

Factors Associated with Extirpation of Sage-Grouse

Michael J. Wisdom, Cara W. Meinke, Steven T. Knick,
and Michael A. Schroeder

Abstract. Geographic ranges of Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*C. minimus*) have contracted across large areas in response to habitat loss and detrimental land uses. However, quantitative analyses of the environmental factors most closely associated with range contraction have been lacking, results of which could be highly relevant to conservation planning. Consequently, we analyzed differences in 22 environmental variables between areas of former range (extirpated range), and areas still occupied by the two species (occupied range). Fifteen of the 22 variables, representing a broad spectrum of biotic, abiotic, and anthropogenic conditions, had mean values that were significantly different between extirpated and occupied ranges. Best discrimination between extirpated and occupied ranges, using discriminant function analysis (DFA), was provided by five of these variables: sagebrush area (*Artemisia* spp.); elevation; distance to transmission lines; distance to cellular towers; and land ownership. A DFA model containing these five variables correctly classified >80% of sage-grouse historical locations to extirpated and occupied ranges. We used this model to estimate the similarity between areas of occupied range with areas where extirpation has occurred. Areas currently occupied by sage-grouse,

but with high similarity to extirpated range, may not support persistent populations. Model estimates showed that areas of highest similarity were concentrated in the smallest, disjunct portions of occupied range and along range peripheries. Large areas in the eastern portion of occupied range also had high similarity with extirpated range. By contrast, areas of lowest similarity with extirpated range were concentrated in the largest, most contiguous portions of occupied range that dominate Oregon, Idaho, Nevada, and western Wyoming. Our results have direct relevance to conservation planning. We describe how results can be used to identify strongholds and spatial priorities for effective landscape management of sage-grouse.

Key Words: *Centrocercus minimus*, *Centrocercus urophasianus*, extirpated range, extirpation, Greater Sage-Grouse, Gunnison Sage-Grouse, range contraction, sagebrush.

Factores Asociados a la Extirpación del Sage-Grouse

Resumen. Las distribuciones geográficas del Greater Sage-Grouse (*Centrocercus urophasianus*) y el Gunnison Sage-Grouse (*C. minimus*) se han

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contraído a través de extensas áreas en respuesta a la pérdida de hábitat y a usos perjudiciales del suelo. Sin embargo, se carece de análisis cuantitativos de los factores ambientales que más se asocian a la contracción del territorio, cuyos resultados podrían ser altamente relevantes al planeamiento de la conservación. Por lo tanto, analizamos diferencias en 22 variables ambientales entre las áreas del territorio original (territorio extirpado), y las áreas todavía ocupadas por las dos especies (territorio ocupado). Quince de las 22 variables, representando un amplio espectro de condiciones bióticas, abióticas, y antropogénicas, tuvieron valores medios que resultaron significativamente diferentes entre los territorios extirpados y ocupados. La mejor discriminación entre los territorios extirpados y ocupados, usando el análisis de función discriminante (DFA), fue proporcionada por cinco de estas variables: área del sagebrush (*Artemisia* spp.); elevación; distancia a las líneas de transmisión; distancia a las torres celulares; y propiedad del terreno. Un modelo de DFA que contenía estas cinco variables clasificó correctamente >80% de las ubicaciones históricas del sage-grouse como territorios extirpados y ocupados. Utilizamos este modelo para estimar la semejanza entre las áreas del territorio

ocupado con las áreas donde ha ocurrido la extirpación. Las áreas ocupadas actualmente por sage-grouse, pero con alta semejanza al territorio extirpado, pueden no ser capaces de sostener a las poblaciones persistentes. Las estimaciones del modelo demostraron que las áreas de mayor semejanza están concentradas en las porciones más pequeñas y divididas del territorio ocupado, y a lo largo de las periferias del territorio. Extensas áreas en la porción este del territorio ocupado también tuvieron gran semejanza con el territorio extirpado. Por el contrario, las áreas de menor semejanza con el territorio extirpado están concentradas en las porciones más grandes y más contiguas del territorio ocupado que dominan Oregon, Idaho, Nevada, y Wyoming occidental. Nuestros resultados tienen relevancia directa al planeamiento de la conservación. Describimos cómo los resultados pueden utilizarse para identificar baluartes y prioridades espaciales para el eficaz manejo del paisaje de sage-grouse.

Palabras Clave: artemisa, *Centrocercus minimus*, *Centrocercus urophasianus*, contracción del rango geográfico, extirpación, Greater Sage-Grouse, Gunnison Sage-Grouse, rango geográfico extirpado.

Species across the world are threatened by human activities that degrade and eliminate habitats at a massive scale. The World Conservation Union estimates that >12,000 species are at risk of extinction from the pervasive and accelerating effects of human-associated causes of habitat loss (Baillie et al. 2004). Habitat loss is reflected in range contraction for many widely distributed species. Large, contiguous ranges of many terrestrial species have become smaller and fragmented, resulting in population isolation and increased vulnerability to extirpation and extinction. In western North America, a myriad of widely distributed birds and mammals have experienced large contractions in their historical ranges in response to habitat loss and detrimental human activities (Wisdom et al. 2000a, Laliberte and Ripple 2004).

Range contraction for many species is well documented and the causes generally accepted. However, the specific changes in environmental conditions associated with contraction often are not well studied and thus poorly quantified. Consequently,

specific factors and their threshold values associated with range contraction, or regional extirpation of a species, have rarely been documented (see Laliberte and Ripple 2004 as an exception). The advent of continuous coverage spatial data now allows environmental conditions to be summarized across vast areas, encompassing extirpated and occupied portions of a species historical range. These spatial data provide novel and compelling opportunities for formal analysis of conditions associated with extirpation in areas where species ranges have contracted (Aldridge et al. 2008). Differences in environmental conditions between extirpated and occupied portions of a species' historical range could provide important insights for conservation planning and recovery. This is particularly true for many species whose populations are declining and considered imperiled, yet data are insufficient to conduct a formal population viability analysis (Morris and Doak 2002).

Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*C. minimus*) (collectively

referred to as sage-grouse) are typical of many widely distributed species whose ranges have contracted in response to habitat loss and detrimental land uses. Habitats and populations have declined steadily over long periods and across large areas (Connelly and Braun 1997, Braun 1998, Schroeder et al. 1999, Connelly et al. 2004, Aldridge et al. 2008) resulting in widespread range contraction (Schroeder et al. 2004). Notably, sage-grouse are strongly associated with sagebrush (*Artemisia* spp.), and like many other sagebrush-associated vertebrates, are highly vulnerable to regional extirpation because of extensive habitat loss and degradation (Raphael et al. 2001).

Our goal was to identify environmental factors associated with regional extirpation of sage-grouse. Our specific objectives were to: (1) identify spatially explicit environmental factors most strongly associated with, and providing the best discrimination between, currently occupied versus extirpated ranges of sage-grouse; (2) use these factors in a spatially explicit model to estimate the similarity of remaining areas of occupied range with areas where extirpation has occurred as a means of identifying areas where sage-grouse may be vulnerable to extirpation; (3) interpret results for conservation planning at regional and range-wide spatial extents, and (4) describe data deficiencies and research needs to enhance knowledge about environmental conditions that potentially contribute to sage-grouse extirpation at regional extents.

METHODS

We used six steps to meet our objectives: (1) delineate boundaries of currently occupied versus extirpated portions of sage-grouse historical range; (2) obtain or derive continuous-coverage spatial layers for all environmental variables likely to differ between occupied and extirpated ranges based on known or hypothesized environmental associations with sage-grouse at landscape scales; (3) develop an unbiased system of sampling or census of these environmental variables in occupied versus extirpated ranges at a spatial extent compatible with that used by sage-grouse populations to meet year-round needs, and consequently, the extent at which regional extirpation may occur; (4) use the system to analyze patterns and differences in environmental variables between occupied and extirpated ranges; (5) build and

validate spatial models based on these patterns and differences that best discriminate between occupied and extirpated ranges; and (6) apply the best-performing model to different regions of occupied range to estimate each region's similarity with areas where extirpation has occurred.

Step 1: Range Delineation

We used the range map for Greater and Gunnison Sage-Grouse as the basis for identifying their occupied and extirpated ranges (Schroeder et al. 2004). The historical ranges of the two species could not always be distinguished. Until recently, the two species were considered one, and historical records often were identified simply as sage-grouse (Schroeder et al. 2004). As a result, our analysis combines both species, recognizing that most areas of their collective ranges were and continue to be dominated by Greater Sage-Grouse (Schroeder et al. 2004). Both species have similar environmental requirements and respond similarly to habitat loss from human activities, and both have undergone substantial range contractions in response to habitat loss (Oyler-McCance et al. 2001, Rowland 2004).

The range map of Schroeder et al. (2004) depicts the potential pre-settlement and current range of sage-grouse. Potential pre-settlement was defined as the range before 1800, when settlement of western North America by large numbers of Euro-Americans had not yet occurred. We assumed that the potential pre-settlement range not currently occupied represented areas where sage-grouse once existed but now are extirpated. This assumption is supported by the large number of sage-grouse collected or observed during the latter phases of Euro-American settlement (late 1800s and early 1900s) in areas where sage-grouse no longer exist. Collected specimens or unambiguous observations of sage-grouse provided clear evidence of areas where sage-grouse occurred historically, although collections and observations were not systematic across the range and exact locations not always documented. Given this background information, we assumed that potential pre-settlement range, minus the current range, represented the best estimate of areas where sage-grouse have been extirpated. We refer to current range as occupied and to potential pre-settlement range, excluding current range, as extirpated.

