

Public lands and private waters: scarce mesic resources structure land tenure and sage-grouse distributions

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Abstract. Water scarcity in semiarid environments provides a model system to evaluate the role of mesic resources in structuring the distribution and abundance of wildlife. We used remote sensing and point process analyses to evaluate spatio-temporal variability in limited mesic resources in relation to greater sage-grouse (*Centrocercus urophasianus*) distributions in Oregon, California, and northwest Nevada, USA, 1984–2011. We then link population distribution to changes in resource availability over time, space, and land tenure. Despite encompassing only 2.4% of landscape area, mesic sites influenced sage-grouse breeding distributions as evidenced by significantly shorter lek to mesic resource distances in observed (5.3 km) vs. predicted (8.2 km) values. Population abundance increased with proximity to mesic sites. Lag effects evident in abundance and proximity trends of mesic resources suggest a level of drought tolerance that moderated climatic variability. Mesic abundance and proximity remained relatively stable during the study period in comparison to more dynamic climatic patterns. Drought effects were most pronounced during multiyear events as evidenced by the 1987–1992 period that decreased mesic abundance >25% and approximately doubled mean lek to mesic resource distances (4.8–8.3 km). In our study area, 75% of all mesic resources were in private ownership, where the predominant land use is livestock ranching. Results suggest a holistic conservation strategy inclusive of private and public lands is needed to ensure sage-grouse habitat requisites are met throughout the life cycle of this landscape species.

Key words: California; *Centrocercus urophasianus*; Great Basin; greater sage-grouse; Landsat; late brood rearing; Nevada; Oregon; point pattern analysis; private land; proximity; remote sensing.

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INTRODUCTION

Water scarcity shaped western settlement, and today is a driver of human economic growth and urbanization in semiarid ecosystems (Gleick

2010). Intensive agriculture and ranching traditionally accounted for >85% of water use in the West (National Research Council 1982). Recent growth in exurban and rural populations now places unprecedented pressure on limited water

resources in the “New” West (Hansen et al. 2002). Sustainability of irrigated rangeland is at risk as water demand shifts from agricultural to domestic and industrial uses (MacDonald 2010), including water intensive activities such as gold mining (Gunson et al. 2012). Predicted long-term fluctuations in climate patterns portend future shortages in already stressed semiarid systems (Elliott et al. 2013).

Water scarcity intensifies threats to biodiversity (Lemly et al. 2000) because 60–80% of wildlife is dependent on mesic habitats (e.g., wetlands and riparian areas; Thomas et al. 1979, Patten 1998, Belsky et al. 1999, Peck and Lovvorn 2001). Wet-dry cycles in these systems provide high biological productivity for wildlife during favorable environmental conditions (McKinstry 2004). Availability of these resources provides an important source of food and cover for wildlife. To date, half of all mesic habitats in the continuous United States have been lost (Dahl 1990) and future impacts are expected as water resources are purchased to support exurban demand (Peck et al. 2005). Changes in traditional water use to satisfy human development threatens remaining mesic systems and biodiversity conservation (Goldstein et al. 2011).

Greater sage-grouse (*Centrocercus urophasianus*; herein “sage-grouse”) is a gallinaceous bird native to sagebrush (*Artemisia* spp.) communities of western North America (Schroeder et al. 1999). Degradation of sagebrush communities has contributed to declines in sage-grouse populations and to extirpation of the species from half of its range (Schroeder et al. 2004). Severity and extent of changes have led to heightened concern over the species’ population status and recent designation of the species as “warranted but precluded” under the federal Endangered Species Act (ESA; United States Fish and Wildlife Service 2010). Key threats leading to sagebrush habitat loss and fragmentation include large-scale wildfire, invasion of exotic annual grasses, urbanization, energy development, mining, agricultural conversion, unsustainable grazing management (domestic and feral animals), and encroachment of conifer species into native rangeland (Knick et al. 2013).

Sage-grouse inhabit semiarid systems characterized by relatively stable sagebrush communities (Miller et al. 2011). Climate-driven variation

in underlying herbaceous production creates an important but unpredictable resource, representing selective pressures around which sage-grouse have evolved their life history strategy (Blomberg et al. 2012). Seasonal drying and senescence of herbaceous vegetation (July–August) cause female sage-grouse to move their broods from breeding areas to more productive sites including temporary wetlands, wet meadows, riparian areas, high elevation mesic sagebrush communities, and irrigated alfalfa; hereafter “mesic resources” (Fischer et al. 1996, Atamian et al. 2010, Connelly et al. 2011b). Mesic resources represent an important and potentially limiting component of sage-grouse late brood rearing habitat (Atamian et al. 2010). It is currently unknown how the extent and availability of these resources structures sage-grouse population abundance and distribution.

Sage-grouse in the semiarid sage-steppe provides a model system to evaluate the role of mesic resources in structuring wildlife distributions. At local scales, relationships among sage-grouse recruitment and resource availability are known, but to date no one has evaluated spatio-temporal variability in landscape conditions that spatially structure populations. The objective of this study was to evaluate how variability in mesic resource conditions structures the spatial distribution of sage-grouse populations across 130 000 km² in southeast Oregon, northeast California, and northwest Nevada, USA, using data from 1984 to 2011. First, we mapped mesic resources and assessed variability in resource abundance over 28 yr using remotely sensed imagery. We then evaluated the dependence of population distribution and abundance on spatio-temporal variation in mesic resources using point pattern analysis. Last, we evaluated land tenure to inform a more holistic sage-grouse conservation strategy inclusive of mesic resource requisites.

