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Research Article

Nest-Site Selection and Reproductive Success of Greater Sage-Grouse in a Fire-Affected Habitat of Northwestern Nevada

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ABSTRACT Identifying links between micro-habitat selection and wildlife reproduction is imperative to population persistence and recovery. This information is particularly important for landscape species such as greater sage-grouse (*Centrocercus urophasianus*; sage-grouse). Although this species has been widely studied, because environmental factors can affect sage-grouse populations, local and regional studies are crucial for developing viable conservation strategies. We studied the habitat-use patterns of 71 radio-marked sage-grouse inhabiting an area affected by wildfire in the Virginia Mountains of northwestern Nevada during 2009–2011 to determine the effect of micro-habitat attributes on reproductive success. We measured standard vegetation parameters at nest and random sites using a multi-scale approach (range = 0.01–15,527 ha). We used an information-theoretic modeling approach to identify environmental factors influencing nest-site selection and survival, and determine whether nest survival was a function of resource selection. Sage-grouse selected micro-sites with greater shrub canopy cover and less cheatgrass (*Bromus tectorum*) cover than random sites. Total shrub canopy, including sagebrush (*Artemisia* spp.) and other shrub species, at small spatial scales (0.8 ha and 3.1 ha) was the single contributing selection factor to higher nest survival. These results indicate that reducing the risk of wildfire to maintain important sagebrush habitats could be emphasized in sage-grouse conservation strategies in Nevada. Managers may seek to mitigate the influx of annual grass invasion by preserving large intact sagebrush-dominated stands with a mixture of other shrub species. For this area of Nevada, the results suggest that ≥40% total shrub canopy cover in sage-grouse nesting areas could yield improved reproductive success. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Artemisia*, *Bromus tectorum*, *Centrocercus urophasianus*, cheatgrass, greater sage-grouse, habitat selection, micro-habitat, nest survival, Nevada, percent shrub cover, sagebrush.

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) have been the focus of increased study because of range-wide population declines (Connelly et al. 2011, Stiver 2011). Within Nevada, sage-grouse populations are estimated to have decreased by 50% from historical levels and some local populations have been reduced by 80% (Klebenow 2001). These declines have been linked to fragmentation of sagebrush (*Artemisia* spp.) ecosystems attributed to changing land-use practices and their effects on fire regimes, the occurrence of invasive and non-native species, disease transmission, and changes in predator composition and densities (Connelly et al. 2004, State of Nevada 2012). For example, largely as a result of increased fire frequency, the Great Basin has experienced landscape-scale conversions from sagebrush to areas dominated by cheatgrass (*Bromus tectorum*; Balch et al. 2013). Areas such as these may affect sage-grouse population persistence because of increased wildfire risks. Nevada's Strategic Plan for Conservation of Greater Sage-Grouse (State of Nevada 2012) identified habitat protection as the greatest priority for sage-grouse conservation, and wildfire with the subsequent conversion to invasive species as the most prominent threat. Large-scale changes in vegetation communities as a result of wildfires may also indirectly affect sage-grouse population vital rates through ecological mechanisms such as changes in predator composition and predation rates (Seymour et al. 2003, Evans 2004).

Multiple factors spanning sage-grouse life stages likely are influencing population dynamics including sage-grouse nest survival as a central component of reproductive success. Nest survival appears to be a limiting factor in some sage-grouse

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populations (Taylor et al. 2012). Nesting success in female sage-grouse is dependent on ecological, physiological, environmental, and behavioral factors (Coates and Delehanty 2010, Dzialak et al. 2011, Kaczor et al. 2011). Furthermore, the environmental factors influencing sage-grouse nesting behavior likely vary both spatially and temporally across the species' range (Doherty et al. 2010, Connelly et al. 2011).

Previous studies have evaluated nest-site selection (Kolada et al. 2009*a*, Connelly et al. 2011, Dzialak et al. 2011, Kirol et al. 2012) and nest survival (Moynahan et al. 2007, Rebholz et al. 2009, Coates and Delehanty 2010) at various spatial scales. However, because of the range-wide variability in habitats and vegetation conditions, research regarding sage-grouse responses to dynamic local environmental conditions is needed to guide inter- and intrastate conservation efforts (Connelly et al. 2011). Additionally, few published studies have sought quantitatively to link nest-site selection to nest survival (Aldridge and Boyce 2007, Dzialak et al. 2011, Kaczor et al. 2011). Identifying specific environmental factors selected by female sage-grouse that influence the probability of nest survival could identify female sensitivity to specific environmental factors, such as wildfire, that promote or inhibit reproductive success (Dzialak et al. 2011, Hess and Beck 2012).

According to Arkle et al. (2014), past wildfire restoration efforts have had limited success, and these habitats likely require ≥20 years before re-establishment of native shrub species. Given these concerns, the researchers suggested protection of the best habitats as the most effective management strategy. As a result of limited restoration success in the past, managers need to be able to identify key areas for protection while simultaneously prioritizing the most promising areas for restoration (Pyke 2011). We modeled nest-site selection and survival using multiple vegetation and topographical parameters at multiple spatial scales in a population of sage-grouse on the western edge of the sagebrush-steppe in the Virginia Mountains of northwestern Nevada. This area was previously affected by wildfire 10 years prior to our study. Our goal was to identify environmental factors associated with nest-site selection at multiple spatial scales and then evaluate the extent to which those factors were associated with nest survival in a fire compromised habitat.

STUDY AREA

We conducted our study within a topographically diverse sagebrush-steppe ecosystem in the Virginia Mountains of northwestern Nevada, USA (Fig. 1). The study area encompassed approximately 691 km^2 with elevations ranging from 1,218 m to 2,683 m. Mean annual precipitation was 18.7 cm and temperatures ranged from 6.8 °C to 18.2 °C (Western Regional Climate Center; http://www.wrcc.dri.edu/, accessed 01 Feb 2012). Significant seasonal and annual variation in both temperature and precipitation occurred over the duration of this study. The nesting season in 2009 was colder and received more precipitation than in 2010 and 2011. Conditions in 2010 and 2011 remained closer to average; however, in 2010 a late spring snow storm blanketed the study area while many birds were nesting and the later part of the nesting season in 2011 received higher daily temperatures than normal. The Bureau of Land Management (BLM) administered most of the land (588 km^2) in the study area. Private lands (95 km^2) consisting of 3 ranches constituted the remaining acreage. Grazing and recreation were the primary land-use practices that occurred on both public and private lands in the study area. The Pyramid Lake Reservation bordered the eastern portion of the Virginia Mountains and California's state boundary line bordered to the west. Anthropogenic features and activities (e.g., roads, transmission lines, fences, ranching operations, etc.) were primarily found at the lowest elevations. Common ravens (*Corvus corax*), American badgers (*Taxidea taxus*), and coyotes (*Canis latrans*) were the most common nest predators found within the study area (Lockyer et al. 2013).

