second ed. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland, USA.
- Gesch, D., Oimoen, M., Greenlee, S., Nelson, C., Steuck, M., Tyler, D., 2002. The National Elevation Dataset. *Photogramm. Eng. Remote. Sens.* 68, 5–11.
- Gessler, P.E., Moore, I.D., McKenzie, N.J., Ryan, P.J., 1995. Soil-landscape modeling and spatial prediction of soil attributes. *Int. J. GIS* 9, 421–432.
- Gibson, R.M., 1996a. A re-evaluation of hotspot settlement in lekking sage grouse. *Anim. Behav.* 52, 993–1005.
- Gibson, R.M., 1996b. Female choice in sage grouse: The roles of attraction and active comparison. *Behav. Ecol. Sociobiol.* 39, 55–59.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550–555.
- Greenberg, J.A., Mattiuzzi, M., 2014. gdalUtils: wrappers for the geospatial data abstraction library (GDAL) utilities. (R package version 0.3.1) <https://CRAN.R-project.org/package=gdalUtils>.
- Greenwood, R.J., Sargeant, A.B., Johnson, D.H., Cowardin, L.M., Shaffer, T.L., 1995. Factors associated with duck Nest success in the prairie pothole region of Canada. *Wildl. Monogr.* 128, 1–57.
- Gregory, A.J., Beck, J.L., 2014. Spatial heterogeneity in response of male greater sage-grouse lek attendance to energy development. *PLoS One* 9.
- Herman-Brunson, K.M., Jensen, K.C., Kaczor, N.W., Swanson, C.C., Rumble, M.A., Klaver, R.W., 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. *Wildl. Biol.* 15, 237–246.
- Hijmans, R.J., 2015. Raster: Geographic Data Analysis and Modeling. R Package Version Vol. 2 pp. 4–18 (<https://CRAN.R-project.org/package=raster>).
- Holloran, M.J., 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming (Dissertation) University of Wyoming, Laramie.
- Holloran, M.R.J., Anderson, S.H., 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. *Condor* 107, 742–752.
- Holloran, M.J., Kaiser, R.C., Hubert, W.A., 2010. Yearling greater sage-grouse response to energy development in Wyoming. *J. Wildl. Manag.* 74, 65–72.
- Horn, B.K.P., 1981. Hill shading and the reflectance map. *Proc. Inst. Electr. Electron. Eng.* 69, 14–47.
- Hurvich, C.M., Tsai, C.L., 1989. Regression and time-series model selection in small samples. *Biometrika* 76, 297–307.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *J. Wildl. Manag.* 70, 347–357.
- Knick, S.T., Connelly, J.W. (Eds.), 2011. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats*. Studies in Avian Biology, University of California Press, Berkeley, California, USA.
- Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, W.M., van Riper, C., 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105, 611.
- Knick, S.T., Hanser, S.E., Preston, K.L., 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, USA. *Ecol. Evol.* 3, 1539–1551.
- LANDFIRE, 2008. LANDFIRE 1.1.0 Existing Vegetation Type Layer. U.S. Geological Survey (<http://landfire.cr.usgs.gov/viewer/>).
- Lark, T.J., Salmon, J.M., Gibbs, H.K., 2015. Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environ. Res. Lett.* 10.
- Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R News* 2, 18–22.
- Liu, C.R., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P. (Eds.), 2002. *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*, second ed. Kluwer, Boston, Massachusetts, USA.
- McNab, H.W., 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. *Can. J. For. Res.* 23, 1100–1107.
- Meyer, J.S., Irwin, L.L., Boyce, M.S., 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. *Wildlife Monographs*, pp. 5–51.
- Montana Greater Sage-Grouse Habitat Conservation Advisory Council, 2014C. *Greater Sage-Grouse Habitat Conservation Strategy* (Helena, Montana, USA).
- Murphy, M.A., Evans, J.S., Storfer, A., 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91, 252–261.