MATERIALS AND METHODS

Study area

The study area comprised ~20% (>130 000 km²) of current sage-grouse range in the western and most arid portions of their distribution as defined by Schroeder et al. (2004). Areas studied encompassed northwestern and western regions of the Great Basin and include the entire population

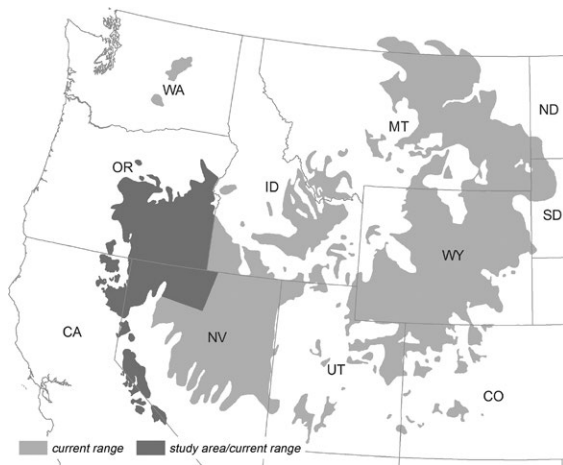


Fig. 1. Study area (>130 000 km²), encompassing ~20% of current sage-grouse range in regions of Oregon, California, and northwest Nevada, USA (Schroeder et al. 2004).

of Oregon, California, and associated populations in northwest Nevada (Fig. 1). The ecological setting of the region is characterized as semiarid mid-latitude shrub steppe and desert marked by hot summers and cold winters. Aridity is the result of the rain shadow of the Sierra Nevada and Cascade Mountains intercepting wet air masses brought by westerly winds. Annual precipitation ranges from 15 cm to over 100 cm at higher elevations (Flaschka et al. 1987, Commission for Environmental Cooperation 1997), although high annual variability is characteristic with precipitation typically falling below 70% of the annual mean one in 5 yr (Miller et al. 1991, Hurd et al. 1999, Fig. 5A). Mesic conditions are largely driven by accumulating winter snowpack (Lemly et al. 1993, Engilis and Reid 1996, Lovvorn et al. 1999). Snowmelt in mountain streams peaks from late spring to early summer and results in intermittent surface flows that feed natural wetland basins and irrigated agriculture. High evaporative rates in late summer limit the extent of mesic resources.

Lek distribution and population abundance

We modeled sage-grouse distributions using lek locations and lek survey data. Results were used to estimate landscape configuration of grouse distributions and applied as a variable to examine patterns of spatial dependence

relative to mesic resource locations. High fidelity to leks and surrounding nesting sites are well documented in sage-grouse (Connelly et al. 2011a). Leks typically occur in the same location each year with documented rates of continual use exceeding 85 yr in some cases (Connelly et al. 2011a). Lek surveys have been widely used by resource agencies to monitor trends in sage-grouse populations, and are considered a reasonable index of relative distribution and abundance (Reese and Bowyer 2007). We presumed all lek locations to be fixed within the context of broad landscape patterns examined in the study, but acknowledge that shifts in lek locations may occur due to persistent disturbance or alteration of vegetative cover (Walker et al. 2007).

To account for high variability in survey intervals and sampling intensity, we used average maximum male counts for known lek locations over a 28 yr period (1984–2011) as the basis for estimating breeding distributions and relative population abundance (Fig. 2). Leks, outside defined sage-grouse range ($n = 15$; Schroeder et al. 2004) were incorporated by buffering lek locations using known distributions of nesting females (Holloran and Anderson 2005) and merging their extent into the study area (Fig. 2). Lek counts were collected by the Oregon Department of Fish and Wildlife, Nevada Department of Wildlife, and California Department of Fish and Game. Only leks averaging one or more males counted within the 28-yr period examined were included in the study ($n = 1277$). Lek counts that averaged less than one male ($n = 496$) were omitted from analyses. Omitted leks were characterized by high rates of zero count surveys. Exclusion of these sites eliminated the majority of leks that may have been considered abandoned or inactive during the study period. We felt their removal provided a conservative, but more accurate estimation of population distribution. All leks included in the study were assumed to be active through the period examined (1984–2011).

Lek survey data were used to delineate relative population abundance. We applied a weighted kernel function to aggregate populations among proximal lek locations and then ranked the weighted abundance from high to low and grouped leks into four classes (high, moderate,

low, and sparse), containing 25%, 50%, 75%, and 100% of the known breeding population respectively (Doherty et al. 2011, Fig. 2). Averaged maximum male counts (total averaged males $\mu = 14\,039$) from 1984 to 2011 were used as a population abundance measure and to weight lek locations during kernel function calculations. Starting with the highest kernel weighted lek; we summed the number of counted males (non-weighted) until a given percentage of the population threshold was met. This resulted in a segmentation of population abundance from high to low, each defined by a population percentage. We avoided the bandwidth choice problem present when applying kernel density functions (Horne and Garton 2006) by using known distributions of nesting females around leks (Holloran and Anderson 2005, table B-1 in Colorado Division of Wildlife 2008) to delineate the outer boundaries of the functions search radius. We applied abundance classes as categorical factors during examination of grouse distribution dependence on mesic resource locations.