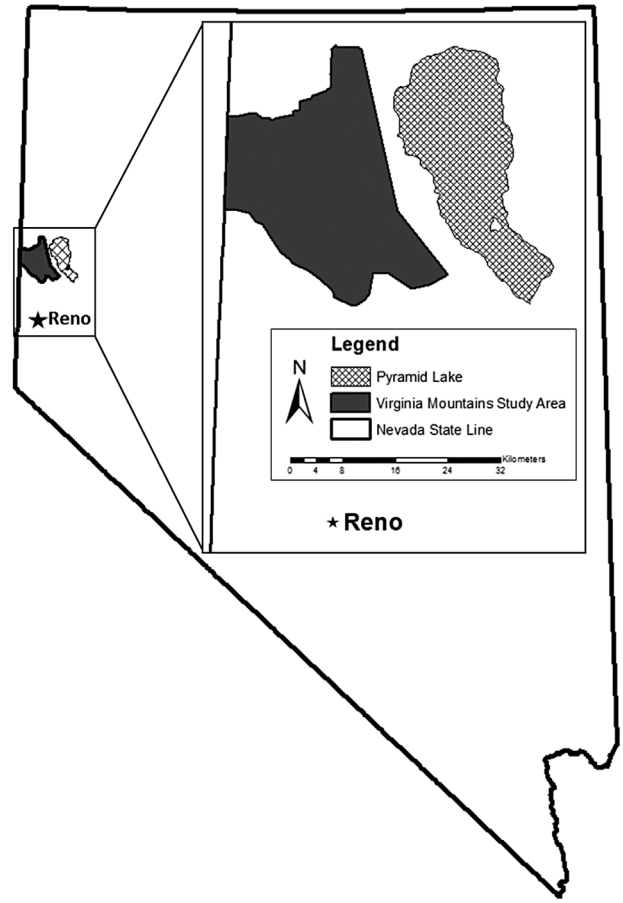

Figure 1. Map of study area location, Virginia Mountains, located in northwestern Nevada.

Habitat within our study area was consistent with shrub steppe habitats found within the Great Basin. Dominant overstory at lower elevations consisted of Wyoming big sagebrush (*A. tridentata* spp.) and rabbitbrush (*Chrysothamnus* spp.), whereas higher elevations were dominated by big sagebrush, black sagebrush (*A. nova* spp.), low sagebrush (*A. arbuscula* spp.), and several species of mountain shrub. Coates et al. (2011) describes in detail the dominant shrub and understory species found within the study site. The plant

community in the study site reflected regrowth from a 19,288-ha fire (Fish Fire) that occurred in 1999, 10 years prior to the start of this study. The fire reduced shrub abundance and increased the presence of cheatgrass within burned areas. Rehabilitation efforts by aerial reseeding occurred post-fire in February of 2000 on approximately 12,626 ha. Seed mixes primarily consisted of various wheatgrasses (*Agropyron* spp.), smooth brome (*Bromus inermis*), basin wildrye (*Leymus cinereus*), Idaho fescue (*Festuca idahoensis*), alfalfa (*Medicago sativa*), fourwing saltbush (*Atriplex canescens*), big sagebrush, and antelope bitterbrush (*Purshia tridentata*).

METHODS

Capture and Monitoring

We captured sage-grouse at nocturnal roosting locations by walking using spotlights and nets attached to 3-m extension handles (Giesen et al. 1982, Wakkinen et al. 1992), and hand-held net launching devices (SuperTalon®, Advanced Weapons Technology, La Quinta, CA) during the spring and fall of 2008–2011. We fitted captured grouse with 18–22-g (<3% body mass; Schroeder et al. 1999) necklace-style, battery-powered radio-transmitters (Advanced Telemetry Systems, Isanti, MN) with 22-cm antennas bent back along the contour of the body to reduce interference with activities. Capture, handling, and marking procedures were approved by Idaho State University (#02-02-2010) and U.S. Geological Survey Western Ecological Research Center's Animal Care and Use Committees.

We classified captured grouse as adult or yearling (Eng 1955, Dalke et al. 1963). Following release on site, we monitored radio-marked sage-grouse from the ground using 3-element Yagi antennas (Advanced Telemetry Systems, Isanti, MN) and handheld receivers (Communication Specialist Inc., Orange, CA) to document sage-grouse nest habitat selection and survival during the spring and summer (Mar–Aug). To estimate sage-grouse locations, observers circled radio-marked grouse using directional telemetry signals, maintaining a 30–50-m buffer around the grouse. This approach minimized disturbance to individual sage-grouse while ensuring precise grouse locations. We recorded distance and compass bearing to each grouse as well as the observer's location using handheld global positioning system receivers. We attempted to find all radio-marked sage-grouse $\geq$2 times per week. We performed fixed-wing aerial telemetry flights monthly to locate radio-marked grouse that otherwise could not be detected by ground crews.

Observers verified nests visually after we found sage-grouse in the same location on 2 consecutive observations. We classified nests as successful if $\geq$1 egg hatched (Rearden 1951). We included renesting attempts in our analyses because we were interested in identifying environmental factors that influenced nest-site selection and survival across the nesting season.

Model Development

Following nest fate, we measured habitat vegetation characteristics (Connelly et al. 2003) at varying distances from the nest bowl. We measured visual obstruction at the nest bowl using a cover board technique (modified from Jones 1968) to determine how cover found directly at the nest bowl may influence probabilities of nest survival. This method has been employed in several other sage-grouse nesting studies (Gregg 1991, Coates and Delehanty 2010, Conover et al. 2010, Bell 2011) and was the most suitable method to address our research objectives. We measured visual obstruction at 2 m from the board at 0°, 45°, and 90° angles from the ground. We randomly assigned board direction from the nest bowl for the first set of measurements and took a total of 3 measurement sets, each separated by a 120° rotation of the cover board. We measured horizontal cover using the 0° and 45° angle measurements (Jones 1968, Ritchie et al. 1994) and total cover included all 3 angles combined.

We used a line-intercept method (Canfield 1941) to quantify percent shrub canopy cover. We randomly assigned orientation of the first of 4 transects for shrub canopy cover and sequentially oriented the remaining 3 transects at 90° intervals relative to the previous transect. We recorded shrub species and crown width (cm) along 4 25-m transects, 2 50-m transects, and 1 100-m transect extending from the nest bowl. The 2 50-m transects and single 100-m transect were extensions on 2 of the 4 25-m transects, 180° apart. Thus, the total length of line intercept quantified along all 4 transects was 200 m. We recorded shrub crown widths and species in intervals of 5-m, 10-m, 25-m, 50-m, and 100-m radii from the nest bowl to allow for analysis at multiple spatial scales for micro-habitat data. These radii resulted in 5 micro-site spatial scales of 0.01 ha, 0.03 ha, 0.2 ha, 0.8 ha, and 3.1 ha. We also obtained a random sample of shrub heights along all transects to quantify average shrub height within the 3.1-ha scale by measuring the tallest crown height of 10 shrubs, when available, encountered along each transect.

We estimated the percentage cover of perennial grass, cheatgrass, perennial forb, annual forb, residual cover, litter, bare ground, rock, and shrub at 9 subplots (20 cm $\times$ 50 cm) located $\leq$25 m from the nest bowl (Daubenmire 1959). Additionally, we recorded the tallest droop height (cm), excluding seed stalks, of the nearest plant within a 0.5-m arc of the center of each plot for sagebrush and other shrub species, perennial grass, perennial forb, and residual grass (Daubenmire 1959). Each individual subplot was centered at the 10-m and 25-m locations along each of the 4 line-intercept transects used for quantifying shrub canopy cover. One subplot was centered at 0 m along the first randomly assigned transect.

In addition to micro-habitat factors, we evaluated macro-habitat explanatory variables across the landscape using a geographical information system (GIS; ArcGIS, ESRI, Redlands, CA). Within a GIS, we incorporated the Nevada Vegetation Synthesis Map (Nevada National Heritage Program 2008) to quantify larger scale environmental factors. Vegetation types contained within this map were developed at the 1:100,000 scale with a spatial resolution of 30 m. We condensed unique vegetation types within the original map to include the most dominant landscape-level

overstory habitat types. Classification types consisted of basin sagebrush (Wyoming and basin sagebrush), montane sagebrush (little and black sagebrush), invasive grassland (grassland dominated by cheatgrass), montane grassland (grassland dominated by perennial bunchgrasses and forbs), coniferous forest, pinyon-juniper (woodland consisting of singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*), playa, saltshrub, wet meadow, and riparian.