- Naugle, D.E., Doherty, K.E., Walker, B.L., Holloran, M.J., Copeland, H.E., 2011. Energy development and greater sage-grouse. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats*. Studies in Avian Biology, University of California Press, Berkeley, California, USA, pp. 489–503.
- Neudecker, G.A., Duvall, A.L., Stutzman, J.W., 2011. Community-based landscape conservation: a roadmap for the future. In: Naugle, D.E. (Ed.), *Energy Development and Wildlife Conservation in Western North America*. Island Press, Washington, DC, USA, pp. 2011–2230.
- Newburn, D., Reed, S., Berck, P., Merenlender, A., 2005. Economics and land-use change in prioritizing private land conservation. *Conserv. Biol.* 19, 1411–1420.
- Phillips, S.J., Elith, J., 2013. On estimating probability of presence from use-availability or presence-background data. *Ecology* 94, 1409–1419.
- Phillips, M.L., Clark, W.R., Sovada, M.A., Horn, D.J., Koford, R.R., Greenwood, R.J., 2003. Predator selection of prairie landscape features and its relation to duck nest success. *J. Wildl. Manag.* 67, 104–114.
- Phillips, S.J., Dudik, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Pike, R.J., Wilson, S.E., 1971. Elevation-relief ratio, hypsometric integral, and geomorphic area-altitude analysis. *Geol. Soc. Am. Bull.* 82, 1079–1083.
- Pocewicz, A., Kiesecker, J.M., Jones, G.P., Copeland, H.E., Daline, J., Meador, B.A., 2011. Effectiveness of conservation easements for reducing development and maintaining biodiversity in sagebrush ecosystems. *Biol. Conserv.* 144, 567–574.
- Pressey, R.L., 1994. Ad hoc reservations - forward or backward steps in developing representative reserve systems. *Conserv. Biol.* 8, 662–668.

- PRISM Climate Group, Oregon State University, 2014. <http://prism.oregonstate.edu>.
- Ramsey, F.L., McCracken, M., Crawford, J.A., Drut, M.S., Ripple, W.J., 1994. Habitat association studies of the northern spotted owl, sage grouse, and flammulated owl. In: Lange, N., Ryan, L., Billard, L., Brillinger, D., Conquest, L., Greenhouse, J. (Eds.), *Case Studies in Biometry*. John Wiley & Sons, Inc., Hoboken, New Jersey, USA, pp. 189–210.
- Rand, T.A., Tylilanakis, J.M., Tschardtke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603–614.
- Rashford, B.S., Walker, J.A., Bastian, C.T., 2011. Economics of grassland conversion to cropland in the prairie pothole region. *Conserv. Biol.* 25, 276–284.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analysis of plant-climate relationships for the western United States. *Int. J. Plant Sci.* 167, 1123–1150.
- Renner, I.W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S.J., Popovic, G., Warton, D.I., 2015. Point process models for presence-only analysis. *Methods Ecol. Evol.* 6, 366–379.
- Riley, S.J., DeGloria, S.D., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermt. J. Sci.* 5, 23–27.
- Roberts, D.W., Cooper, S.V., 1989. Concepts and techniques of vegetation mapping. *Land Classifications Based on Vegetation: Applications for Resource Management*. USDA Forest Service GTR INT-257, Ogden, Utah, USA, pp. 90–96.
- Schroeder, M.A., Hays, D.W., Livingston, M.F., Stream, L.E., Jacobson, J.E., Pierce, D.J., McCall, T., 2000. Changes in the distribution and abundance of sage grouse in Washington. *Northwest. Nat.* 81, 104–112.
- Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C., Estes, J., 2001. Nature reserves: Do they capture the full range of America's biological diversity? *Ecol. Appl.* 11, 999–1007.
- Smith, R.E., 2013. *Conserving Montana's Sagebrush Highway: Long Distance Migration in Sage-grouse* (Thesis) The University of Montana, Missoula, Montana, USA.
- Soil Survey Staff, Natural Resources Conservation Service, USDA, 2012. Soil survey geographic (SSURGO) database. <http://sdmdataaccess.nrcs.usda.gov> (Accessed [11/23/2012]).