Mapping mesic resources

We modeled extent and availability of mesic resources by estimating rates of vegetative productivity derived from Landsat 4-5 satellite imagery. Measurements were based on normalized difference vegetation indices (NDVI), which quantify photosynthetic activity and correlate closely to fluctuations in net primary productivity (Box et al. 1989, Paruelo and Lauenroth 1995, Stoms 2000, Pettorelli et al. 2005). Satellite images were used to monitor habitats once annually over a 28 yr span (1984–2011) to account for annual environmental variation affecting availability (Miller et al. 1991, Hurd et al. 1999). Selected images were acquired during late summer during a typically dry and hot period when the extents of mesic resources are most restricted (Mock 1996). This period is biologically meaningful for sage-grouse, because they use mesic sites during this time to raise their young (Fischer et al. 1996, Aldridge and Boyce 2007, Atamian et al. 2010).

Thirteen individual satellite images were required to cover the study area for each monitoring period. Images were attained through download from the United States Geological Survey Earth Explorer website (<http://earthexplorer.usgs.gov/>). Atmospheric irregularities among satellite images were normalized using a model II linear regression process in program ERDAS

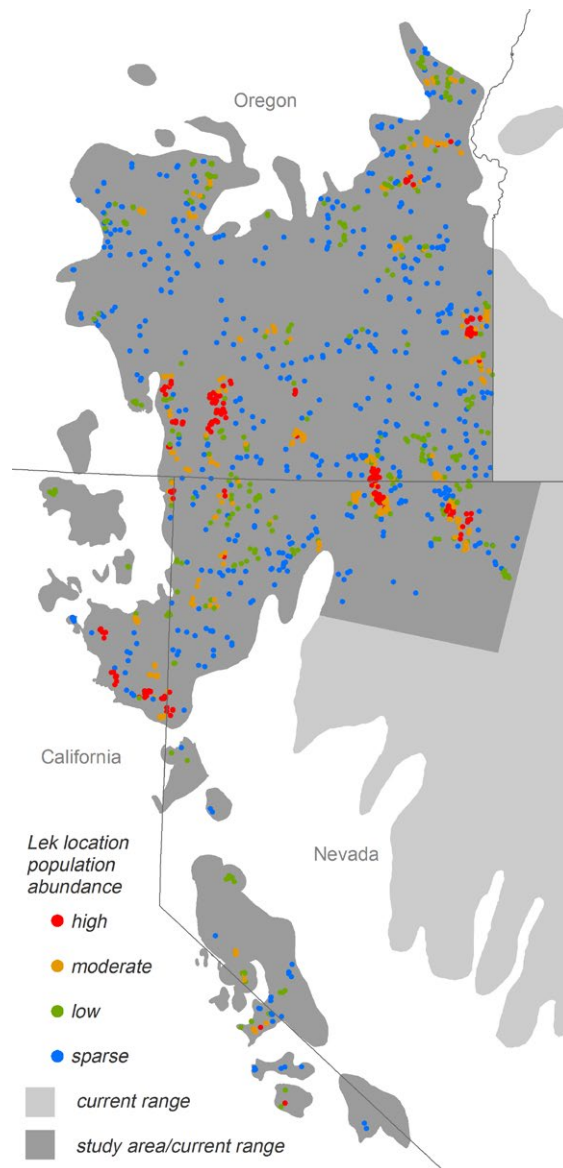


Fig. 2. Sage-grouse lek locations ($n = 1277$) and relative population abundance estimates. Population abundance classes were derived using a weighted kernel function to aggregate populations among proximal lek locations using known nesting female distributions (Holloran and Anderson 2005, Doherty et al. 2011). Leks were then ranked from high to low using weighted abundance and grouped into four classes (high, moderate, low, and sparse), each containing 25, 50, 75, and 100% of the known breeding population respectively.

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Imagine 2013 (Hexagon Geospatial, Norcross, Georgia) following methods outlined in Schroeder et al. (2006) and Beaty et al. (2008). To account for registration errors all images were geometrically corrected to a common base image (RMS error ≤ 0.5 pixels). Image availability and inconsistency in image quality (e.g., cloud cover and smoke) prevented us from using images captured on identical dates for each monitoring period. Monitoring dates ranged from 2 August to 28 September ($\bar{x} = 26$ August; $SD = 12$ days). We did not account for variations in plant phenology resulting from differences in image acquisition dates as we found overall correlation between NDVI response within mesic sites and timing of image acquisition to be low ($R^2 < 0.01$, $F = 0.003$, $P = 0.96$).

It was necessary to develop a polygon data set representative of individual mesic sites to summarize NDVI values. In semiarid environments, mesic resources are easily identified using remote sensing techniques as they are typically rare and easily discernable from surrounding less productive regions (Ozesmi and Bauer 2002). Mesic polygons were derived from Landsat 5 NDVI imagery using image segmentation applied in program eCognition 8.1 (Trimble Geospatial Imaging, Westminster, Colorado, USA). Landsat imagery used for polygon extraction were coincident with peak annual photosynthetic activity (May–June; Caldwell 1985) to capture the maximum extent of mesic resources. Associated Natural Resources Conservation Service (NRCS) Snow Telemetry (SNOTEL) weather data were reviewed to confirm select image years were representative of near or above mean annual precipitation rates for the study period as below average years may have underestimated mesic resource extent. Images from the most recent near or above mean year were selected.

Mesic polygon values were calculated in program ERDAS Imagine 2013 (Hexagon Geospatial, Norcross, Georgia) by averaging the NDVI pixel values they encompassed. Only polygons containing NDVI values indicative of higher primary productivity (≥ 0.3 ; Weier and Herring 2000), were included mesic polygon data set ($n = 52\ 017$). LANDFIRE vegetation type layer representative of 2011 landscape condition (LANDFIRE 2012, available from: <http://www.landfire.gov/vegetation.php>) was used to mask

and remove high NDVI value polygons not associated with sage-grouse mesic resources (e.g., forest or woodlands). Additional photo interpretation and editing was conducted by overlaying mesic polygons onto high resolution National Agricultural Imagery Program (NAIP) imagery (acquired 2009–2010; 1-m resolution) to affirm polygons were representative of visibly identifiable mesic resource extents.