In a GIS, we intersected all female sage-grouse nest locations from 2009 to 2011 ($n = 71$) using Universal Transverse Mercator (UTM, North American Datum 1983, Zone 11) with the Nevada Vegetation Synthesis Map (Nevada National Heritage Program 2008). We evaluated nest locations (hereafter used) at 5 spatial scales: 39 ha, 148 ha, 617 ha, 2,470 ha, and 15,527 ha. We established these spatial scales from field observations by using the minimum and maximum (354-m and 686-m radii to get 39 ha and 148 ha, respectively) recorded distance female sage-grouse ($n = 6$) moved during incubation recess from a used location, and the mean and maximum individual home range size (2,470 ha and 15,527 ha, respectively) using fixed kernel density estimation (Worton 1989) for marked females in the Virginia Mountains. Additionally, we used the 50% core use area (617 ha) as another spatial scale for factor assessment (Coates et al. 2011). To obtain the core use area and home range estimates, we included relocation data from the 2009 and 2010 seasons in a GIS for space-use analyses. We incorporated kernel density estimates to provide a measure of the utilization distribution at the population level (Worton 1989). Area within the upper 50% and upper 95% isopleths of the kernel estimates was classified as the core use area and home range, respectively (Coates et al. 2011). Evaluating spatial scales relative to core use area, home range, and movements from used locations during incubation allowed us to analyze nest-site selection decisions by female sage-grouse and nest survival probabilities at spatial scales that could influence nesting sage-grouse. We buffered used locations in a GIS using radii of 354 m, 686 m, 1,402 m, 2,804 m, and 7,030 m to achieve the area for the macro-habitat spatial scales described above. We calculated the proportion of each vegetation type within each spatial scale using the Spatial Analyst extension in ArcGIS 10.0 (ESRI). To evaluate topographical factors in relation to used locations, we incorporated a digital elevation model (DEM) into a GIS and extracted desired data for model factors (elevation, slope, and aspect).

To develop resource selection functions (RSF; Manly et al. 2002) for the nest-site selection analysis, defined as disproportionate use relative to availability (Hall et al. 1997), we contrasted environmental characteristics at nest sites to random locations. Each year, 2009–2011, we generated independent random points equal to the number of nests detected ($n = 18$, 2009; $n = 20$, 2010; $n = 33$, 2011) within a GIS. For random points, we employed the same measurements conducted at nest sites but centered measurements around the nearest qualifying shrub (Connelly et al. 2004) to characterize available habitat. To make inferences at the population level, we employed sampling protocol A, described in Manly et al. (2002), in which random points are independent of used points and are evaluated across the study site. This was appropriate for our study because sage-grouse are capable of long-distance movements (Fedy et al. 2012). We standardized all factors from used and random locations $[(X - \text{mean})/\sigma]$ for analyses and back transformed coefficients for data interpretation.

Analysis I: Nest-site selection.—We developed RSFs for nesting sage-grouse by following a Design II (Manly et al. 2002) approach by contrasting measurements of each environmental factor from used and random locations using generalized linear mixed models (GLMM, binomial distribution; Zuur et al. 2009). To account for temporal variation over the duration of the study, we fit a random intercept to year in all models. This random effect accounts for inter-annual variation in differences between random locations and nests to avoid confounding fixed effects (Zuur et al. 2009). To avoid multicollinearity, we omitted variables that covaried ($r \geq |0.65|$; Menard 1995).

Although variables were based on a priori hypotheses (Burnham and Anderson 2002), we compared and evaluated models using a multi-step exploratory approach. First, we formed groups of models with the models in each group composed of factors that shared common environmental features such as micro-habitat or canopy cover (Table 1). We compared models within each group to identify the most explanatory single-factor models within each group (Table 2). In this process, we evaluated each factor at each of the micro-site spatial scales (0.01 ha, 0.03 ha, 0.2 ha, 0.8 ha, and 3.1 ha) for which we obtained field measurements or at macro-habitat scales (39 ha, 148 ha, 617 ha, 2,470 ha, and 15,527 ha). No single model within a group included ≥ 1 spatial scale. We evaluated 16 single-factor models for micro-site habitat selection (Table 1). The model set examining shrub canopy (sagebrush spp., other shrub, and total shrub cover) consisted of 15 models (Table 1). At macro-habitat scales, we evaluated pinyon-juniper woodlands, basin sagebrush spp., montane sagebrush spp., total sagebrush cover, invasive grasslands (i.e., grass), and perennial grasslands creating 30 total models, 1 model for each scale per variable (Table 1). We developed 3 models to examine the topographical attributes of elevation, slope, and aspect (Table 1). Evaluation of single-factor models at multiple spatial scales allowed us to identify the most explanatory factor at the most appropriate spatial scale within a group of related factors.

Model support was determined using Akaike's Information Criterion (AIC; Akaike 1973) with second-order bias correction (c; Anderson 2008). We evaluated model uncertainty by calculating differences between AIC_c (ΔAIC_c). We calculated model probabilities ($w_{\text{model } i}$; Anderson 2008) and evidence ratios ($\text{ER} = w_{\text{model } i}/w_{\text{model } j}$) for the most explanatory model compared to other models within the group of models (Anderson 2008). We used likelihood ratio tests (Anderson 2008) to evaluate each model fit relative to a null model (intercept and random effects only; $\alpha = 0.05$).

Table 1. Means ± standard error (SE) of factors used in model analyses of nest-site selection and nest survival for greater sage-grouse nests in the Virginia Mountains, Nevada, 2009–2011.