Step 2: Environmental Variables

We identified 22 environmental variables relevant to sage-grouse or sagebrush landscapes whose values likely differed between occupied and extirpated ranges (Table 18.1). Most variables were identified from earlier research as being associated with sage-grouse extirpation at large spatial extents ($>100,000$ ha; Oyler-McCance et al. 2001, Wisdom et al. 2002c, Aldridge and Boyce 2007, Aldridge et al. 2008), or that have modified sagebrush habitats across large areas of sage-grouse range (Schroeder et al. 1999, Rowland 2004). Other variables represented common landscape features potentially helpful for accurate discrimination between occupied and extirpated ranges. Inclusion of these additional variables was important because of the paucity of prior landscape research on sage-grouse–environmental relations and our objective to identify the best discriminators between occupied and extirpated ranges, regardless of whether such variables had previously been evaluated as causal factors of extirpation.

Nine of the 22 variables were biological measures such as area, patch size, and fragmentation of sagebrush. Five variables were abiotic measures including precipitation, elevation, and soil characteristics. Eight variables were anthropogenic measures such as distance to roads, area in agriculture, and human population density. Of the 22 variables, 16 were raster-based and 6 were vector-based (polygon- or contour-based) estimates (Table 18.1).

Map resolution (cell size, polygon size, or contour interval) differed by variable, but most raster-based estimates used a 90-m cell size, and contour-based estimates used a resolution as fine as 10 m (Table 18.1). Variables also had to be available as continuous-coverage layers in a geographic information system (GIS) and encompass most areas of pre-settlement range. Some fringes of pre-settlement range in the United States and in Canada could not be analyzed because variables were not available in continuous coverage or in compatible GIS formats. These small areas not included in our analysis composed $<2\%$ of sage-grouse pre-settlement range. Estimates of variables were made for 2000–2004, and thus were compatible with the time frame in which sage-grouse ranges were delineated (Schroeder et al. 2004).

Variables used in our analysis were assumed to affect or be associated with changes in sage-grouse habitats or populations at regional spatial extents ($\geq 100,000$ ha). Analysis at regional extents was purposefully different than more typical analyses conducted at smaller spatial extents ($<100,000$ ha), such as evaluation of factors within a seasonal range or a specific use area (e.g., evaluating a lekking, nesting, brood-rearing, or wintering area used by individual sage-grouse or a subpopulation). Consequently, variables included in our analysis did not include all factors associated with smaller areas of fine-scale habitat use or subpopulation dynamics (Connelly et al. 2000c; Connelly et al., this volume, chapter 4). In addition, some variables potentially associated with population dynamics of sage-grouse at regional extents, such as livestock stocking rates and grazing systems, were not available in continuous coverage formats, and thus could not be considered for analysis.

Step 3: Sampling Design

We used historical locations of sage-grouse for analyzing differences in environmental variables between occupied and extirpated ranges. Historical locations came from two sources (Schroeder et al. 2004): museum specimens collected mostly during the early 1900s and published observations documented for this period. Historical locations represent documented areas of occurrence in pre-settlement range (Schroeder et al. 2004).

We used 375 of $>1,300$ historical locations after eliminating multiple collections or observations from the same locations and excluding locations or observations clearly outside the established pre-settlement range where individual birds may have occasionally occurred (Schroeder et al. 2004). Use of historical locations focused our analysis on documented areas of species occurrence before and during European settlement, in contrast to an analysis of randomly selected areas within pre-settlement range that might include regions not having direct physical evidence of species occurrence.

Each historical location was classified as occupied or extirpated range. A circle with an 18-km radius, encompassing an area of 101,740 ha, was then centered on each historical location (Fig. 18.1). Of the 375 historical locations, 239 were in occupied range and 136 were in extirpated

TABLE 18.1

Descriptions of the 22 environmental variables used in discriminant function analysis.

Estimates of the variables were made for the time period 2000–2004, and thus are compatible with the time period in which sage-grouse ranges were estimated (Schroeder et al. 2004). Estimates of the 22 variables were based on conditions within the circles of 18-km radius that encompassed each of the 375 historical locations of sage-grouse. Raster-based variables were derived or estimated using a 90 × 90-m cell size unless stated otherwise.

Variable	Type	Definition and estimation method
Sagebrush area (%)	Raster	Percentage of 18-km radius composed of sagebrush cover types ^a .
Patch size	Raster	Mean size (ha) of sagebrush patches, where a patch is defined as the cells of sagebrush cover types that are contiguous with one another (touching on at least one side) ^b .
Patch density	Raster	Number of sagebrush patches divided by the area ^b .
Edge density 1	Raster	Number of edges between sagebrush patches and non-sagebrush cover types, weighted by sagebrush area. Weighting by sagebrush area differentiates between a low number of edges when little sagebrush is present versus a low number of edges when sagebrush occupies most or all of the area. Resulting values were transformed as 1/n, such that high edge density indicates a high amount of edge, and low edge density indicates low edge ^b .
Edge density 2	Raster	Total length (m) of all edges between sagebrush patches and non-sagebrush cover types divided by area ^b .
Nearest neighbor	Raster	The mean distance (m) between sagebrush patches, where distance between each patch is measured as the shortest distance (edge to edge) to another patch within the circle ^{b, c} .
Proximity index	Raster	The mean proximity (unitless scale) among sagebrush patches. Mean proximity is calculated as the area of each sagebrush patch divided by the squared mean distance of all distances between the patch and all other patches in the circle, with these values summed for all patches in the circle and divided by the total number of patches ^b .
Core area	Raster	The mean size (ha) of core areas of sagebrush. A core area is defined as a sagebrush patch plus all additional cells of sagebrush within 100 m of the edge of each patch (i.e., all additional sagebrush within the distance of two cells from the edge of each sagebrush patch).
Distance to occupied–extirpated boundary	Vector	Distance (m) from the sage-grouse historical location (the center of each circle) to the boundary between occupied and extirpated range ^b .
Precipitation	Raster	Mean annual precipitation (cm) within each 18-km circle for the period 1961–2004. Precipitation estimates were derived from parameter-elevation regression on independent slopes model (PRISM), which uses point data and a digital elevation model (DEM) to generate grid-based estimates of annual, monthly, and event-based climatic parameters ^d .
Elevation	Raster	Mean elevation (m) among all cells, using a 1:24,000-scale digital elevation model downloaded from the United States Geological Survey National Elevation Dataset ^d .
Soil water capacity	Raster	The total amount of water available in all soil profiles (cm of water/cm of soil) for each cell, averaged over all cells. Estimates were derived from the USDA Natural Resources Conservation Service ^d .

TABLE 18.1 (continued)

TABLE 18.1 (CONTINUED)

Variable	Type	Definition and estimation method
Soil rock depth	Raster	The mean depth (cm) to bedrock, or soil depth, as averaged over all cells. Estimates were derived from the USDA Natural Resources Conservation Service ^d .
Soil salinity	Raster	The mean salinity (mmhos/cm) of soil, as averaged over all cells. Estimates were derived from the USDA Natural Resources Conservation Service ^d .
Agriculture area	Raster	Percentage of cells of agricultural cover types ^d .
Human density	Raster	Number of humans/ha in 2000 ^e .
Distance to roads	Vector	Distance (m) to the nearest road. All roads identified in the 2000 United States Census Bureau 1:100,000 scale line files ^d .
Road density	Vector	Linear km of road per unit area. All roads identified in the 2000 United States Census Bureau 1:100,000 scale line files ^d .
Distance to highways	Vector	Distance (m) to the nearest major highway ^f .
Distance to transmission lines	Vector	Distance (m) to the nearest electrical transmission line.
Distance to cellular towers	Vector	Distance (m) to the nearest cellular tower, based on locations of towers registered with the Federal Communications Commission.
Land ownership	Raster	Dominant land ownership, either public or private, based on state and federal sources of ownership data ^d . These data were summarized as the percentage of circles dominated by public land.

^a Sagebrush cover types were defined and estimated by Comer et al. (2002) and further described by Wisdom et al. (2005b).

^b Landscape statistics estimated using FRAGSTATS (McGarigal et al. 2002).

^c Gustafson and Parker (1994).

^d Data available at <http://sagemap.wr.usgs.gov>.

^e United States census block data (United States Census Bureau 2001).

^f Major highways documented in the National Atlas (<http://nationalatlas.gov/>) (Comer et al. 2002, Wisdom et al. 2005b).

range. Portions of some of the associated circles overlapped the boundary between occupied and extirpated ranges. We retained these locations for analysis because the majority of area in the circle was always in the same portion of range as its historical location, and we wanted to include the full spectrum of environmental conditions across areas far from, and close to, the occupied–extirpated range boundary.

Step 4: Environmental Conditions

We used each historical location and associated 18-km radius as our unit of observation to analyze conditions for each environmental variable in occupied versus extirpated range (Table 18.1). For this analysis, we first calculated the composite

value of each environmental variable within each circle. The composite value was the average of all values for a variable that composed the cells, polygons, or contours within the circle. We then calculated the mean and associated 95% confidence interval (CI) for the composite values among all circles associated with occupied ($N = 239$) and extirpated range ($N = 136$) (Fig. 18.1).