Mesic polygons were then used to evaluate availability of late summer mesic resources by summarizing annual NDVI values from August–September Landsat 4-5 imagery (1984–2011).

Polygons containing NDVI values ≥ 0.3 were considered indicators of mesic condition (i.e., high primary productivity; Weier and Herring 2000) and identified as productive late summer mesic resources. Polygons with NDVI values < 0.3 were considered unproductive and unavailable as a mesic resource for sage-grouse. This approach provided an estimate of change in annual mesic resource abundance and landscape configuration within the study period.

As moderate pixel resolution of Landsat imagery (30 m) can limit identification of minor habitat features (Ozesmi and Bauer 2002), we tested detectability of small mesic sites by comparing our results to National Wetlands Inventory (NWI) data. NWI data are produced using high resolution aerial imagery (≤ 1 m), allowing for detection of small wetland features. NWI data were assumed to be representative of mesic resources utilized by sage-grouse. We conducted our assessment by measuring spatial co-occupancy rates of individual mesic polygons and NWI features. Only NWI features representative of potential sage-grouse mesic resources (e.g., palustrine emergent wetland types) were compared. All sites selected were slightly below the expected minimum mapping unit of Landsat imagery (≤ 0.4 ha; Knight and Lunetta 2003). Thirty-five percent of these sites were detected as mesic polygons in our data set. This detection rate was relatively low, however, of those sites not detected, $\sim 60\%$ occurred ≤ 500 m from existing mesic polygons. In addition, the extent of undetected NWI features accounted for $< 0.001\%$ of all detected mesic areas. Thus, we concluded our results to be a reasonable representation of mesic resource configuration and abundance due to the high

rate of proximity and limited spatial extent of undetected sites.

Analysis of spatial dependence

We evaluated the dependence of lek locations on mesic resource distributions using Berman's test (Berman 1986) implemented in program Programita (Wiegand and Moloney 2004, 2014). Berman's test measured the dependence of lek locations on mesic resource distributions by comparing lek to mesic resource distances to distances generated by heterogeneous null model simulations ($n = 999$) of lek locations. To overcome spatial autocorrelation inherent to clustering patterns in lek distributions (Knick and Hanser 2011), we applied a generalized simple Thomas process to account for small- and large-scale clustering patterns in null models generated. This procedure allowed us to retain the inherent clustered structure of lek distributions during null model simulations and provided a more robust estimation of spatial dependence. To ensure accuracy of null model predictions, model parameters were fit ($\alpha \leq 0.05$) to a combination of second order point pattern statistics [L -function $L(r)$, pair correlation $g(r)$, distances to the k th neighbor $D_k(r)$, and spherical contact distribution $H_s(r)$] as outlined in Wiegand et al. (2013). We accounted for variability in mesic resource distributions by applying null models to annual mesic polygon configurations ($n = 28$; 1984–2011).

LANDFIRE 2011 vegetation type layer (LANDFIRE 2012) was used to restrict modeling extent to areas of sagebrush plant communities. Six communities were used to define sagebrush extent: Great Basin xeric mixed sagebrush shrubland, inter-mountain basins big sagebrush shrubland, Columbia Plateau low sagebrush steppe, inter-mountain basins big sagebrush steppe, inter-mountain basins montane sagebrush steppe, and Columbia Plateau silver sagebrush seasonally flooded shrub-steppe (NatureServe Explorer 2012; available from <http://explorer.natureserve.org/>). This process reduced model bias by eliminating regions unlikely to support sage-grouse populations (e.g., woodlands and forest). Lek to mesic resource distances were modeled as straight lines. Statistical significance was assumed at $\alpha \leq 0.05$.

Lek to mesic resource proximity was evaluated as a function of population abundance (high, moderate, low, and sparse; see Materials and Methods: Lek distribution and population abundance) using proximity analysis. We measured the nearest mesic resources to leks ($n = 1277$) annually for each population abundance class to determine variance in proximity throughout the study period. Proximity analyses were completed in program ArcGIS 10.1 (Environmental Systems Research Institute, Redlands California). Next, we compared mesic proximity rates between different population abundance classes using a separate variance two-sample t -test ($\alpha \leq 0.05$). Testing was completed by binning proximity measurements by abundance classes and averaging distances annually. Annual proximity means for each abundance class were then compared. We depicted proximity estimates graphically by plotting lek density as a function of mesic resource proximity $\rho(\text{distance})$ using kernel-smoothing estimators as described in Baddeley et al. (2012); where distance is the continuous measure of distance between leks and mesic resources and ρ is the density of lek distribution. Rho (distance) estimates were implemented in spatstat package; program R (Baddeley and Turner 2005, R Core Team 2015).

We accounted for edge effects in mesic resources during proximity measurements by extending mesic site delineations >20 km beyond the project boundary. As proximity estimates of leks and mesic resources vary (Connelly et al. 1988, Fedy et al. 2012, Coates et al. 2013), visual inspections of leks within 20 km of the project boundary were conducted to ensure all proximal mesic sites were included in the analysis.