			Available		Used	
Group	**Variable**	**Scale (ha)**	**Mean**	**SE**	**Mean**	**SE**
Micro-habitat	Overhead cover (%)	0	68.4	8.1	72.1	8.6
	Horizontal cover (%)	0	74.0	8.8	77.8	9.2
	Vertical cover (%)	0	56.1	6.7	60.5	7.2
	Perennial grass (%)	0.2	8.9	1.1	11.4	1.4
	Cheatgrass (%)	0.2	13.3	1.6	7.1	0.8
	Perennial forb (%)	0.2	7.9	0.9	10.8	1.3
	Annual forb (%)	0.2	4.9	0.6	6.2	0.7
	Residual cover (%)	0.2	10.2	1.2	9.6	1.1
	Litter (%)	0.2	15.9	1.9	18.8	2.2
	Bare ground (%)	0.2	22.8	2.7	19.1	2.3
	Rock (%)	0.2	16.3	1.9	17.9	2.1
	Sagebrush height (cm)	0.2	14.7	1.8	11.0	1.3
	Other shrub height (cm)	0.2	22.1	2.6	29.8	3.5
	Perennial grass height (cm)	0.2	30.1	3.6	30.5	3.6
	Perennial forb height (cm)	0.2	15.7	1.9	19.9	2.4
	Residual grass height (cm)	0.2	23.4	2.8	25.7	3.1
Shrub canopy cover	Sagebrush (%)	0.01	2.2	0.3	4.2	0.5
		0.03	2.8	0.3	4.8	0.6
		0.2	3.6	0.4	4.7	0.6
		0.8	3.5	0.4	4.6	0.5
		3.1	3.4	0.4	4.3	0.5
	Other shrub (%)	0.01	4.9	0.6	10.4	1.2
		0.03	5.6	0.7	11.1	1.3
		0.2	6.1	0.7	11.3	1.4
		0.8	6.2	0.7	11.0	1.3
		3.1	6.1	0.7	10.7	1.3
	Total shrub (%)	0.01	7.6	0.9	14.6	1.7
		0.03	8.8	1.1	15.8	1.9
		0.2	10.1	1.2	16.1	1.9
		0.8	10.1	1.2	15.6	1.9
		3.1	10.1	1.2	15.0	1.8
Macro-habitat	Pinyon-Juniper (ha)	39	8.2	1.0	9.3	1.1
		148	32.6	3.9	35.5	4.2
		617	143.4	17.0	151.8	18.0
		2,470	586.6	69.6	648.1	76.9
		15,527	4,033.7	478.7	4,987.3	591.9
	Montane sagebrush (ha)	39	7.2	0.9	10.4	1.2
		148	27.8	3.3	38.7	4.6
		617	117.0	13.9	168.1	20.0
		2,470	464.6	55.1	646.8	76.8
		15,527	2,552.4	302.9	3,345.4	397.0
	Basin sagebrush (ha)	39	7.1	0.8	4.1	0.5
		148	28.7	3.4	17.7	2.1
		617	128.6	15.3	73.8	8.8
		2,470	457.6	54.3	291.1	34.5
		15,527	2,849.9	338.2	2,133.1	253.2
	Total sagebrush (ha)	39	14.3	1.7	14.4	1.7
		148	56.5	6.7	56.4	6.7
		617	245.6	29.2	242.0	28.7
		2,470	922.2	109.4	937.8	111.3
		15,527	5,402.3	641.1	5,478.5	650.2
	Perennial grasslands (ha)	39	0.0	0.0	0.0	0.0
		148	0.1	0.0	0.1	0.0
		617	0.5	0.1	0.7	0.1
		2,470	4.6	0.5	3.0	0.4
		15,527	50.2	6.0	52.7	6.3
	Invasive grasslands (ha)	39	11.0	1.3	13.7	1.6
		148	38.1	4.5	49.4	5.9
		617	140.8	16.7	195.1	23.2
		2,470	534.0	63.4	673.0	79.9
		15,527	2,641.2	313.5	2,855.2	338.9
Topographical	Elevation (m)	0.03	1,736.2	206.1	1,934.5	229.6
	Slope (°)	0.03	12.0	1.4	12.4	1.5
	Aspect	0.03	n/a	n/a	n/a	n/a

Table 2. Resource selection models ($\Delta AIC_c \geq 2$ less than the $null_{YEAR}$) of sage-grouse nests ($n = 71$) from data collected in the Virginia Mountains, Nevada, 2009–2011. K = number of parameters; LL = log-likelihood; ΔAIC_c = difference between Akaike's Information Criterion with second-order bias correction for the model of interest and the most explanatory model; w = model probability, ER = evidence ratio (e.g., $w_{model\ 1}/w_{model\ 2}$; Anderson 2008). χ^2 = Chi-square statistic to test log ratio model fit relative to null.

Step[a]	Group[b]	Model[c]	Model	K	LL	ΔAIC_c	w	ER	χ^2
I	Micro-habitat	Cheatgrass (%) (−)	1	3	−91.0	0.0	0.96		14.8
		Other shrub height (cm) (+)	2	3	−95.3	8.6	0.01	74.8	6.2
		Perennial grass (%) (+)	3	3	−95.6	9.1	0.01	95.6	5.7
		Perennial forb height (cm) (+)	4	3	−95.7	9.3	0.01	105.6	5.5
	Shrub canopy cover	Total_0.01 (%) (+)	5	3	−89.7	0.0	0.33		17.5
		Total_0.03 (%) (+)	6	3	−90.9	2.4	0.10	3.3	15.2
		Total_0.8 (%) (+)	7	3	−92.0	4.6	0.03	9.8	12.9
		Total_0.2 (%) (+)	8	3	−92.2	5.0	0.03	12.4	12.5
		Total_3.1 (%) (+)	9	3	−93.0	6.7	0.01	28.1	10.9
	Macro-habitat	Montane sage_617 (ha) (+)	10	3	−91.2	0.0	0.35		14.5
		Montane sage_2470 (ha) (+)	11	3	−91.3	0.2	0.32	1.1	14.3
		Montane sage_15527 (ha) (+)	12	3	−91.5	0.7	0.25	1.4	13.8
		Montane sage_148 (ha) (+)	13	3	−93.6	4.8	0.03	11.0	9.7
		Montane sage_39 (ha) (+)	14	3	−94.4	6.3	0.02	23.8	8.1
	Topographical	Elevation (m) (+)	15	3	−91.4	0.0	0.8		14.1
		Aspect	16	9	−86.7	2.6	0.21	3.7	23.5
II	Combined (Individual)	Total_0.01 (%) (+)	17	3	−89.7	0.0	0.59		17.5
		Cheatgrass (%) (−)	18	3	−91.0	2.7	0.15	3.8	14.8
		Montane sage_617 (ha) (+)	19	3	−91.2	3.1	0.13	4.6	14.5
		Elevation (m) (+)	20	3	−91.4	3.4	0.10	5.6	14.1
		Aspect	21	9	−86.7	6.1	0.03	20.7	23.5
	Combined (Additive)	Total_0.01 (%) (+) + Cheatgrass (%) (−)	22	4	−84.0	0.0	0.43		28.9
		Total_0.01 (%) (+) + Montane sage_617 (ha) (+)	23	4	−84.3	0.5	0.33	1.3	28.4
		Total_0.01 (+) + Aspect	24	10	−78.6	1.1	0.24	1.8	39.7

[a] Step I – compared models ($n = 55$) within each scale. Models that met 2 criteria ($\Delta AIC_c \geq 4$ less than the $null_{YEAR}$ and fit data significantly better than the $null_{YEAR}$ model based on likelihood ratio tests) were included in Step II. Step II compared models that were developed with ≤2 single-factor combinations based on a priori hypotheses (total models, $n = 14$).

[b] Analysis grouped by common biological factors.

[c] Model statements represent fixed factors in each binomial model and random intercept for year was fit to each model. Signs within parentheses indicate units and direction of association with the factor of interest. Total represents percentage of total shrub cover. We show the scale of the parameter (in ha) for total shrub cover and macro-habitat after the underscore following the parameter name.

In step II, we extracted the most explanatory single-factor models from step I and compared them to one another and also developed 9 multi-factor additive models based on a priori hypotheses consisting of combinations of factors from the most explanatory single-factor models from step I. We included only those models from step I that satisfied the following requirements: 1) $\Delta AIC_c \geq 4$ less than the $null_{YEAR}$ and 2) the model fit the data better than the $null_{YEAR}$ model. No additive model in step II included >2 factors to avoid over parameterizing models beyond our sample sizes.

Analysis II: Nest survival.—Using an information-theoretic approach (Burnham and Anderson 2002), we evaluated the same candidate models from analysis I (Table 1) using R statistical software with the RMark package (R Version 2.13; Laake and Rexstad 2007) that implements MARK (White and Burnham 1999) to estimate the effects of multiple environmental factors on nest survival probability. We used the same candidate models from analysis I because we were interested in links between RSF and survival probability. In this analysis, we used a 3-step modeling approach where 1) we investigated variation in survival among years, 2) we investigated groups of models that shared similar factors (identical to groups used in analysis I; Table 1) based on a priori hypotheses, and 3) we developed and compared models within a final set based on those factors identified as important in step II of this analysis. We used change in AIC_c and AIC_c weights to evaluate individual model strength relative to the $null_{YEAR}$ model (Anderson 2008). We considered individual models supported by factors when AIC_c was less than the $null_{YEAR}$ model and $\Delta AIC_c \geq 2$ relative to the $null_{YEAR}$ model.