We treated each circle as a sample unit, although most (279 of 375) circles overlapped one another on their outer edges. However, most of the area within circles did not overlap other circles (\bar{x} overlap = 22%). Moreover, circle overlap occurred most often along the occupied–extirpated range boundary, where we chose to retain circles because of their contribution to the occupied–extirpated gradient.

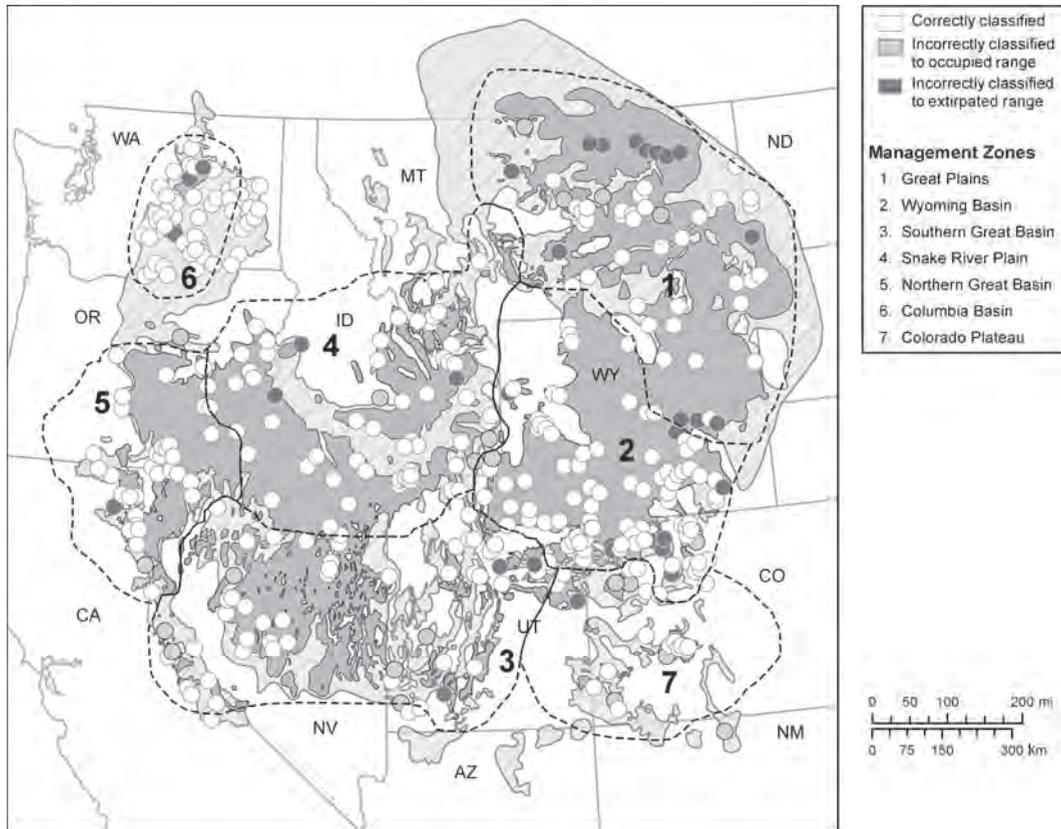


Figure 18.1. Distribution of 375 historical locations (circles) of sage-grouse (Schroeder et al. 2004). Locations are overlaid on occupied (dark grey) and extirpated (light grey) ranges of sage-grouse. Shaded locations represent the classification accuracy of discriminant function analysis (model 2, Table 18.3). Black locations are those present in occupied range but incorrectly classified to extirpated range. Grey locations are those present in extirpated range but incorrectly classified to occupied range. White locations were correctly classified to occupied and extirpated ranges.

Step 5: Discriminant Analysis

We used discriminant function analysis (DFA; SAS Institute 1990) to identify which environmental variables discriminated best between historical locations in occupied versus extirpated range. Discriminant function analysis is an appropriate method for discriminating between two or more groups when variables used for discrimination are quantitative and normally distributed (Hair et al. 1992). When these assumptions are met, DFA generally has more discriminatory power than analogues such as logistic regression (Efron 1975). Prior probabilities of classification were set proportional to sample sizes in occupied and extirpated ranges. Variance-covariance structure for the two classification groups were not pooled (i.e., we used quadratic discriminant

functions), as recommended when equal variances between groups is not assured (SAS Institute 1990, Hair et al. 1992). Examination of the frequency distributions of each variable showed that data were normally distributed for all variables within both classification groups, thus meeting this assumption. Discriminatory variables also should not be highly correlated if stepwise procedures are used. Correlation coefficients among all discriminatory variables were <0.35 , positive or negative, indicating that stepwise procedures could be used.

Results from the discriminant function analysis were used in cross-validation analysis by withholding data for a different circle for each run to jackknife the assessment of classification accuracy of each combination of discriminatory variables in a given model (SAS Institute 1990, Hair

et al. 1992). Results were expressed as the percentage of locations correctly classified to occupied range, to extirpated range, and incorrectly classified to each (SAS Institute 1990).

We used cross-validation results to rank model performance. First, we summed the percentage of historical locations correctly classified to occupied or extirpated range to obtain a cumulative percentage of correct classifications (Table 18.2). For a model to perform perfectly, the cumulative percentage would be 200%—100% of locations correctly classified to occupied range and to extirpated range. Second, we subtracted the percentage of locations correctly classified to occupied range from the percentage correctly classified to extirpated range. This absolute difference measured the evenness of correct classifications between occupied and extirpated ranges. The best evenness value would be 0, indicating that a model was equally consistent in correct classifications between occupied and extirpated ranges. Third, we subtracted the evenness value from the cumulative percentage of correct classifications. This difference, or performance value, provided an overall measure of model performance, considering both accuracy and evenness of classifications (Table 18.2). For example, a given model might correctly classify 100% of locations associated with occupied range but only 75% of locations associated with extirpated range, yielding a cumulative percentage of 175, an evenness of 25, and an overall performance value of 150. By contrast, a second model that correctly classified 90% of locations to occupied range and 85% of locations to extirpated range also results in a cumulative percentage of 175, but an evenness of 5, and an overall performance value of 170. The second model has a higher performance value, owing to its superior capability to correctly classify locations to both occupied and extirpated ranges.

We used this process to evaluate DFA models containing different combinations of the 22 discriminatory variables. The combinations included evaluation of: (1) each environmental variable individually; (2) biotic variables as a group; (3) abiotic variables as a group; (4) anthropogenic variables as a group; (5) all combinations of the three groups of biotic, abiotic, and anthropogenic variables; (6) all variables that had nonoverlapping 95% confidence intervals between their

mean values for occupied versus extirpated ranges; (7) all groups of variables whose individual performance values were ≥ 75 and ≥ 100 ; and (8) all variables identified in forward stepwise DFA (Hair et al. 1992) as statistically significant ($P < 0.05$) discriminators. All of these DFA models were identified a priori of any modeling results.

Step 6: Spatial Modeling

The combination of variables with highest performance value in discriminating between extirpated and occupied ranges was used in a predictive DFA to estimate the probability that different regions of occupied range had environmental conditions similar to conditions in extirpated range. Our purpose was to identify and map areas of occupied range where environmental conditions indicated that sage-grouse may be at higher risk of regional extirpation, versus areas with conditions likely to serve as regional strongholds for population persistence.

We first subdivided the occupied range into 100,000-ha blocks. These blocks were compatible in size with the circular areas used to evaluate performance of various models at historical locations, and likewise compatible with regional effects on sage-grouse. We then applied the model to each of 2,661 blocks that encompassed occupied range. Results were expressed as the probability of environmental similarity of a given block of occupied range with conditions in extirpated range.

The probability of similarity for each block was placed in one of six categories: 0.0–0.10, >0.10–0.25, >0.25–0.50, >0.50–0.75, >0.75–<0.90, and 0.90–1.0. These categories were most narrow for the lowest and highest probabilities because these values represent extreme conditions where similarity to extirpated range is either highly probable or improbable. Categories for intermediate probability values were wider, reflecting higher uncertainty about environmental differences between occupied and extirpated ranges. We summarized results by these categories across occupied range within each Sage-Grouse Management Zone (SMZ; Stiver et al. 2006). We also mapped similarity values as a continuous variable by state and SMZ to compare and contrast these results with values summarized by categories.

TABLE 18.2
Classification accuracy and resulting performance of biotic, abiotic, and anthropogenic variables contained in discriminant function models that were used to discriminate between historical locations of sage-grouse in occupied versus extirpated ranges under cross-validation.

See methods for details regarding cross-validation.