Analysis of resource type and land tenure

Mesic polygons were classified by resource type and land tenure (public vs. private) to examine patterns of annual resource reliance among different sage-grouse population densities. Ownership was assigned using data provided by the Bureau of Land Management (BLM 2004; available from http://sagemap.wr.usgs.gov/westUS_own.shp). We classified mesic resource types broadly by association with underlying system or land use process as outlined in Cowardin et al. (1979). Classes included wet meadow, riparian, seasonal

wetland, temporary wetland, reservoir/lake, playa, and alfalfa. Wet meadow, seasonal wetland, and riparian classes occur as components of upper elevation mesic sagebrush communities identified as important mesic resources during late brood rearing periods (Atamian et al. 2010). We assumed these sites to be correlated with more productive sagebrush landscapes not directly evaluated in our analysis. Alfalfa fields were included as a mesic type because they are an abundant irrigated crop and known late summer resource for sage-grouse (Connelly et al. 2011b). Habitat classes were assigned through photo interpretation of NAIP imagery (2009–2010).

We summarized mesic resource type and land tenure in proximity to known lek distributions. This eliminated bias from nonsagebrush regions (e.g., forest and woodlands) within the study boundary that do not support sage-grouse populations. Summary boundaries were generated by buffering lek locations using known nesting female distributions within breeding abundance classes (see Materials and Methods: Lek distribution and population abundance; Fig. 3). We extended the distance from 8.5 to 10.0 km for sparse populations because a *post hoc* analysis indicated 8.5 km was too short a distance to account for observed mesic resource distributions within this abundance class. Large blocks of continuous mesic sites remaining within the summary boundaries were buffered inward ~400 m to remove internal polygons. Internal buffering eliminated the center portions of extensive wet meadow and alfalfa complexes unlikely to be used by sage-grouse (Casazza et al. 2011). Available mesic resources within these boundaries were summarized by type and ownership annually (1984–2011). All data summaries and analyses were completed in program ArcGIS 10.1 (Environmental Systems Research Institute, Redlands California).

We compared precipitation patterns to late summer mesic resource abundance and lek proximity annually (1984–2011). Precipitation data were obtained from 10 NRCS SNOTEL sites distributed within or adjacent to the study area boundary (Fig. 3). Annual precipitation measurements were averaged and compared to mesic resource abundance and proximity measures using linear regression. Annual precipitation patterns

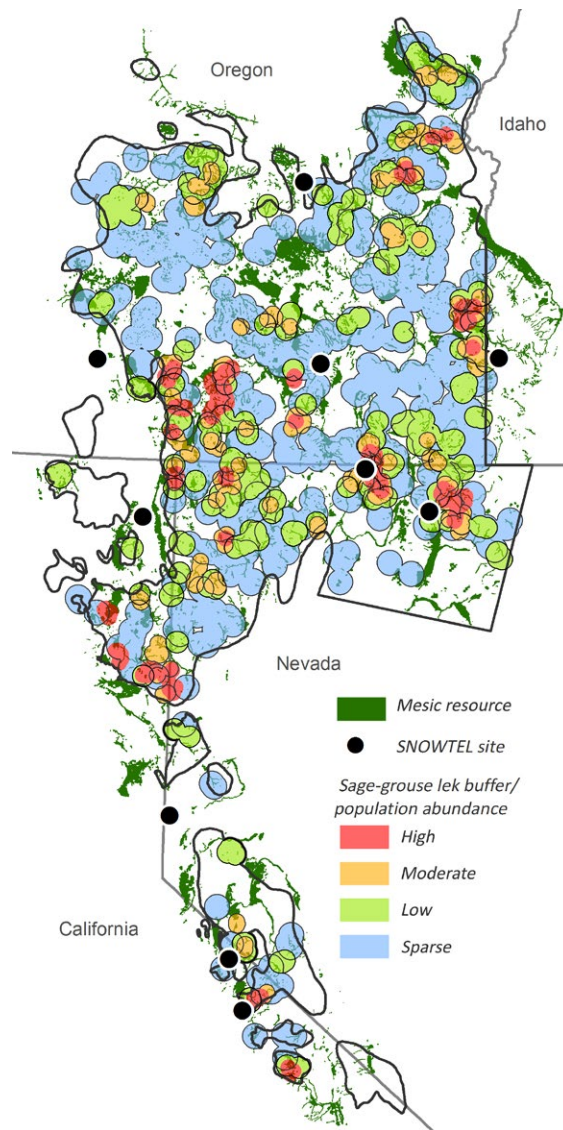


Fig. 3. Mapped mesic resource distribution, SNOWTEL site locations, and buffered lek locations. Lek buffering distances were derived using known nesting female distributions within population abundance classes (high-moderate = 6.4; low 8.5, sparse = 10 km; Holloran and Anderson 2005, Doherty et al. 2011, see Materials and Methods: Analysis of habitat type land tenure) Map scale does not permit illustration of minor mesic features.

were similar across sites (relative standard deviation [%RSD] \pm 8.6%). Annual SNOTEL measurements were provided within water years (1 October–30 September).

RESULTS

Berman's test results determined that observed lek to mesic resource distances (5.3 km) were significantly smaller than null model predictions (8.2 km) averaged across all years estimated ($P < 0.001$, $\bar{Z}_1 = 4.09$; 1984–2011), indicating lek locations were positively associated with the limited spatial distribution of mesic resources. Plots estimating lek density as a function of distance to mesic resources $\rho(\text{distance})$ show clustering of leks around mesic sites within a 10 km band containing 85% of all lek locations (Fig. 4). Highest lek densities were within 3 km of mesic resources and contained ~30% of lek locations.