- Stage, A.R., 1976. An expression of the effects of aspect, slope, and habitat type on tree growth. *For. Sci.* 22, 457–460.
- Stiver, S.J., Apa, A.D., Bohne, J.R., Bunnell, S.D., Deibert, P.A., Gardner, S.C., Hilliard, M.A., McCarthy, C.W., Schroeder, M.A., 2006. *Greater Sage-Grouse Comprehensive Conservation Strategy*. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
- Suring, L.H., Rowland, M.M., Wisdom, M.J., 2005. Identifying species of conservation concern. In: Wisdom, M.J., Rowland, M.M., Suring, L.H. (Eds.), *Habitat Threats in the Sagebrush Ecosystem - Methods of Regional Assessment and Applications in the Great Basin*. Alliance Communications Group, Lawrence, Kansas, USA, pp. 150–162.
- Swenson, J.E., Simmons, C.A., Eustace, C.D., 1987. Decrease of sage grouse *Centrocercus urophasianus* after plowing of sagebrush steppe. *Biol. Conserv.* 41, 125–132.
- Sylvester, K.M., Brown, D.G., Deane, G.D., Kornak, R.N., 2013. Land transitions in the American plains: Multilevel modeling of drivers of grassland conversion (1956–2006). *Agric. Ecosyst. Environ.* 168, 7–15.
- Tack, J.D., 2009. *Sage-grouse and the human footprint: implications for conservation of small and declining populations* (Thesis) The University of Montana, Missoula, Montana, USA.
- Taylor, R.L., Walker, B.L., Naugle, D.E., Mills, L.S., 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. *J. Wildl. Manag.* 76, 336–347.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Acad. Sci. U. S. A.* 108, 20260–20264.
- Tschardtke, T.J.M., et al., 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biol. Rev.* 87, 661–685.
- US Census Bureau, 2013. Tiger/line shapefiles. <https://www.census.gov/geo/maps-data/data/tiger.html>.
- US Department of Interior, 2010. *Endangered and Threatened Wildlife and Plants; 12-Month Findings for Petitions to List the Greater Sage-Grouse (Centrocercus urophasianus) as Threatened or Endangered*. Federal Register, pp. 13910–13958.
- US Department of Interior, 2015. *Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition To List Greater Sage-Grouse (Centrocercus urophasianus) as an Endangered or Threatened Species*. Federal Register, pp. 59858–59942.
- USDA, 2012. User guide for the National Commodity Crop Productivity Index (NCCPI) version 2.0. http://www.nrcs.usda.gov/wps/PA_NRCSCconsumption/download?cid=nrcs142p2_050734&ext=pdf (Accessed [11/23/2012]).
- USDA NRCS, 2015. Sage grouse initiative 2.0: Investment strategy, FY 2015–2018. http://www.nrcs.usda.gov/wps/PA_NRCSCconsumption/download?cid=nrcseprd391816&ext=pdf.
- USDA-NASS, 2014a. Cropland data layer. <http://nassgeodata.gmu.edu/CropScape/>.
- USDA-NASS, 2014b. QuickStats 2.0. <http://quickstats.nass.usda.gov>.
- USFWS, 2013. *Greater Sage-Grouse (Centrocercus urophasianus) Conservation Objectives: Final Report*. USFWS, Denver, Colorado, USA.
- Vander Haegen, W.M., 2007. Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. *Ecol. Appl.* 17, 934–947.
- Vander Haegen, W.M., Dobler, F.C., Pierce, D.J., 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, USA. *Conserv. Biol.* 14, 1145–1160.
- Walker, B.L., Naugle, D.E., Doherty, K.E., 2007. Greater sage-grouse population response to energy development and habitat loss. *J. Wildl. Manag.* 71, 2644–2654.
- Warton, D.I., Shepherd, L.C., 2010. Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. *Ann. Appl. Stat.* 4, 1383–1402.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615.