Discriminatory variables	Correctly classified to occupied range (%) ^a	Correctly classified to extirpated range (%) ^a	Total % correctly classified ^b	Evenness of correctly classified ^c	Performance value (rank) ^d
Sagebrush area (%) ^{e, f}	76	65	141	11	130 (2)
Patch density	100	0	100	100	0
Patch size ^f	41	96	137	55	82 (8)
Edge density 1	98	6	104	92	12 (17)
Edge density 2 ^e	96	4	100	92	8 (18)
Proximity index ^f	35	86	121	51	70 (12)
Nearest neighbor	99	0	99	99	0
Mean core area ^f	39	95	134	56	78 (11)
Distance to occupied–extirpated boundary ^{e, f}	92	24	116	68	48 (16)
All biotic variables	52	92	144	40	104 (6)
Precipitation	98	0	98	98	0
Elevation ^{e, f}	85	50	135	35	100 (8)
Soil water capacity ^f	90	29	119	61	58 (13)
Soil rock depth	100	0	100	100	0
Soil salinity ^{e, f}	100	0	100	100	0

TABLE 18.2 (continued)

TABLE 18.2 (CONTINUED)

Discriminatory variables	Correctly classified to occupied range (%) ^a	Correctly classified to extirpated range (%) ^a	Total % correctly classified ^b	Evenness of correctly classified ^c	Performance value (rank) ^d
All abiotic variables	89	47	136	42	94 (9)
All biotic and abiotic variables	54	92	146	38	108 (5)
Agriculture area (%) ^f	92	40	132	52	80 (10)
Distance to roads	100	0	100	0	0
Human density ^f	99	25	124	74	50 (15)
Road density ^{e, f}	93	28	121	65	56 (14)
Distance to highways ^f	100	0	100	0	0
Distance to transmission lines ^{e, f}	64	63	127	1	126 (4)
Distance to cellular towers ^{e, f}	81	51	132	30	102 (7)
Land ownership ^f	64	74	138	10	128 (3)
All anthropogenic variables	96	42	138	54	84 (10)
All anthropogenic and abiotic variables	94	52	146	42	104 (6)
All anthropogenic and biotic variables	75	81	156	6	150 (1)

^a Percentage of historical locations in currently occupied or extirpated range correctly classified to that range based on the associated discriminatory variable or variables using cross-validation.

^b Sum of correct classification percentages for occupied and extirpated ranges based on the associated discriminatory variable or variables.

^c Absolute difference between percentages of locations correctly classified to occupied versus extirpated ranges.

^d Performance value is the evenness subtracted from total percent correctly classified. A value of 200 represents highest performance, which is possible if all locations are correctly classified to occupied (100%) and to extirpated (100%) ranges, for a total percent of 200 and an evenness of 0 (100% minus 100%). Variables are ranked, shown in parentheses, according to their performance values, with a rank of 1 representing the best performance considering all discriminant function models listed in Table 18.2. Each line of the table represents a discriminant function model that was evaluated.

^e Variables with significant discriminatory value ($P < 0.05$) as estimated by forward stepwise discriminant analysis.

^f Variables with non-overlapping 95% confidence intervals between mean values in occupied versus extirpated ranges (Figs. 18.2–18.4).

RESULTS

Differences Between Extirpated and Occupied Ranges

Fifteen of the 22 environmental variables had mean values with nonoverlapping 95% CIs between extirpated and occupied ranges (Figs. 18.2–18.4). These variables included five biotic, three abiotic, and seven anthropogenic variables.

The five significant biotic variables were sagebrush area, patch size of sagebrush, proximity of sagebrush patches, size of sagebrush core areas, and distance to the boundary between occupied and extirpated ranges. Historical locations in occupied range contained almost twice as much area in sage-

brush as those in extirpated range (Fig. 18.2). Mean patch size of sagebrush was >9 times larger, and mean core area >11 times larger, in occupied versus extirpated range (Fig. 18.2). Sagebrush patches also were substantially closer to one another in occupied range (Fig. 18.2). In addition, historical locations in occupied range were closer to the boundary between occupied and extirpated ranges than locations in extirpated range (Fig. 18.2).

The three significant abiotic variables were elevation, soil water capacity, and soil salinity. Elevation was almost 50% higher in occupied range than in extirpated range (Fig. 18.3). Occupied range had lower soil water capacity and higher soil salinity (Fig. 18.3).

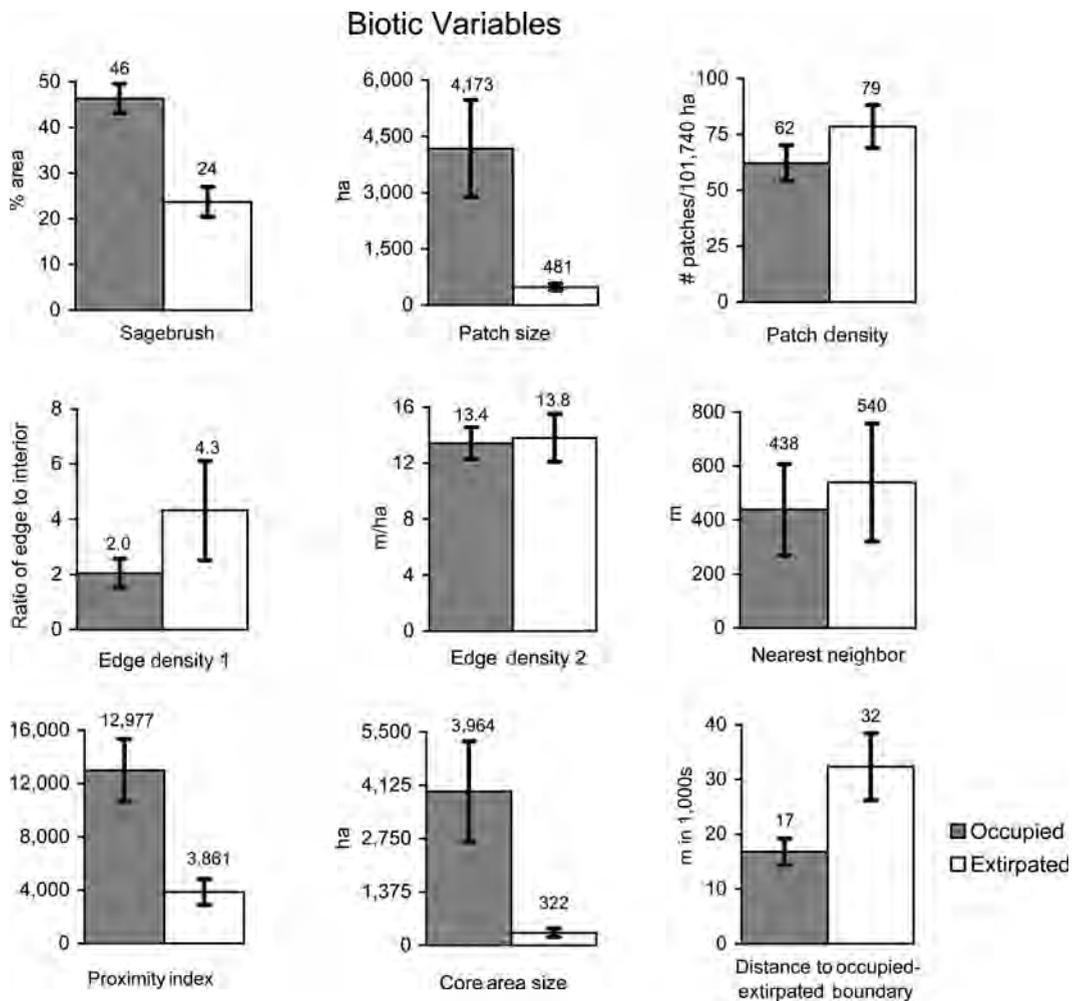


Figure 18.2. Mean values and 95% confidence intervals for nine biotic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

Abiotic Variables

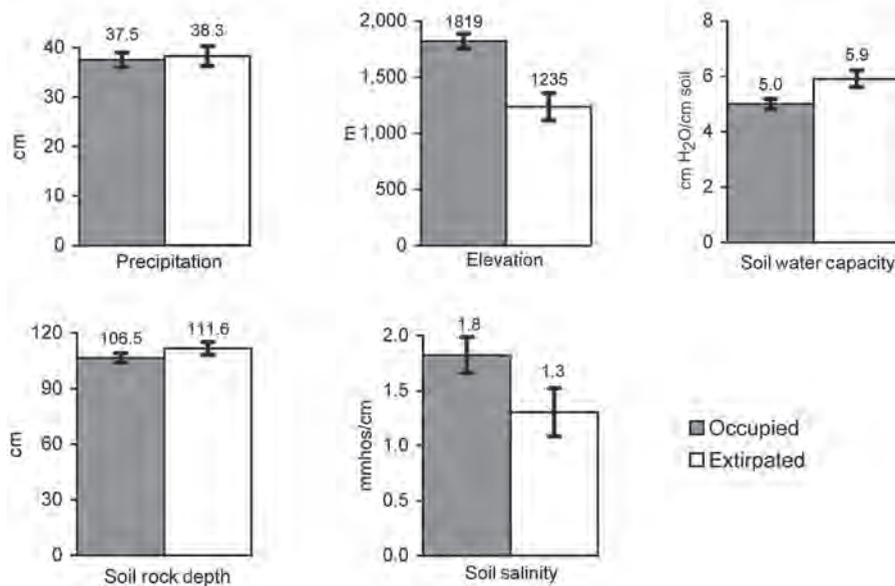


Figure 18.3. Mean values and 95% confidence intervals for five abiotic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

The seven significant anthropogenic variables were area in agriculture, human density, road density, distance to highways, distance to electric transmission lines, distance to cellular towers, and landownership. Area in agriculture was almost three times lower and mean human density was 26 times lower in occupied than in extirpated range (Fig. 18.4). Road density also was lower and highways substantially farther from historical locations in occupied range (Fig. 18.4). Mean distance to electric transmission lines was >2 times farther in occupied range than in extirpated range (Fig. 18.4). The distance to cellular towers averaged almost twice as far in occupied range (Fig. 18.4). Occupied range also had substantially more public ownership (Fig. 18.4); 64% of circles encompassing historical locations in occupied range were dominated by public ownership compared to 26% in extirpated range.