Population abundance was positively correlated with mesic resource proximity (Fig. 5C). Mean mesic resource proximity was double in sparse (6.8 km) vs. high abundance (3.3 km) populations (Table 1). Low and sparse breeding populations occurred 1.8–3.5 km further ($r = 0.45, 0.86$; $P < 0.02$) from mesic resources than higher abundance populations. Average distance to mesic resource was 5.3 km. Variation

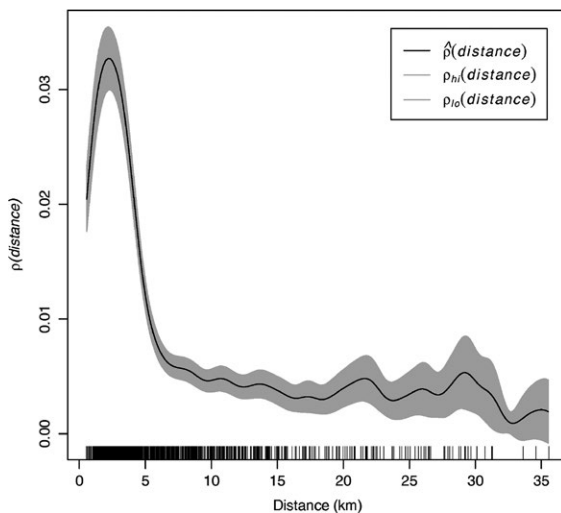


Fig. 4. Estimate of lek density as a function of averaged distance to mesic resource $\rho(\text{distance})$ using kernel-smoothing estimators as described in Baddeley et al. (2012; $\hat{\rho} = \text{mean}$, $\rho_{hi} = \text{upper bounds}$, $\rho_{lo} = \text{lower bounds}$); where *distance* is the continuous measure of distance between leks and mesic resource and ρ is the density of lek distribution.

in annual lek to mesic resource distance was low (%RSD $\pm 15.8\%$, $\bar{SD} < 1.0$ km) for all population densities (Table 1).

Mesic resources accounted for 1.6–2.9% (mean = 2.4%) of land area within buffered lek boundaries annually. Private ownership accounted for <20% of land overall, but contained 75% of mesic resources annually (public lands mean = 25%; Table 2, Figs. 5B and 6). Proportion of mesic resources on public lands was higher for high abundance populations (Table 1). Wet meadow, riparian, and alfalfa resources accounted for 78.1% of mesic resources during the study period (Table 2). Private ownership accounted for the majority of wet meadow, alfalfa, riparian, and temporary wetland types; while the majority of lake/reservoir, playa, and seasonal wetland types occurred on public lands. All alfalfa and >90% of privately owned wet meadows were associated with irrigation practices.

Annual precipitation patterns accounted for ~42% of the variation ($R^2 = 0.42$, $F = 20.7$, $P = 0.13$) in mesic resource abundance and ~20% of variation in lek to mesic resource proximity ($R^2 = 0.2$, $F = 7.9$, $P = 0.01$; Fig. 5A–C). Patterns of lag effects in delayed response to climatic variation were evident in observations of mesic resource abundance and proximity trends (Fig. 5A–C).

DISCUSSION

In our study region of the semiarid Great Basin, mesic resources are keystone features that structure sage-grouse distributions far beyond the spatial extent of the resources themselves. Despite encompassing only 2.4% of landscape area, mesic sites influenced sage-grouse breeding distributions as evidenced by significantly shorter lek to mesic resource distances in observed (5.3 km) vs. predicted (8.2 km) values ($P < 0.001$, $\bar{Z}_1 = 4.09$). Configuration of mesic resources at broad spatial scales influenced lek distributions, clustering populations within landscapes. Previous studies demonstrate the importance of landscape features on lek distribution and habitat selection by nesting sage-grouse females (Doherty et al. 2010) and identify thresholds necessary to maintain populations (Knick et al. 2013). Our data suggest that in landscapes where other known ecological minimums are satisfied, mesic