Analysis III: Linking nest-site selection to nest survival.—To link nest-site selection to nest survival probability, we used only those factors identified as important for influencing nest-site selection (step I; Table 2) in this analysis. We used the same modeling approach outlined in analysis II using R statistical software with the RMark package (R Version 2.13; Laake and Rexstad 2007) to evaluate nest survival relative to nest-site selection parameters. To do this, we first characterized nest-site selection parameters based on availability (i.e., independent random locations) by taking the mean of those variables. Then, to create selection coefficients, we divided values of habitat variables for used locations by the mean of available and log transformed the data. Doing so, normalized selection coefficients to be used in the nest survival analysis relative to what was available at the population level. By incorporating the log ratios of nest-site selection coefficients in a nest survival analysis, we were able to analyze whether sage-grouse selection for a particular factor or combination of factors translated into significant changes in survival probability for sage-grouse nests. We used the same criterion ($AIC_c \geq 2$ less than the $null_{YEAR}$) to evaluate model support.

RESULTS

Nest-Site Selection

We evaluated 71 nest and 71 independent random locations ($n = 18$, 2009; $n = 20$, 2010; $n = 33$, 2011). Seven nests were abandoned. We included these nests in our analysis because abandonment was not investigator induced. Nest initiation rate across all females and all years was 88.8% (SE = 0.10). Most nests were located under shrubs (88.7%), consisting of sagebrush species (31.0%), rabbitbrush (26.7%), and other shrub species (31.0%). Bunchgrasses were the primary nesting cover for 9.9% of nests.

Micro-habitat.—Female sage-grouse avoided nesting in areas with increased cheatgrass abundance. Cheatgrass abundance was the single greatest micro-habitat feature distinguishing nests from random sites ($w_{\text{model 1}} = 0.96$; Table 2). The evidence ratio for model 1 ($w_{\text{model 1}}/w_{\text{model 2}}$) indicated that this model was 75 times more likely to represent resource selection of nest sites within this group of factors than the next best model, which was other shrub height ($w_{\text{model 2}} = 0.01$; Table 2). Average abundance of cheatgrass at nests and random sites was 7.1% (SE = 1.0) and 13.3% (SE = 1.2), respectively (Table 1).

Based on model selection, we also found strong support for increased percent shrub canopy cover influencing nest-site selection, but we did not observe a distinctive effect of solely sagebrush. Factors composed of shrub canopy cover estimated at 5 micro-site spatial scales (0.01 ha, 0.03 ha, 0.2 ha, 0.8 ha, and 3.1 ha) did not show support for selection of sagebrush species alone. We found strong support, however, that sage-grouse selected for increased percent of the total shrub cover at each of these micro-site spatial scales (Table 2). The strongest support for selection of increasing percent shrub cover occurred at the 0.01-ha scale ($w_{\text{model 5}} = 0.33$; Table 2). This scale was 3.3 times more likely to be the most explanatory scale for percent shrub selection than the next best model at 0.03 ha (i.e., $w_{\text{model 6}} = 0.10$; Table 2). At the 0.01-ha spatial scale, females selected nest sites with an average 14.6% (SE = 1.2) shrub cover compared to 7.6% (SE = 1.1) at available locations (Table 1).

Macro-habitat.—Analysis of habitat features at the landscape scale revealed the strongest support for selection of habitats with higher percentages of montane sagebrush species (Table 2). We did not find support for selection or avoidance of pinyon-juniper woodlands, perennial grasslands, or invasive grasslands based on availability at macro-habitat scales. Selection for montane sagebrush was best supported at the 617-ha ($w_{\text{model 10}} = 0.35$), 2,470-ha ($w_{\text{model 11}} = 0.32$), and 15,527-ha ($w_{\text{model 12}} = 0.25$; Table 2) scales. The evidence ratio ($w_{\text{model 10}}/w_{\text{model 11}}$) indicated that montane sagebrush at the 617-ha scale was 1.1 times more likely to represent resource selection compared to the next best model at the 2,470-ha scale.

Topographical features.—More nest sites occurred at higher elevations and on east or northeasterly facing aspects compared to available sites. The strongest model describing selection for topographical features consisted of elevation ($w_{\text{model 15}} = 0.8$) followed by aspect ($w_{\text{model 16}} = 0.21$; Table 2). Elevation was 3.7 times more likely to describe resource selection compared to aspect. We did not find support for selection of slope.

Step II evaluated single-factor models and also additive models that were based on a priori hypotheses. The set of models to be compared in step II began with 8 single-factor models (cheatgrass abundance; shrub cover within 0.01 ha and 0.03 ha; montane sagebrush at the 617-ha, 2,470-ha, and 15,526-ha scales; elevation; and aspect) from step I. To include only the most explanatory spatial scale for each single factor, we reduced this set of models to 5 single-factor models after estimating that shrub cover at the 0.01-ha scale was 3.3 times more likely to represent resource selection than the 0.03-ha scale (Table 2) and montane sagebrush at the 617-ha scale was 1.1 and 1.4 times more likely to represent resource selection compared to the 2,470-ha and 15,526-ha scales, respectively (Table 2). Therefore, we dropped the 3 single-factor models consisting of shrub cover at the 0.03-ha scale and montane sagebrush at the 2,470-ha and 15,526-ha spatial scales. We also evaluated 9 additive models consisting of 2-factor combinations derived from the 5 single-factor models in step I in the final model set for step II.

The most explanatory model for nest-site selection was a 2-factor additive model consisting of total shrub cover at the 0.01-ha scale and cheatgrass abundance ($w_{\text{model 22}} = 0.4$; Table 2). This model was 1.3 times more likely to represent resource selection compared to the next best 2-factor additive model consisting of shrub cover at the 0.01-ha scale and montane sagebrush at the 617-ha scale ($w_{\text{model 23}} = 0.3$; Table 2). The most explanatory single-factor model was shrub canopy cover at the 0.01-ha scale ($w_{\text{model 17}} = 0.59$; Table 2).

Nest Survival

Daily survival rates were evaluated over 37 days consisting of 7 days of egg-laying and 30 days of incubation under the assumption that incubation begins with the penultimate egg (Coates and Delehanty 2010). The intercept-only survival model estimated cumulative survival probability to be 22.4% (95% CI: 13.0–33.4%). Year accounted for significant variation in nest survival ($w_{\text{model 1}} = 0.93$; Table 3) compared to the intercept-only survival model ($w_{\text{model 2}} = 0.07$). Thus, we included year in all subsequent models as a fixed effect to account for inter-annual variation (Table 3).

Micro-habitat.—Among micro-habitat factors, the most explanatory model predicting nest survival was horizontal cover at the nest site ($w_{\text{model 3}} = 0.98$; Table 3). Odds of nest survival increased by 4.4% (CI 95%: 2.1–6.7%) with each additional 1% increase in amount of horizontal cover present at the nest bowl (Fig. 2). Shrub canopy cover was positively related to nest survival at the 0.8-ha ($w_{\text{model 4}} = 0.50$; Table 3) and 3.1-ha ($w_{\text{model 5}} = 0.43$) spatial scales. We did not find support for an effect on survival when we examined shrub canopy cover differentiated by sagebrush species or by other shrub species separately. Model support was formed by the combined total shrub cover component at these spatial scales.