Environmental Discrimination Between Extirpated and Occupied Ranges

Individual Variables and Biotic, Abiotic, and Anthropogenic Groups

We first evaluated performance of DFA models containing individual discriminatory variables and those containing all combinations of biotic,

abiotic, and anthropogenic groups of variables (Table 18.1). The best-performing of these models contained all biotic and anthropogenic variables, which correctly classified 72% of historical locations to occupied range and 80% to extirpated range (Table 18.2). The second-best model contained just one variable, sagebrush area, which correctly classified 76% of historical locations to occupied range and 65% to extirpated range. The landownership model had third-best performance, followed by models containing distance to transmission lines, all biotic and abiotic variables, distance to cellular towers, elevation, all biotic variables, and all anthropogenic and abiotic variables (Table 18.2). Additional models containing the remaining individual variables performed poorly as discriminators between occupied and extirpated ranges (Table 18.2).

Best-Performing Combinations of Variables

We evaluated four additional models that contained combinations of variables with potential for high classification accuracy (Table 18.3), based on our a priori modeling approaches described in step 5 of Methods. The best-performing model, model 2, contained just five variables: sagebrush area, elevation, distance to transmission lines,

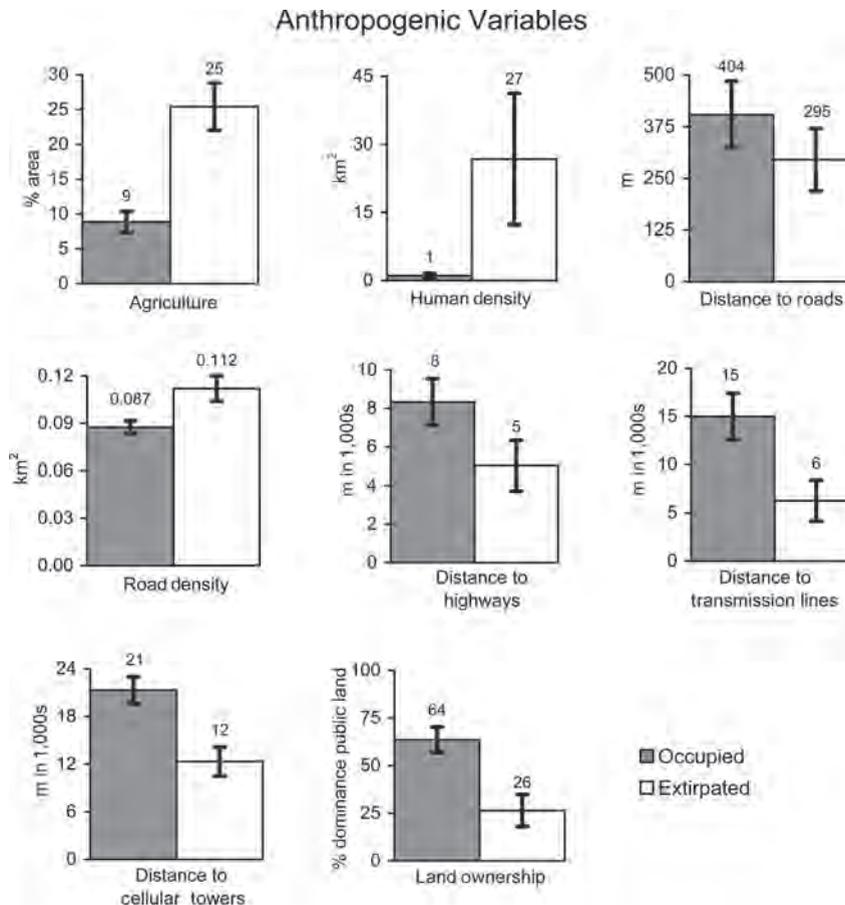


Figure 18.4. Mean values and 95% confidence intervals for eight anthropogenic variables associated with 239 historical locations in occupied range and 136 historical locations in extirpated range for sage-grouse.

distance to cellular towers, and landownership (Table 18.3). This model correctly classified 85% of locations to occupied range and 83% to extirpated range (performance value 166; Table 18.3). Model 4, which contained the 15 variables with nonoverlapping confidence intervals between mean values in occupied and extirpated ranges, performed slightly worse than model 2 (performance value 154) and substantially better than models 1 and 3 (Table 18.3). Both models 2 and 4 outperformed all single-variable models and all models based on biotic, abiotic, and anthropogenic groups of variables (Tables 18.2, 18.3).

Nearly all errors in correctly classifying historical locations to occupied and extirpated ranges with model 2, our best-performing model, occurred under two conditions: they were located in the Great

Plains SMZ ($N = 17$), or they were substantially closer to the boundary between occupied and extirpated ranges ($N = 41$) (Fig. 18.1). Locations incorrectly classified to occupied and extirpated ranges and not within the Great Plains SMZ were <10 km from the boundary between occupied and extirpated ranges. By contrast, $>80\%$ of correctly classified locations were >20 km from the boundary between occupied and extirpated ranges. Incorrectly classified locations close to the occupied–extirpated range boundary had large portions of the associated circles that overlapped both occupied and extirpated ranges. Thus, locations associated with these circles represented a mix of conditions from both ranges. As a result, performance of model 2 was diminished with the inclusion of these circles that overlapped both classification groups (occupied versus

TABLE 18.3

Classification accuracy and performance of four models used to discriminate between historical locations of sage-grouse in occupied versus extirpated range using cross-validation.

Discriminatory variables in each model were selected using different criteria (see table notes).

Discriminatory models	Correctly classified to occupied range (%)	Correctly classified to extirpated range (%)	Total % correctly classified	Evenness of correctly classified	Performance value ^a
Model 1 ^b					
SB, PS, MCA, E, AA, DL, CT, LO	54	93	147	39	106
Model 2 ^b					
SB, E, TL, CT, LO	85	83	168	2	166
Model 3 ^c					
SB, ED, RB, E, S, RD, TL, CT	90	70	160	20	140
Model 4 ^d					
SB, PS, PI, MCA, RB, E, SWC, S, AA, HD, RD, DH, TL, CL, LO	77	88	165	11	154

ABBREVIATIONS: Variables used in one or more of the models included sagebrush area (SB), patch size (PS), edge density 2 (ED2), proximity index (PI), mean core area (MCA), distance to occupied–extirpated range boundary (RB), elevation (E), soil salinity (S), soil water capacity (SWC), agriculture area (AA), road density (RD), human density (HD), distance to highways (DH), distance to transmission lines (TL), distance to cellular towers (CL), and land ownership (LO).

^a Evenness subtracted from total percent correctly classified.

^b Models 1 and 2 included variables with individual performance values ≥ 75 and ≥ 100 (Table 18.1).

^c Model 3 contained variables selected under stepwise discriminant analysis.

^d Model 4 included the 15 variables with non-overlapping 95% confidence intervals between mean values in occupied versus extirpated ranges (Figs. 18.2–18.4).

extirpated ranges). However, classification accuracy was high for model 2 (>80%; Table 18.3) despite the inclusion of these circles along the occupied–extirpated range boundary.

Similarity of Occupied Range with Extirpated Range

Estimates based on application of model 2 to all 100,000-ha blocks of occupied range showed that similarity to extirpated range was highest along most range peripheries (Fig. 18.5). Similarity to extirpated range also was highest in the smaller, disjunct areas of occupied range in Washington, southwest Oregon, northeast California, Idaho, northeast Utah, southern Montana, and in larger areas of east-central Montana and eastern and north-central Wyoming (Fig. 18.5).

Environmental similarity to extirpated range was lowest in the expansive area of occupied range in southeast Oregon, southwest Idaho, northern and east-central Nevada, and west-central and southwest Wyoming (Fig. 18.5); these areas compose the largest, most contiguous blocks of occupied range of Greater Sage-Grouse. By contrast, the small, disjunct areas occupied by Gunnison Sage-Grouse in southeast Utah and southern Colorado had similarity values that were mostly intermediate with those of extirpated range (Fig. 18.5).