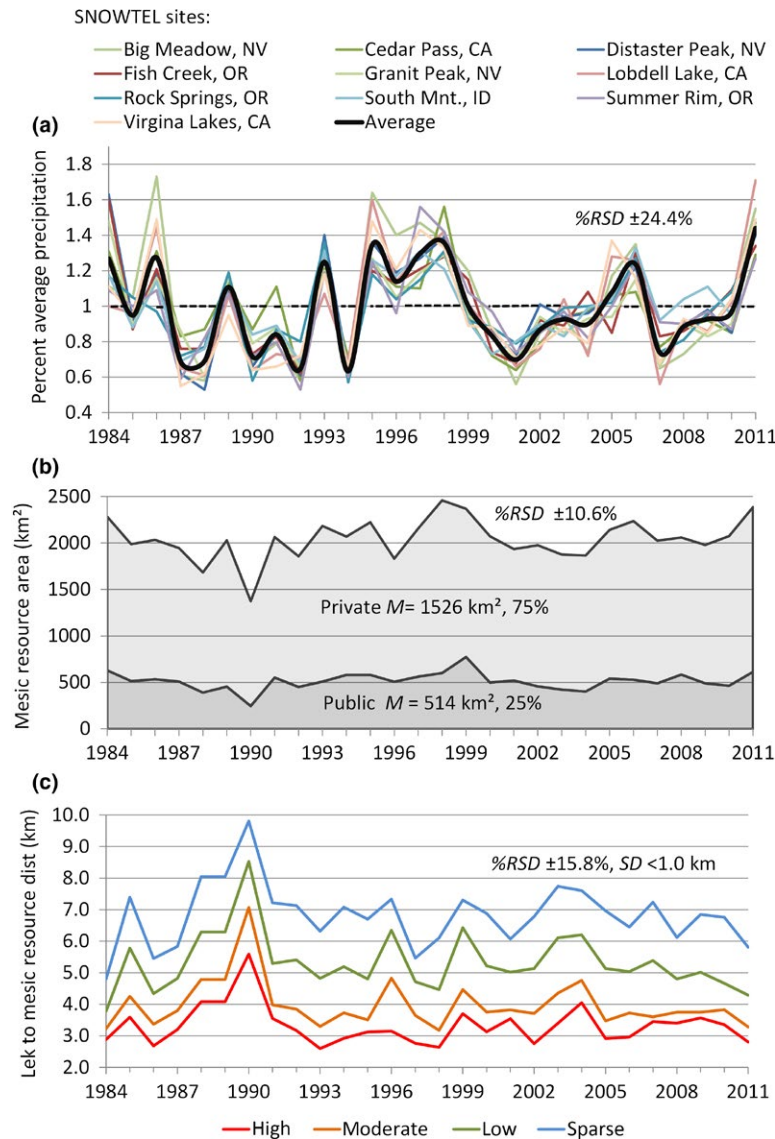


Fig. 5. (a) Snow Telemetry (SNOWTEL) percent average precipitation and snow water equivalent (1984–2011). Data obtained for 10 sites distributed within or adjacent to study area (see Fig. 3 for site locations). Data representative of water year totals (October 1–September 30). Long-term mean calculated 1981–2010. (b) Annual mesic resource availability (km²; 1984–2011) by public and private lands contributions. (c) Mean annual lek to nearest mesic resource distance (1984–2011) binned by sage-grouse population abundance classes (high, moderate, low, and sparse).

resource distributions may act as another key delimiter of breeding habitats as inferred by clustering of leks within 3 km of mesic sites (Figs. 4 and 6). Quantification of these patterns is made possible by high detectability of mesic areas within semiarid environments (Ozemi and Bauer 2002) from free publicly accessible, moderate-resolution satellite imagery.

While causal mechanisms behind observed patterns were not explored here, we speculate that sage-grouse may be juxtaposing their breeding distributions to exploit the highly restricted distribution of mesic resources during periods of resource depletion, when birds are reliant on herbaceous forbs and invertebrates (Fischer et al. 1996, Aldridge and Boyce 2007, Gregg and

Table 1. Average sage-grouse breeding site (lek) to mesic resources distances (km) observed 1984–2011, reported by population abundance classes for Oregon, California, and northwest Nevada, USA.

Population	<i>n</i>	Mean dist. (km)	SD	%RSD	Median
High	203	3.3	0.61	19.1	3.2
Moderate	264	4.0	0.76	20.4	3.8
Low	298	5.3	0.91	17.8	5.1
Sparse	512	6.8	0.97	14.2	6.9
All	1277	5.3	0.82	15.8	5.2

Note: Distances were measured as straight lines from lek locations (*n* = 1277) to the nearest mesic resource.

Table 2. Proportional abundance and ownership of mesic resource types by sage-grouse abundance class (high, moderate, low, and sparse).

	High, %	Mod, %	Low, %	Sparse, %	All, %	%RSD	km ²	Private, %	Public, %
Alfalfa	11.4	13.5	9.4	18.3	17.1	9.1	349	98.8	1.2
Wet meadow	38.0	40.4	43.1	45.9	41.5	10.4	848	92.1	7.9
Lake/ reservoir	5.5	2.0	4.9	0.7	3.6	65.5	74	25.9	74.1
Playa	3.2	3.3	2.3	0.5	1.6	72.4	34	12.3	87.7
Riparian	22.0	30.9	25.1	21.2	19.5	11.5	397	60.9	39.1
Seasonal wetland	5.2	2.0	8.6	7.5	8.5	12.6	174	17.2	82.8
Temporary wetland	14.8	7.9	6.5	6.0	8.1	38.2	165	63.7	36.3
Mesic resource (km ²)	211	247	786	1406	2040	10.6			
Private	58.0	75.5	68.3	78.0	74.8	18.0			
Public	42.0	24.5	31.7	22.0	25.2	9.5			

Notes: Mesic resource abundance and public/private ownership were estimated from annual observations (1984–2011) and averaged. Estimations were summarized in proximity of known lek distributions. Nonsagebrush areas (e.g., forest and woodlands) were omitted from summary results. Summary areas were generated by buffering lek locations within population abundance classes using known nesting female distributions (Holloran and Anderson 2005, Doherty et al. 2011, see Materials and Methods: Lek distribution and population abundance; Fig. 3). Large blocks of continuous mesic sites remaining within the summary boundaries were buffered inward ~400 m to remove internal polygons unlikely to be used by sage-grouse (Casazza et al. 2011).

Crawford 2009). Lek to mesic resource proximity estimates were measured as straight line distances, however we acknowledge that patch characteristics and boundary permeability are likely to affect bird movements (Wiens et al. 1993). Fidelity also may influence movement wherein birds bypass a comparable site in favor of another (e.g., Connelly et al. 1988); nonetheless, patterns we observed correspond well with previous observations in seasonal movements (Fedy et al. 2012).