Macro-habitat.—We found support for increased nest survival in areas with reduced montane perennial grasses at

Table 3. Nest survival models for sage-grouse nests ($n = 71$) in the Virginia Mountains, Nevada, 2009–2011. We considered models ≥ 2 AIC_c units less than the $null_{YEAR}$ to be significant at contributing to probabilities of nest survival. We do not include other, unsupported models in this table. LL = log-likelihood; K = number of parameters; AIC_c = Akaike's Information Criterion with second-order bias correction; ΔAIC_c = difference between model of interest and most explanatory model with second-order bias correction; w = model probability.

Step[a]	Group[b]	Model[c]	Model	LL	K	AIC_c	ΔAIC_c	w
I	Annual variation	Year	1	−115.8	3	237.6	0.0	0.93
		Intercept-only	2	−120.4	1	242.8	5.2	0.07
II	Micro-habitat	Horizontal cover (%)	3	−109.1	4	226.1	0.0	0.98
		$Null_{YEAR}$		−115.8	3	237.6	11.5	0.02
	Shrub canopy cover	Total_0.8 (%)	4	−112.9	4	233.7	0.0	0.50
		Total_3.1 (%)	5	−113.0	4	234.0	0.3	0.43
		$Null_{YEAR}$		−115.8	3	237.6	3.9	0.07
	Macro-habitat	Montane grass_39 (ha)	6	−113.5	4	234.9	0.0	0.50
		Total sage_15527 (ha)	7	−113.8	4	235.6	0.6	0.36
		$Null_{YEAR}$		−115.8	3	237.6	2.7	0.13
III	Combined	Horizontal cover (%)	8	−109.1	4	226.1	0.0	0.93
		Total_0.8 (%)	9	−112.9	4	233.7	7.6	0.02
		Total_3.1 (%)	10	−113.0	4	234.0	7.9	0.02
		Montane grass_39 (ha)	11	−113.5	4	234.9	8.8	0.01
		Total sage_15527 (ha)	12	−113.8	4	235.6	9.4	0.01
		$Null_{YEAR}$		−115.8	3	237.6	11.5	0.00

[a] Step I compared variation between years to an intercept-only survival model. Step II investigated groups of models that shared similar factors based on a priori hypotheses. Step III compared individual models identified as important in step II to determine most explanatory models predicting probabilities of nest survival.

[b] Factors for the topographical group were not found to explain variation in nest survival more than the $null_{YEAR}$, and therefore we do not list them in the table.

[c] Total represents percentage of total shrub cover. We show the scale (in ha) for total shrub cover and montane grass after the underscore following the parameter name.

the 39-ha scale ($w_{model\,6} = 0.50$; Table 3). Additionally, we found support for increased survival at the largest spatial scale (15,527 ha) for total sagebrush ($w_{model\,7} = 0.36$). No topographical (elevation, slope, aspect) factors explained nest survival for sage-grouse at macro-habitat spatial scales.

In step III (Table 3), we compared models to one another from the set of models identified as important in step II. Horizontal cover was strongly supported and was the most explanatory model ($w_{model\,8} = 0.93$; Table 3) followed by shrub canopy cover at the 0.8-ha scale, and shrub canopy cover at the 3.1-ha scale ($w_{models\ 9\ and\ 10} = 0.02$). We evaluated only single-factor models in this step to increase ease of interpretation, to avoid over-parameterizing models, and to prevent confounding results by incorporating multiple habitat factors with the same spatial resolution in a single model.

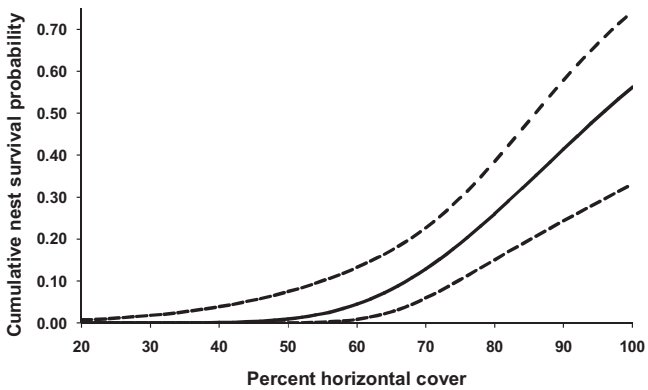

Figure 2. Cumulative nest survival probability for sage-grouse nests in the Virginia Mountains, Nevada from 2009 to 2011 with increasing horizontal cover at the nest bowl. Solid line represents parameter estimates for the effect of horizontal cover on nest survival and dashed lines indicate 95% CI.

Linking nest-site selection to nest survival.—We found support only for shrub canopy cover at the 0.8-ha and 3.1-ha spatial scales ($w_{models\ 1\ and\ 2} = 0.18$ and 0.16, respectively; Table 4). Nest survival increased by 4.4% (95% CI: 1.6–12.0%) when female sage grouse selected nest sites with an additional 1% increase in shrub cover within 0.8 ha (Table 4; Fig. 3). We did not find support that other factors selected by female sage-grouse explained nest survival.

DISCUSSION

In the Virginia Mountains, an area affected by a large wildfire 10 years prior to our study, we analyzed factors influencing sage-grouse nest-site selection, nest survival probability, and modeled the capacity of nest-site selection factors to predict nest survival. Estimated cumulative nest survival was 22.4%, a rate that is lower than other Great Basin estimates (Rebholz et al. 2009, Coates and Delehanty 2010, Bell 2011), and remains a concern regarding the long-term viability of this population if this low rate of nest survival were to continue. Additionally, we found that percentage shrub canopy cover best explained nest-site selection and survival for sage-grouse, despite a rarity of shrubs compared to unburned sagebrush steppe habitats in other regions of core sage-grouse range. Furthermore, sage-grouse in the Virginia Mountains did not select nest sites in areas dominated by cheatgrass. These findings emphasize the fundamental importance of shrub communities for nesting sage-grouse and the sensitivity of female sage-grouse in selecting these areas for nesting (Connelly et al. 2011).

Table 4. Nest survival models for sage-grouse nests ($n = 71$) in the Virginia Mountains, Nevada, 2009–2011 based on selection coefficients from analysis of nest-site selection. We considered models ≥ 2 AIC_c units less than the $null_{YEAR}$ to be significant at contributing to probabilities of nest survival and are indicated with an asterisk (*). LL = log-likelihood; K = number of parameters; AIC_c = Akaike's Information Criterion with second-order bias correction; ΔAIC_c = difference between model of interest and most explanatory model with second-order bias correction; w = model probability.

Model[a]	Model	LL	K	AIC_c	ΔAIC_c	w
Total_0.8 (%)*	1	−113.6	4	235.2	0.0	0.18
Total_3.1 (%)*	2	−113.7	4	235.4	0.2	0.16
Total_0.2 (%)	3	−113.9	4	235.7	0.6	0.14
Total_0.03 (%)	4	−114.1	4	236.2	1.1	0.11
$Null_{YEAR}$	5	−115.8	3	237.6	2.4	0.05
Cheatgrass (%)	6	−114.9	4	237.8	2.7	0.05
Elevation (m)	7	−115.1	4	238.1	3.0	0.04
Total_0.01 (%)	8	−115.1	4	238.2	3.1	0.04
Perennial grass (%)	9	−115.4	4	238.9	3.7	0.04
Montane sage_2470 (ha)	10	−115.5	4	239.0	3.8	0.03
Perennial forb height (cm)	11	−115.5	4	239.1	3.9	0.03
Montane sage_617 (ha)	12	−115.6	4	239.1	4.0	0.02
Montane sage_39 (ha)	13	−115.6	4	239.2	4.0	0.02
Montane sage_15527 (ha)	14	−115.7	4	239.3	4.2	0.02
Other shrub height (cm)	15	−115.7	4	239.5	4.3	0.02
Montane sage_148 (ha)	16	−115.8	4	239.6	4.4	0.02

[a] Total represents percentage of total shrub cover. We show the scale (in ha) for total shrub cover and montane sage after the underscore following the parameter name.