The Columbia Basin had the highest percentage of environmental similarity with extirpated range: 65% of the zone was in the two highest similarity classes (probabilities >0.75) and mostly in the highest class (0.90–1.0; Fig. 18.5, Table 18.4). The Great Plains had the next-highest percentage of occupied range in the two highest similarity

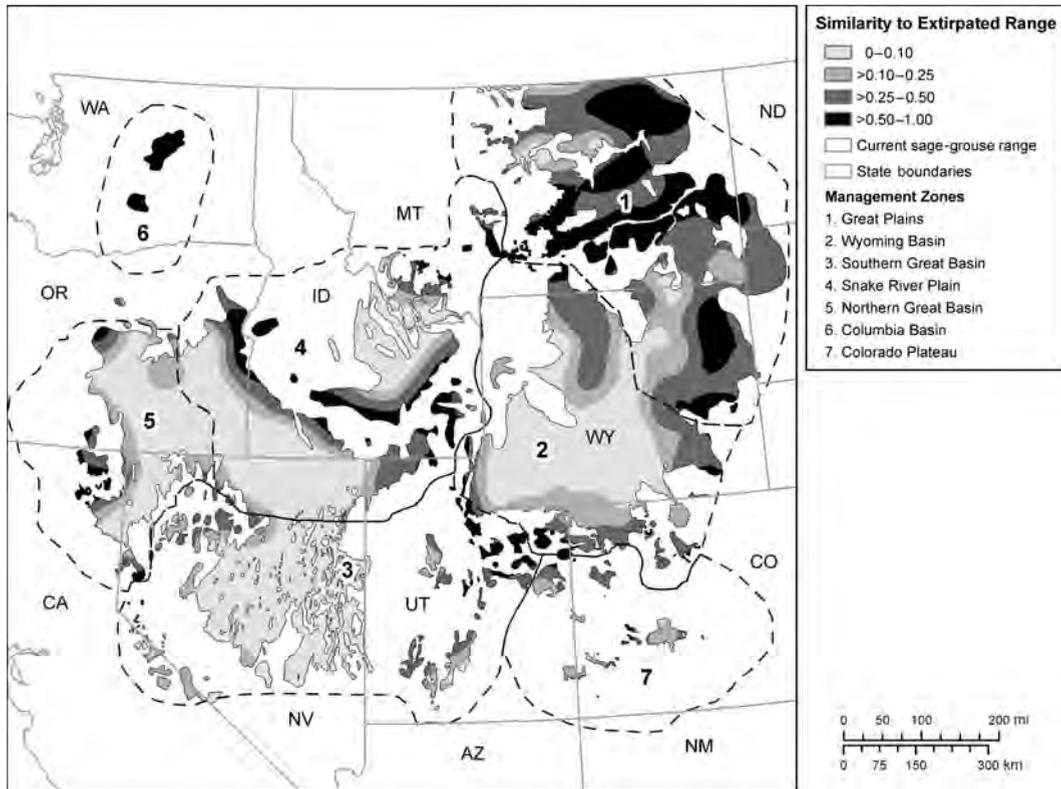


Figure 18.5. Probabilities of environmental similarity of areas currently occupied by sage-grouse with areas where extirpation has occurred, based on estimates from model 2 discriminant function analysis. Probabilities range from 0.0–1.0 and are mapped as a continuous variable. Areas in black show high similarity with extirpated range. Areas in light grey show low similarity.

classes (37%), followed by Colorado Plateau at 10% (Table 18.4). SMZs with lowest similarity to extirpated range were Northern Great Basin, Southern Great Basin, Snake River Plain, and Wyoming Basin. The large majority of occupied range in these four SMZs had probabilities of similarity of ≤ 0.10 . All four, however, had high similarity with extirpated range along range peripheries or in smaller, disjunct areas (Fig. 18.5).

DISCUSSION

Factors Associated with Extirpation

Biotic Variables

Sage-grouse occupation versus extirpation was strongly associated with measures of sagebrush abundance and distribution, including sagebrush area, patch size, proximity of patches, and size of core areas. These results support past studies that identified sage-grouse as a sagebrush obligate,

dependent on sagebrush for persistence (Braun et al. 1976, Schroeder et al. 1999, Rowland 2004).

Sagebrush area was the single best discriminator between occupied and extirpated ranges among the 22 variables evaluated. The DFA model containing this single variable was one of the top-performing models. These results agree with recent findings that sagebrush area is one of the best landscape predictors of sage-grouse persistence (Wisdom et al. 2002c; Walker et al. 2007a, Doherty et al. 2008, Aldridge et al. 2008).

The upper 95% CI for sagebrush area in extirpated range was 27%. Landscapes occupied by sage-grouse with sagebrush $< 27\%$ would thus have a $> 97.5\%$ probability of being no different than a random sample of extirpated ranges, suggesting that associated populations in these occupied ranges could be more vulnerable to extirpation. Similarly, the lower 95% CI for sagebrush area in occupied range was 50%. Landscapes occupied by sage-grouse with values above this lower bound thus have a $> 97.5\%$ probability of being no different than a

TABLE 18.4
Percent area of occupied range by categories of the probability of similarity with extirpated range, summarized by Sage-Grouse Management Zone.
 Probabilities of similarity are summarized in six categories: (1) 0.0–0.10; (2) >0.10–0.25; (3) >0.25–0.50; (4) >0.50–0.75;
 (5) >0.75–<0.90; and (6) 0.90–1.0. Probabilities were estimated for each of 2,661 100,000-ha
 blocks that encompass the occupied range of sage-grouse.

Sage-Grouse Management Zone	Categories of similarity to extirpated range												
	1 (0.0–0.10)		2 (>0.10–0.25)		3 (>0.25–0.50)		4 (>0.50–0.75)		5 (>0.75–<0.90)		6 (0.90–1.0)		
	ha	% area	ha	% area	ha	% area	ha	% area	ha	% area	ha	% area	Total area
Great Plains	9,783,456	49.9	876,405	4.5	962,934	4.7	778,925	4.0	1,068,834	5.4	6,176,855	31.5	19,611,209
Wyoming Basin	11,176,049	76.4	1,088,868	7.4	781,287	5.3	359,034	2.5	502,765	3.4	715,584	4.9	14,623,587
Southern Great Basin	8,426,483	82.2	756,360	7.4	336,628	3.3	454,331	4.4	108,158	1.1	175,149	1.7	10,257,109
Snake River Plain	11,531,252	79.7	451,982	3.1	555,622	3.8	434,949	3.0	443,068	3.1	1,044,541	7.2	14,461,414
Northern Great Basin	5,978,359	86.4	211,164	3.1	203,219	2.9	102,251	1.5	134,475	1.9	286,249	4.1	6,915,717
Columbia Basin	69,720	14.7	0	0.0	0	0.0	97,724	20.6	84,004	17.7	222,305	46.9	473,753
Colorado Plateau	507,907	56.2	174,546	19.3	36,991	4.1	94,962	10.5	52,531	5.8	36,666	4.1	903,603

random sample of occupied ranges, suggesting a higher capability to support persistent populations.

Recent landscape studies of Greater Sage-Grouse identified similar threshold values for sagebrush area to maintain population persistence. Aldridge et al. (2008:990), using a 30.77-km radius around sampling locations, estimated that at least 25% and preferably 65% of the landscape needed to be dominated by sagebrush for long-term sage-grouse persistence. These estimates mirror our values of 27% and 50% for sagebrush area, with values <27% indicating a high risk of extirpation, and values above 50% indicating a high probability of persistence. Our estimates also are for large landscapes, based on the 18-km radius circles that we analyzed. Similarly, Walker et al. (2007a) estimated that the lowest probability of lek persistence, approximately 40–50%, occurred for landscapes with <30% area in sagebrush within 6.4 km of a lek center. These probabilities declined even more for landscapes with <30% sagebrush that were subjected to energy development (see fig. 5 in Walker et al. 2007a).

Abiotic Variables

Three abiotic variables—elevation, soil salinity, and soil water capacity—also differed between occupied and extirpated ranges. Elevation was a good discriminator, probably because most sagebrush loss has occurred disproportionately at lower elevations where human activities and developments have been concentrated (Hann et al. 1997; Knick et al., this volume, chapter 12; Leu and Hanser, this volume, chapter 13), and where invasive grasses have displaced large areas of sagebrush (Suring et al. 2005b, Meinke et al. 2009). Lower soil salinity and higher soil water capacity in extirpated range also indicate a higher suitability for agricultural development (Knick, this volume, chapter 1), which also was associated with sage-grouse extirpation.

Anthropogenic Variables

Seven of the eight anthropogenic variables differed between occupied and extirpated ranges. The number of these variables, their diversity, and the strength of differences between occupied and extirpated ranges suggest that a variety of human activities and land uses have contributed to or been associated with sage-grouse extirpation. This inference agrees with findings from recent landscape studies that documented negative effects of anthropogenic

variables on sage-grouse populations, including human density and percent agriculture (Aldridge et al. 2008), roads and traffic (Lyon and Anderson 2003, Holloran 2005), and energy development (Holloran 2005; Aldridge et al. 2007; Walker et al. 2007a; Doherty et al. 2008; Naugle et al., this volume, chapter 20). We did not specifically evaluate energy development. However, extirpated range contained almost 27 times the human density, had almost three times more area in agriculture, was 60% closer to highways, and had 25% higher density of roads, in contrast to occupied range. These patterns agree with research cited above that evaluated these or similar variables. Moreover, the four variables of human density, area in agriculture, distance to highways, and road density were part of model 4, which outperformed all models except the top-ranked model 2.