Our findings also show that sage-grouse population abundance was spatially structured by the distribution of mesic resources (Table 1; Figs. 5C and 6). Breeding population abundance was a function of mesic resource proximity with the largest populations occurring closer

to productive sites. In contrast, low-abundance populations were distributed sparsely at twice the average distance to limited mesic resources (Table 1; Fig. 6). The correlative nature of this observation provides a passive agent in linking mesic resources and sage-grouse population dynamics. Confounding factors associated with landscape quality that may have contributed to patterns observed were not explored. For example, the mesic resources detected in our analysis may be closely correlated with adjacent productive landscapes, typically higher in elevation and with greater precipitation. The presence of such landscapes can provide more diffuse late season habitats perhaps not detected by our methods. Regardless, the relative landscape abundance of mesic resources we identified (<3%) were similar

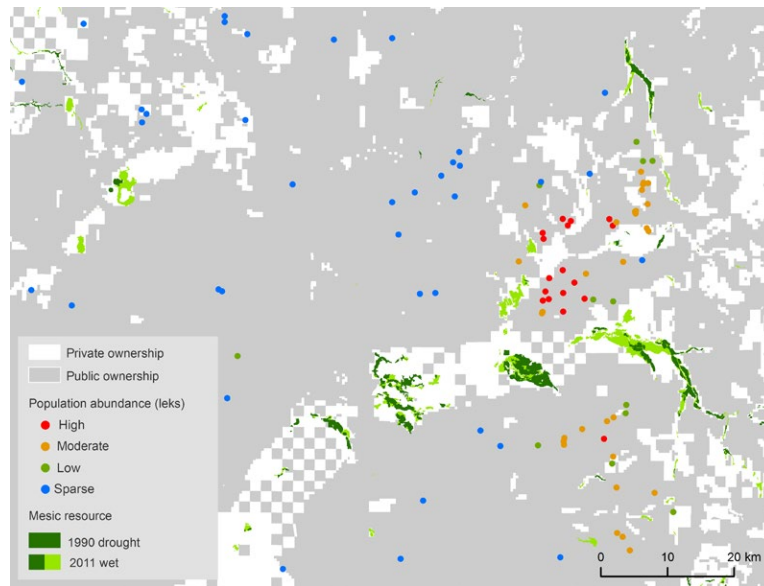


Fig. 6. Example of characteristic ownership and population distribution patterns observed. Private lands encompassed on average 75% of summer mesic resources. Breeding distribution (leks) was a function of mesic resource proximity with the highest population abundances nearest reliable mesic sites.

to those observed in other areas of the sage-grouse range using different techniques (Aldridge and Boyce 2007, Atamian et al. 2010). The restricted spatial distribution of mesic resources and montane sagebrush communities indicates that such features play a role in limiting sage-grouse populations (Atamian et al. 2010), providing justification for their conservation and restoration.

Lag effects evident in mesic abundance and proximity estimates indicate a level of drought tolerance that moderated climatic variability in sage-grouse summer resources. Mesic abundance and proximity exhibited moderately stable patterns within the study period (%RSD \pm 10.6, \pm 15.8%) in comparison to more dynamic precipitation rates (%RSD \pm 24.0%; Fig. 5). Private lands water storage, groundwater pumping, and irrigation are likely factors contributing to drought tolerance in mesic resources (Sando et al. 1988, Peck and Lovvorn 2001, Lovvorn and Hart 2004). These hydrologic modifications may also generate tradeoffs that reduce drought tolerance in some areas at the expense of increasing resilience in others. Drought effects were most pronounced during multiyear events. For example, an extended drought from 1987 to 1992 decreased mesic abundance >25% and approximately doubled

lek to mesic resource distances (\bar{x} = 4.8–8.3 km; Fig. 5C). Relatively stable patterns in late summer mesic resources availability suggest recruitment benefits linked to elevated precipitation and plant production (Blomberg et al. 2012) are more likely due to variability in habitat quality or encompass periods beyond late brood rearing.

Water resources were predictive of land tenure as shown by 75% private ownership of mesic areas (Table 2, Figs. 5B and 6), inextricably linking sage-grouse conservation to privately owned ranchlands in this study area. BLM accounted for 63% of mesic resources on public lands. Higher rates of public land ownership in high abundance sage-grouse populations resulted from anomalies in land tenure patterns that include Sheldon-Hart Mountain National Wildlife Refuge that made up <3% of public land within the study area, but contained >25% of all publicly owned mesic riparian resources. Correlative patterns of ownership and mesic resources may differ in regions not assessed. Although our land tenure analysis was extensive, it was not inclusive of the entire sage-grouse range where ownership patterns can vary widely.

Sustainability of scarce water resources hinges on maintaining land use practices that promote

conservation of mesic resources. We encourage the accelerated protection and restoration of these resources regardless of land ownership for their values to biodiversity, food production, and rural way of life in the “New” West. Emerging solutions on private ranchlands include voluntary, incentive-based easements to halt conversion of mesic sites to subdivision and other noncompatible land uses (Copeland et al. 2013). Broad scale efforts already underway to reverse shrub-steppe conifer encroachment affecting sage-grouse populations in the Great Basin (Baruch-Mordo et al. 2013) may also benefit mesic resource availability by improving soil water availability (Roundy et al. 2014) and increasing late season (July–September) surface water availability (Deboodt et al. 2008). Restoration of degraded wet meadows, playas, and other mesic systems near breeding habitats may also increase summer habitat availability. To close the research to implementation gap (Knight et al. 2008) and continue efforts of threat reduction for sage-grouse, the analysis reported here provides mapping products as decision support tools to public and private land managers for targeting easements and restoration actions of greatest ecological value (Natural Resources Conservation Service 2015).

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