* Total shrub cover, at the 3.1-ha and 0.8-ha spatial scales, were the only factors identified that contributed to increased nest survival probabilities when female sage-grouse selected nest sites with greater abundance of total shrub cover at these spatial scales.

The low cumulative nest survival estimate of 22.4%, avoidance of cheatgrass for selection of nest sites, and the propensity to select nest sites in areas with greater percent shrub canopy cover suggest that the habitat in the Virginia Mountains may not be adequate for nesting sage-grouse. This likely is the result of the wildfire that occurred 10 years prior to our study, despite significant efforts to rehabilitate the habitat following the wildfire. Our results suggest a habitat still not recovered 10 years following wildfire and subsequent compromised nesting success as a result of poor habitat quality. This pattern corroborates trends found by Arkle et al. (2014) in their multi-scale occupancy modeling assessment on the effectiveness of post-fire restoration treatments relative to sage-grouse habitat quality throughout the Great Basin that found burned areas require $\geq$20 years to re-establish sagebrush cover using past restoration methodologies. These findings, in conjunction with our results, suggest more thoughtful and intensive conservation practices are needed in the Virginia Mountains to protect the highest quality sage-grouse habitats currently on the landscape while simultaneously working to restore native shrub habitats affected by wildfire.

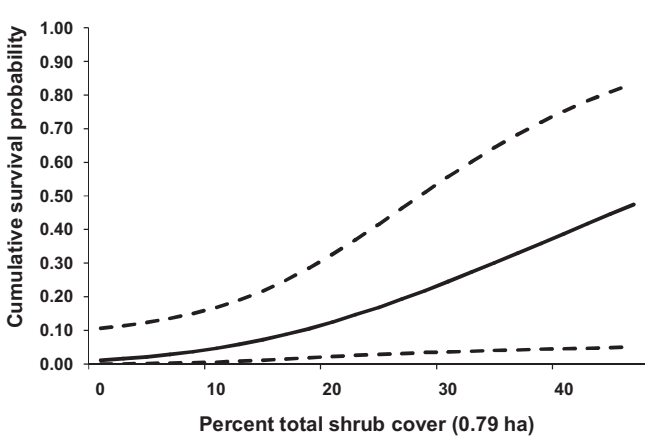

Figure 3. Cumulative nest survival probability for sage-grouse nests in the Virginia Mountains, Nevada from 2009 to 2011 given selection for nest sites with increased shrub canopy cover at the 0.8-ha scale. Solid line represents parameter estimates for the effect of nest site selection of total shrub cover (0.8 ha) on nest survival and dashed lines indicate 95% CI.

Climatic conditions varied greatly across years, and sample sizes were relatively small. As such, continued research efforts for this sage-grouse population are needed to further validate observed outcomes. Despite these limitations, our results suggest that actions in the Virginia Mountains focused on effective fire abatement and improved rehabilitation efforts at sites with disturbed shrub communities could increase long-term nest survival rates for this population of sage-grouse. Our results suggest that at a scale of 0.8 ha, a total percentage shrub canopy cover of $\geq$40% could yield cumulative nest survival estimates similar to other populations in the Great Basin (Fig. 3). For example, Rebholz et al. (2009) estimated nest survival for sage-grouse in the Montana Mountains of Nevada at 36% and calculated the percent total shrub cover within 20 m of the nest bowl at 37.2%. Similarly, Coates and Delehanty (2010) estimated the probability of sage-grouse nest survival at 42% in northeastern Nevada and suggested $\geq$40% total shrub cover within 25 m of the nest bowl for the benefit of sage-grouse. Bell (2011), in Modoc Country, California, estimated nest survival at 45% and attributed increased grass height within 0.03 ha of the nest and greater sagebrush shrub canopy diameter directly over the nest bowl to be the strongest models predicting nest survival; however, the author did not provide precise target management recommendations for grass height and nest shrub canopy diameter.

In the Virginia Mountains, sage-grouse selected areas with large expanses of sagebrush for nesting, but within those larger spatial scales the amount of total shrub cover,

regardless of shrub species, was important in nest-site selection. At macro-habitat spatial scales (39 ha, 148 ha, 617 ha, 2,470 ha, and 15,527 ha), we found support for selection of montane sagebrush communities. This sagebrush community offers a diversity of shrub species, and despite exhibiting lower sagebrush densities may still provide adequate nest concealment for some grouse. However, a critical factor for nest micro-site selection consisted of increased shrub cover at the smallest spatial scale. Large-scale sagebrush removal can result in significant declines in sagebrush obligate bird species (Magee et al. 2011). Beck et al. (2011), in a synthesis analysis, evaluated the influence of prescribed burning on nesting habitat for sage-grouse across 6 states and found prescribed burning to be detrimental for nesting and brood rearing habitats. Based on our results and others in Nevada (Rebholz et al. 2009, Coates and Delehanty 2010), actions or other disturbances that result in significant reduction of shrub cover would likely negatively influence nest survival for sage-grouse in the Great Basin.

Strong emphasis has been placed on the presence of sagebrush for nesting sage-grouse (Klebenow 1970, Braun et al. 1976, Connelly et al. 2000, Holloran et al. 2005), and our results support these findings at a landscape scale. But the apparent sensitivity of female sage-grouse to the amount of total shrub cover as micro-habitat, regardless of whether or not the cover is sagebrush, merits further attention. The importance of total shrub cover identified here corroborates other studies in the southwestern portion of sage-grouse range (Kolada et al. 2009*a*, Coates and Delehanty 2010). In Mono County, California, total shrub cover showed greater support than sagebrush-only cover in nest-site selection models (Kolada et al. 2009*a*) and cover of non-sagebrush shrub species explained the most variation in survival (Kolada et al. 2009*b*). Notably, our Nevada study area experienced a large fire in 1999 that reduced the abundance of shrubs. In fire-affected habitats such as ours, sage-grouse may be selecting areas for nesting that still provide adequate nest concealment, despite a lack of sagebrush species. Our results demonstrate that sage-grouse still select concealment using shrub species other than sagebrush albeit at the expense of nest survival. Given the long recovery time and minimal benefit of past post-fire restoration efforts (Arkle et al. 2014), managers should consider the short-term benefits that other shrub species may provide to nesting sage-grouse along with the long-term goal of establishment of sagebrush cover.

Sage-grouse did not select nest sites in areas with greater percent cover of cheatgrass at the micro-site spatial scale (0.2 ha). The presence of cheatgrass in the Virginia Mountains is largely the result of previous wildfires. Cheatgrass is an invasive annual grass that quickly becomes established in disturbed sagebrush-steppe landscapes before many native species recover from the disturbance (Stewart and Hull 1949, D'Antonio and Vitousek 1992). Cheatgrass may replace sagebrush as the dominant plant (Stewart and Hull 1949, Balch et al. 2013). Cheatgrass invasion has led to declines in numerous species within the Great Basin (Yensen et al. 1992, Humple and Holmes 2006, Hall et al. 2008). The Nevada State Plan (Nevada Department of Wildlife 2004) identified wildfire as a primary factor threatening sage-grouse habitat. In the Virginia Mountains and elsewhere in Nevada, cheatgrass has already established and the potential for further cheatgrass expansion is high given Nevada's susceptibility to wildfire. Rehabilitation efforts that promote establishment of native shrub and perennial grass in burned areas will be an important management practice towards habitat recovery for sage-grouse. However, protection and maintenance of current intact sagebrush habitats should also be considered a priority, recognizing that returning important native shrub habitats to pre-wildfire conditions can be a long process (Arkle et al. 2014).