Three additional anthropogenic variables—distance to transmission lines, distance to cellular towers, and landownership—also differed between occupied and extirpated ranges. These variables were the best discriminators among the eight anthropogenic variables considered and ranked among the best of all individual variables. These variables have received little attention in landscape research on sage-grouse—only distance to transmission lines has been formally evaluated (Connelly et al. 2000a, Aldridge and Boyce 2007, Walker et al. 2007a). Transmission lines can cause sage-grouse mortality via bird collisions with lines (Beck et al. 2006, Aldridge and Boyce 2007) and facilitate raptor predation of sage-grouse (Connelly et al. 2000a). In addition, the electromagnetic radiation emitted from transmission lines has a variety of negative effects on other bird species using areas on or near lines (Fernie and Reynolds 2005). Moreover, transmission lines convert habitat to nonhabitat and fragment the remaining habitat, similar to roads (Naugle et al., this volume, chapter 20).

The strong association between distance to cellular towers and sage-grouse extirpation was an especially intriguing result, given that no previous studies of sage-grouse have evaluated this variable. Whether cellular towers function in a cause-effect manner or simply are aligned with other detrimental factors cannot be addressed without additional research. Recent studies, however, suggest possible cause-effect relationships between high levels of electromagnetic radiation within 500 m of cellular towers and reduced population or reproductive performance of a limited

number of bird and amphibian species (Balmori 2005, 2006; Balmori and Hallberg 2007; Everaert and Bauwens 2007). These negative effects are similar to those documented for bird species exposed to electromagnetic radiation generated by power lines (Ferne and Reynolds 2005). Cellular towers also are likely to cause sage-grouse mortality via collisions with these structures or influence movements by visual obstruction, but no research has investigated these issues.

Distance to cellular towers may also indicate the most intensive human developments and uses, given that cellular towers are concentrated along major highways and within and near larger towns and cities across the range of sage-grouse. Although correlation coefficients between this and the other environmental variables were low, cellular towers represent discrete points within areas of high human use. Consequently, distance to cellular towers may serve as a finely measured indicator of more concentrated human uses, in contrast to other anthropogenic variables that reflect more general landscape measures of human uses. This pattern would explain the variable's low correlation with other anthropogenic variables yet high discriminatory performance.

Landownership also was an ideal indicator of underlying causes of sage-grouse extirpation, given that many private lands have been converted from sagebrush to other land uses (Vander Haegen 2007; Knick et al., this volume, chapter 12). In addition, the conversion of private lands to nonsagebrush land uses has fragmented remaining sagebrush habitats nearby (Vander Haegen et al. 2000) and facilitated the spread of exotic plants in sagebrush habitats near such conversions (Hann et al. 1997; Wisdom et al. 2005a,c).

Combinations of Biotic, Abiotic, and Anthropogenic Variables

Performance of the many discriminant function models, each containing different combinations of environmental variables, largely reflected differences in individual variables between occupied and extirpated ranges. Models that performed best either contained all 15 variables whose mean values had nonoverlapping confidence intervals between occupied and extirpated ranges—model 4—or contained a subset of five of those variables (sagebrush area, elevation, distance to transmission lines, distance to cellular towers, and

landownership) that provided highly distinct and precise differences between ranges—model 2. The superior performance of models 2 and 4 suggests that different combinations of the 15 environmental variables could be used as effective predictors of sage-grouse vulnerability to extirpation for current or projected landscape conditions. These results also clearly demonstrate that sage-grouse extirpation is associated with a varied combination of biotic, abiotic, and anthropogenic influences, and that holistic consideration of these many environmental factors in land management appears important to maintain persistent populations at large landscape extents like those studied here.

Geographic Patterns of Environmental Similarity with Extirpated Range

Our estimates of environmental similarity of areas occupied by sage-grouse to areas where extirpation has occurred have direct implications for range-wide conservation planning. First, populations along the peripheries of occupied range may have a higher risk of extirpation. This higher risk is an expected extension of past extirpation patterns that have largely occurred from the outside inward. That is, sage-grouse extirpation has occurred mostly along the outer portions of pre-settlement range and contracted inward (Schroeder et al. 2004, Aldridge et al. 2008). Most areas along the outer portion of pre-settlement range are at lower elevations where land uses and habitat conversions have been concentrated, particularly on private lands. Moreover, this pattern is expected because populations on the periphery of their range immediately adjacent to areas where extirpation has occurred often are more vulnerable to extirpation than populations closer to the center when anthropogenic factors disproportionately affect the periphery (Brown et al. 1996, Laliberte and Ripple 2004). This is the case for sage-grouse. By contrast, this may not be the case for declining populations of other species when peripheral areas provide refuge from habitat degradation occurring in core areas (Lomolino and Channell 1995, 2000).

Populations of many species at high risk along range peripheries may undergo extirpation during periods of high environmental variation, such as during a severe and prolonged drought. Extirpation also may occur in such areas when a combination of environmental, genetic, stochastic, and demographic sources of variation manifest

over time in ways not easily predicted (Mills 2007). Populations in the periphery of a species range typically experience high temporal variation in abundance in contrast to core populations (Vucetich and Waite 2003); this variation may reflect the many sources of variation described above that contribute to extirpation in small populations of sage-grouse.

Second, populations in small, disjunct areas of occupied range may have a high risk of extirpation. This pattern also is expected, given principles of population viability, which have consistently shown that extinction probability increases for populations that become increasingly small and isolated (Purvis et al. 2000). Populations of Greater Sage-Grouse occupying small, disjunct areas in Washington, northeast California, southwest Oregon, north-central Idaho, eastern Idaho, northeast Utah, and southern Montana, which are separated from larger core populations, fit these conditions.

Third, populations in many areas of occupied range in the Great Plains may have a higher risk of extirpation. This result is not unexpected, given the relatively low sagebrush area in the Great Plains (Knick, this volume, chapter 1), which is dominated more by grasslands (Küchler 1964, 1970; McArthur and Ott 1996). In addition, the southern part of the Great Plains has been altered by extensive energy development, resulting in extensive sagebrush loss and concomitant development of roads, power lines, and other infrastructure (Walker et al. 2007a; Walker 2008; Naugle et al., this volume, chapter 20). Energy development in Wyoming has progressed, at varying rates in relation to varying energy prices, for many decades (Braun et al. 2002; Naugle et al., this volume, chapter 20). Consequently, long-term changes in sage-grouse environments based on energy development in the Wyoming portion of the Great Plains were reflected through the early 2000s in our estimates of sagebrush area and distance to transmission lines—two of the five discriminatory variables included in model 2 that we used to estimate environmental similarity with areas where extirpation has occurred.

Given that sagebrush is substantially less common in the Great Plains in contrast to other areas of sage-grouse range (Knick, this volume, chapter 1), our analyses suggest that sage-grouse in this zone may be vulnerable to further reductions in sagebrush area. Additional loss of sagebrush in the Great Plains would approach potential thresholds for sage-grouse extirpation faster

than in other areas where sagebrush dominates a larger proportion of the landscape. Our results also indicate that other detrimental factors are at play in the Great Plains.

Finally, our mapped estimates of similarity could be used to identify strongholds for sage-grouse, that is, areas of occupied range where the risk of extirpation appears low (e.g., areas with similarity values ≤ 0.10 ; Fig. 18.5) and those that compose the largest areas of contiguous range. Two large strongholds for Greater Sage-Grouse are evident. One, a western stronghold, is the extensive, contiguous area encompassing south-east Oregon, northwest Nevada, southwest Idaho, northeast Nevada, and east-central Nevada that includes most areas in the Northern Great Basin, Southern Great Basin, and Snake River Plain SMZs—the lightest grey areas within these zones in Fig. 18.5. The other, an eastern stronghold, is the area encompassing south-central and southwest Wyoming in the Wyoming Basin SMZ. This second stronghold is approximately one-half the size of the western stronghold. In addition, an area in east-central Idaho has low similarity to extirpated range (Fig. 18.5) but is smaller than either of the two primary strongholds.

No strongholds are evident for Gunnison Sage-Grouse that consist of expansive, contiguous areas where similarity with extirpated range is ≤ 0.10 (Fig. 18.5). Intensive management to conserve existing habitats and populations of the species, combined with efforts to restore habitats, are obvious needs for Gunnison Sage-Grouse (Oyler-McCance et al. 2001, 2005a; Lupis et al. 2006).

Our documented spatial patterns of environmental similarity with extirpated range are similar to recent range-wide estimates of sage-grouse persistence (Aldridge et al. 2008). Similarities between these separate analyses are particularly compelling, given that different methods and variables were used. In that regard, our spatial estimates of environmental similarity with extirpated range, and those of persistence by Aldridge et al. (2008), are mutually reinforcing, thus providing a stronger basis for inferences made from each study (Johnson et al. 2002).

Spatial Priorities for Management

Our mapped estimates of environmental similarity of areas currently occupied by sage-grouse with areas where extirpation has occurred could

be used to help establish management priorities across existing sage-grouse range. Strongholds identified from our analysis are potential areas of focus for maintenance and improvement over time. Management emphasis on strongholds is more effective and efficient than devoting limited resources to restoration of areas where populations are at high risk of extirpation because of widespread habitat deficiencies (Wisdom et al. 2005c; Meinke et al. 2009; Doherty et al., this volume, chapter 21). In the latter situation, it is highly uncertain as to whether populations can persist, or how effective it would be to use limited resources in an attempt to improve a myriad of challenging environmental conditions to assure population persistence. This uncertainty revolves around three related issues: (1) areas with high similarity to extirpated range could be population sinks, given that these areas are mostly along the boundary with extirpated range, and range contraction along this boundary appears to be an ongoing process for sage-grouse; (2) areas with high similarity to extirpated range are associated with a variety of anthropogenic management challenges that may be difficult or impossible to mitigate (e.g., minimizing current infrastructure of roads, highways, transmission lines, cellular towers, and agricultural and urban areas that dominate these areas), thus negating benefits to restore sagebrush, which also is deficient in these areas; and (3) areas with high similarity to extirpated range are mostly at lower elevations characterized by warmer conditions that have low resistance to exotic plant invasions and low resiliency for returning to native vegetation states following any natural or human-caused disturbances, including restoration treatments (Wisdom et al. 2005c, Meinke et al. 2009).

Despite these challenges, the presence of sage-grouse populations in areas with high similarity to extirpated range may help maintain a lower risk of extirpation for populations in strongholds, by maintaining a larger population size overall and thus helping buffer the negative effects of environmental stochasticity and loss of genetic variation. More isolated or disjunct populations, especially at the range periphery, may have different genetic, phenotypic, and behavioral characteristics important to the species. Understanding the role of these high-risk populations in relation to those in strongholds warrants immediate research attention (Nielson et al. 2001).

Regardless of the role of high-risk populations, effective management of strongholds is important because detrimental anthropogenic factors in strongholds are less common and extensive areas of sagebrush remain. Thus, the management challenge in strongholds is one of maintaining or improving current conditions, which largely translates to prevention of detrimental land uses and minimizing undesirable ecological processes (Wisdom et al. 2005c). In many cases, this combination of passive management and passive restoration involves modifications to existing land uses that maintain or improve conditions (McIver and Starr 2001). This contrasts with active restoration, requiring intensive management and large inputs to restore or rehabilitate conditions in areas where extensive degradation and loss of habitat has occurred, and which may be difficult or impossible to reverse for many sites formerly dominated by sagebrush (McIver and Starr 2001; Pyke, this volume, chapter 23).

If management emphasis is placed on strongholds, a comprehensive and detailed assessment of threats to habitats and populations within these areas is appropriate (Wisdom et al. 2005a,b,c). Most areas of sagebrush in the western stronghold are threatened by large-scale invasion of exotic plants, particularly cheatgrass (*Bromus tectorum*) (Suring et al. 2005b; Miller et al., this volume, chapter 10). Minimizing this threat warrants comprehensive management of all human activities that act as vectors for spread and establishment of exotic plants, and that increase their competitive edge over native vegetation. More than 25 different human-associated disturbances would need to be effectively managed to reduce this threat (Wisdom et al. 2005b,c). Among these disturbances are obvious factors such as high densities of roads open to motorized travel and expansive areas of public land open to off-road motorized travel (Barton and Holmes 2007). A myriad of less obvious human-associated disturbances also are prevalent and warrant management attention (Wisdom et al. 2005b).

Another common threat in the western stronghold is displacement of sagebrush by highly invasive pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands (Suring et al. 2005b; Miller et al., this volume, chapter 10). Woodland control can be achieved through aggressive mechanical or burning treatments; which treatments, if any, are appropriate and effective

depends on local site conditions, the potential interaction with exotic plants, and the anticipated responses of affected sagebrush community types (Suring et al. 2005b; Miller et al. 2007; this volume, chapter 10). Comprehensive assessment of risks posed by this threat, mapped across the western stronghold, would provide a basis for developing and implementing effective management controls (Suring et al. 2005b).

The eastern stronghold continues to be a focal area of large-scale energy development, and attempts to mitigate the associated negative effects on sage-grouse populations have been ineffective (Holloran 2005, Walker et al. 2007a, Walker 2008). If the eastern stronghold is to be maintained, a holistic redesign of mitigation practices for energy development is needed (Kiesecker et al. 2009). For mitigations to be effective, they must be implemented over substantially larger areas than current practices, which focus on small areas around leks at a scale too small to sustain year-round needs of sage-grouse populations (Walker et al. 2007a; Walker 2008; Naugle et al., this volume, chapter 20; Doherty et al., this volume, chapter 21).

Research and Information Needs

Our analysis was one of the first to associate a diverse set of environmental factors with sage-grouse extirpation. As part of this process, we noted a number of deficiencies in spatial data. One was the lack of spatial data available for livestock grazing, which constitutes the most pervasive land use across the range of sage-grouse (Knick et al. 2003). Federal agencies are required to closely manage and monitor livestock grazing. However, associated data are not available in consistent, spatially explicit formats across the range of sage-grouse, or even for smaller areas that span multiple administrative boundaries within or among federal agencies. This deficiency precluded our analysis of livestock grazing. Likewise, no other studies of potential effects of livestock grazing on sage-grouse have been conducted at regional or range-wide spatial extents because of this data deficiency (Crawford et al. 2004).

Primitive and secondary roads also may be underestimated in current spatial layers. Our distance- and density-based road analyses might have changed with a more accurate inventory. In addition, exotic plant occurrence, another extensive landscape feature, has not been mapped

accurately across the range of sage-grouse, and this factor may have substantial effects on habitat (Hemstrom et al. 2002, Rowland et al. 2005). Regional models of cheatgrass occurrence recently were developed and validated for western areas of sage-grouse range (Peterson 2005, Bradley and Mustard 2006, Meinke et al. 2009). Ultimately, such an approach is needed to estimate and map range-wide occurrence of the more common exotic plants, such that potential effects on sage-grouse extirpation can be evaluated range-wide. Similarly, more accurate, range-wide maps of the occurrence of pinyon pine and juniper woodlands would provide a basis for analyzing this variable in relation to range-wide patterns of sage-grouse extirpation.

Another data challenge for range-wide analyses is that some factors may be common or pervasive in specific parts of sage-grouse range, but uncommon or absent in most areas. Energy development is concentrated in Wyoming and adjacent areas but is spatially uncommon, concentrated in small areas, or absent elsewhere. Consequently, we could not evaluate energy development as a range-wide variable because we had insufficient sampling coverage, using historical sage-grouse locations in occupied and extirpated ranges, to evaluate different levels of energy development (but see earlier discussion regarding variables evaluated that are associated with energy development).

Other factors that may affect sage-grouse populations are just emerging, such as West Nile virus (Naugle et al. 2005; Walker 2008; Walker and Naugle, this volume, chapter 9). Such variables are not related to past extirpations, and the range-wide prevalence of West Nile virus within all populations is uncertain. Consequently, an evaluation was not possible.

Finally, identifying which environmental factors are operating in a cause-effect manner in relation to extirpation and which may simply be correlative is a challenge not easily addressed except through consideration of our results in relation to the larger body of sage-grouse literature. Our results confirm prior research documenting sage-grouse as a species whose persistence depends on adequate areas of sagebrush. This inference extends to other sagebrush variables—patch size, proximity among patches, and size of core areas—that also were associated with extirpation. These results illustrate the strong effect of sagebrush abundance and

distribution on sage-grouse persistence; without large areas of contiguous sagebrush, sage-grouse cannot persist.

A cause-effect relationship of anthropogenic variables such as area in agriculture, human density, road density, and distance to highways is indicated by past research documenting the widespread conversion of sagebrush habitat to these land uses (Braun 1998; Vander Haegen et al. 2000; Knick et al., this volume, chapter 12); by the facilitation of exotic plant invasions into sagebrush habitats adjacent to these land uses (Hann et al. 1997), especially adjacent to roads (Gelbard and Belnap 2003); and by mortality of sage-grouse along roads and highways (Lyon and Anderson 2003, Aldridge and Boyce 2007).

The strong associations of elevation and landownership with sage-grouse extirpation represent the widespread conversion of low-elevation, private lands to nonsagebrush land uses, such as agricultural and urban development (Vander Haegen et al. 2000; Knick et al., this volume, chapter 12), as well as the substantial loss of sagebrush from widespread exotic plant invasions at lower elevations (Hann et al. 1997, Meinke et al. 2009). In that context, elevation and landownership are ideal indicators of underlying causes of extirpation.

Finally, two variables strongly associated with sage-grouse extirpation, distance to transmission lines and distance to cellular towers, have unknown relations with sage-grouse population dynamics at regional extents. New, mechanistic research is needed to understand the potential relation between these variables and sage-grouse extirpation. Until then, our results suggest that transmission lines and cellular towers warrant consideration as part of holistic conservation strategies for sage-grouse.

CONSERVATION IMPLICATIONS

A variety of biotic, abiotic, and anthropogenic factors are associated with extirpation of sage-grouse. Consequently, holistic attention to a diverse set of environmental factors—beyond those considered for sage-grouse in current guidelines and management—appears necessary to help maintain population persistence.

Maintenance of desired conditions in areas identified as strongholds for Greater Sage-Grouse appears critical to the species' future persistence. Strongholds provide extensive areas of contiguous sagebrush that can be maintained and improved with less active management and fewer resource inputs. Restoration and rehabilitation of areas within and near the small, disjunct areas of Gunnison Sage-Grouse range likewise is important to recovery and viability of this species. The future of sage-grouse will depend on new, holistic management approaches that are strategically designed and effectively implemented range-wide, and that minimize all forms of detrimental factors and maximize best uses of limited resources.

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