Increased horizontal cover was not selected by sage-grouse but explained variation in nest survival. The horizontal cover metric was not specific to any particular type of vegetation but rather an all-inclusive measure of concealment of the nest bowl. Conover et al. (2010) determined that sage-grouse in Wyoming and Utah selected nest sites with greater concealment from visual predators (i.e., ravens) but not olfactory predators (i.e., badgers). These findings support our results in that sage-grouse experienced higher nest survival rates where visual concealment was greater and may be the result of avoidance from visual predators in an area with similar olfactory and visual predators (Lockyer et al. 2013). Conversely, others have suggested that microclimate may be a greater selection pressure than predation in grouse (Bergerud and Gratson 1988, Wiebe and Martin 1998, Yost et al. 2008). Yost et al. (2008) examined nest-site selection for sage-grouse in southeastern Oregon relative to biophysical features using predictive modeling techniques. They found support for selection of topographical features such as elevation and aspect but after further analyses found that when these predictor variables were removed, vegetation predictor variables best explained nest-site selection. In terms of nest survival, managers could consider the benefit of both horizontal and shrub canopy cover for nesting sage-grouse. Where prescribed burning or other shrub manipulation practices remain viable sagebrush management tools, such as described in the Nevada State Plan (Nevada Department of Wildlife 2004), managers could consider avoiding actions that reduce shrub canopy cover below 40% as well as the associated horizontal cover.

Sage-grouse selected nest sites at higher elevations and on east-northeastern facing aspects. Some studies have shown that female sage-grouse have strong fidelity to specific nesting areas (Fischer et al. 1993, Holloran et al. 2010) possibly returning to previously successful nesting or brood-rearing areas (Bergerud and Gratson 1988). In a stable environment, simple behavioral rules such as these could benefit females. However, after landscape-scale plant community change (i.e., wildfire) or a shifting predator community, such site fidelity could be maladaptive. Under these circumstances, management practices that restore disturbed habitats would be valuable for nesting sage-grouse, but will likely require long-term restoration efforts.

Another probable explanation for selection of higher elevation is related to anthropogenic development. For example, females may be avoiding lower elevation areas for

nesting because lower elevations could be more closely associated with human activities (e.g., roads, transmission lines, etc.) with more abundant generalist predators. Increased raven densities have been associated with anthropogenic activities (Kristan and Boarman 2007, Bui et al. 2010), especially linear features such as roads and transmission lines (Howe et al. 2014). If higher elevations offer greater distance from concentrations of predators, one might expect sage-grouse to locate nests sites in these areas. Alternatively, females may be seeking out optimal sites to raise broods following nest hatch such as high elevation plant communities or areas near upland springs that are important for brood survival (Casazza et al. 2011). Sage-grouse nest-site selection relative to topographical features warrants further study to better understand the mechanisms associated with this relationship.

Cumulative nest survival for the Virginia Mountain population (22.4%) was lower than other published results using maximum likelihood within the Great Basin of 36% (Rebholz et al. 2009) and 42% (Coates and Delehanty 2010). Bell (2011) estimated cumulative nest survival for a population of sage-grouse to the northwest of our study in Modoc County, California, to be 45% from 2009 to 2011, the same years of study as for the Virginia Mountain population. Vital rates for other life stages for the Virginia Mountain population have not been analyzed, but contemporaneous estimates from Bell (2011) along with previously mentioned Great Basin nest survival estimates suggest that low nest survival could limit this Nevada population. Multiple factors are likely influencing low nest survival, but a landscape that is recovering from wildfire coupled with high nest depredation rates (Lockyer et al. 2013) are likely important considerations. Nest survival rates are highly variable, both spatially and temporally, across sage-grouse populations (Taylor et al. 2012), and such a low nest survival rate for a small population like the Virginia Mountains is of considerable concern.

This study was not without constraints and limitations. The nest-site selection analysis was based on resources that vary at multiple spatial scales and are subjected to cross-scale correlations (i.e., correlations between predictor variables at multiple spatial scales; Battin and Lawler 2006, Mahonon et al. 2008), which can bias model parameter estimates. However, we evaluated diagnostic correlations between factors across each of the spatial scales and did not detect evidence of multicollinearity between factors considered at different scales. Factors that showed strong support for selection likely were independent of other factors at different spatial scales. An important potential limitation in interpreting the macro-habitat scale (39 ha, 148 ha, 617 ha, 2,470 ha, and 15,527 ha) results was the spatial resolution of the Nevada Vegetation Synthesis Map (Nevada National Heritage Program 2008) where large amounts of sagebrush cover consist of multi-species stands of shrubs, but the resolution of this map was not capable of detecting shrub composition in detail. Thus, the cover type is classified as dominated by sagebrush, even though other types of shrubs are within those areas.

Understanding processes and factors that influence habitat-based selection decisions for wildlife populations is important and informative for conservation (Connelly et al. 1991, Kolada et al. 2009*a*). Although these selection decisions are expected to enhance reproductive success and survival, accurately evaluating population status and trajectories is difficult without identifying specific links between selection decisions and measures of reproductive success (Aldridge and Boyce 2007, Casazza et al. 2011, Dzialak et al. 2011). For sage-grouse and many other imperiled species, analyses that successfully identify links between selection decisions and reproductive success can better guide conservation actions that promote species persistence and recovery. For example, the nest-site selection analysis (analysis I) identified multiple environmental factors influencing nest-site selection, but only the amount of shrub cover selected by females influenced their nest survival probabilities. These findings portray a sage-grouse population with compromised nest survival 10 years following a fire, despite efforts by land managers to rehabilitate this perturbed, high elevation habitat through aerial reseedings. If these low levels of nest survival were to continue, persistence for this population of sage-grouse could be at risk. Management practices focused on fire abatement in conjunction with improved vegetation rehabilitation techniques will likely benefit nesting sage-grouse.

MANAGEMENT IMPLICATIONS

The Virginia Mountains study area resembled an area with 10 years of recovery following a wildfire. Within this fire-affected landscape, sage-grouse selected nest sites with increased shrub canopy cover and achieved higher probabilities of nest survival when greater percentages of shrub cover were selected. These results were not specific to shrub canopy of sagebrush species alone, similar to other published literature (Hagen et al. 2007). Based on our results, we draw attention to land and wildlife managers the benefits to nesting sage-grouse provided by all shrub cover rather than sagebrush alone. Furthermore, our findings suggest that protecting areas within intact sagebrush ecosystems with increased shrub canopy cover ($\geq$40% within 0.8 ha) and perennial grasses should improve reproductive success for sage-grouse. They also suggest that reducing the further spread of cheatgrass should protect sage-grouse nesting habitat currently on the landscape. Close monitoring of the efficacy of any such rehabilitation efforts will be important to understand if sage-grouse populations benefit or if other, new methods may need to be brought to bear. Our results demonstrate that in areas affected by wildfire, the potential to sustain regional sage-grouse populations is practical in the short term (i.e., 10 years). This potential, however, would likely be greatly enhanced through strategic rehabilitation efforts in disturbed areas focused on improving shrub canopy and perennial grass cover.

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