Original Article

Sage-Grouse Breeding and Late Brood-Rearing Habitat Guidelines in Utah

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ABSTRACT Delineation, protection, and restoration of habitats provide the basis for endangered and threatened species recovery plans. Species recovery plans typically contain guidelines that provide managers with a scientific basis to designate and manage critical habitats. As such, habitat guidelines are best developed using data that capture the full diversity of ecological and environmental conditions that provide habitat across the species' range. However, when baseline information, which fails to capture habitat diversity, is used to develop guidelines, inconsistencies and problems arise when applying those guidelines to habitats within an ecologically diverse landscape. Greater sage-grouse (*Centrocercus urophasianus;* sage-grouse) populations in Utah, USA, reflect this scenario—published range-wide habitat guidelines developed through a literature synthesis did not include data from the full range of the species. Although all sage-grouse are considered sagebrush obligates (*Artemisia* spp.), the species occupies a diversity of sagebrush communities from shrub-dominated semideserts in the southwest to more perennial grass-dominated sagebrush-steppe in the northeast portions of their distribution. Concomitantly, local ecological site and environmental conditions may limit the ability of managers to achieve broader range-wide habitat guidelines. We combined microsite habitat vegetation parameters from radiomarked sage-grouse nest and brood locations with state-wide spatially continuous vegetation, climatic, and elevation data in a cluster analysis to develop empirically based sage-grouse habitat guidelines that encompass the range of ecological and environmental variation across Utah. Using this novel approach, we identified 3 distinct clusters of sage-grouse breeding (i.e., nesting and early brood-rearing) and late brood-rearing habitats in Utah. For each cluster, we identified specific vegetation recommendations that managers can use to assess sage-grouse breeding and late brood-rearing habitat. Our results provide relevant guidelines to Utah's sage-grouse populations and are feasible given the unique ecological variation found therein. This approach may have application to other species that occupy diverse habitats and physiographic regions.

KEY WORDS brood habitat, *Centrocercus urophasianus*, greater sage-grouse, habitat clusters, habitat guidelines, nesting habitat, radiotelemetry, random forest, species recovery plans, Utah.

Global biodiversity has declined as a result of habitat loss and fragmentation (Haddad et al. 2015). Conservation plans aimed at recovering and managing biodiversity, including endangered, threatened, or at-risk species worldwide, rely on habitat protection and restoration as basic tenets (Bottrill et al. 2011, Evans et al. 2016). Conservation plans typically incorporate the best available science, often in the form of peer-reviewed literature, to develop guidelines that provide the basis to design and prioritize species-habitat projects and conservation actions (Miller and Hobbs 2007, USFWS 2016). However, habitat guidelines developed through a synthesis of the published literature may lack spatial representation because of the inherent bias in availability and selection by individual study area locations (Dale et al. 2000, Messmer 2013). When baseline

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information fails to capture diversity in habitat and is then used to develop guidelines, inconsistencies and problems arise when applying those guidelines to manage habitats across an ecologically diverse landscape. Connelly et al. (2000) expressed this concern when they published range-wide guidelines for the greater sage-grouse (*Centrocercus urophasianus;* sage-grouse).

Sage-grouse, an obligate to one of the most imperiled ecosystems in the world, occupy sagebrush (*Artemisia* spp.) landscapes across western North America from North and South Dakota to California, USA, and from Alberta and Saskatchewan, Canada, to southern Utah and Colorado, USA (Schroeder et al. 2004, WAFWA 2015). Across this extent, sage-grouse occupy a diversity of sagebrush communities from shrub-dominated semideserts with sparse herbaceous cover in the southwest to more perennial grass-dominated sagebrush-steppe in the northeast portions of their distribution. This variation in ecological and environmental conditions and resulting differences in habitat characteristics and productivity complicates the application of a universal set of range-wide habitat guidelines for specific populations (Connelly et al. 2000).

This is particularly evident when considering the application of current guidelines to a large diversity of sage-grouse habitat across 7 floristic provinces or ecoregions (Stiver et al. 2006). In 2015, the U.S. Fish and Wildlife Service determined that sage-grouse did not warrant protection under the U.S. Endangered Species Act (ESA 1973, as amended) of 1973 because threats to the species had been mitigated by range-wide conservation actions (USFWS 2015). Immediately prior to this decision, the Bureau of Land Management (BLM) and U.S. Forest Service (USFS) published a record-of decision that amended their resource management and land use plans, respectively, to address conservation threats for sage-grouse (BLM 2015, USFS 2015). These revised conservation plans generally adopted habitat guidelines recommended by Connelly et al. (2000) as the best available science to evaluate sage-grouse habitat conditions across western federal lands (BLM 2015, USFS 2015).

Connelly et al. (2000) provided habitat vegetation guidelines for spring breeding (i.e., lekking, nesting, and early brood-rearing), late summer brood-rearing, and winter habitats. These peer-edited guidelines were developed through a synthesis of peer-reviewed literature, theses, and dissertations available at the time. The development of sage-grouse habitat guidelines was extensive, resulting in a valuable resource; however simply due to restricted publication availability, guidelines reflected habitat information from a limited spatial extent (i.e., 5 of 7 floristic provinces) compared with the overall species distribution (Fig. 1; Stiver et al. 2006). Hagen et al. (2007) subsequently expanded on this work while using many of the same published information but included a slightly larger spatial extent of peer-reviewed literature. However, Hagen et al. (2007) excluded the same 2 floristic provinces because of publication availability. They did report descriptive statistics providing a slightly broader set of recommendations for habitat compared with Connelly et al. (2000). Given their approach, Hagen et al. (2007) concluded that guidelines reported in Connelly et al. (2000) were reasonable.

Most of the available published research used in Connelly et al. (2000) and Hagen et al. (2007) was completed in the

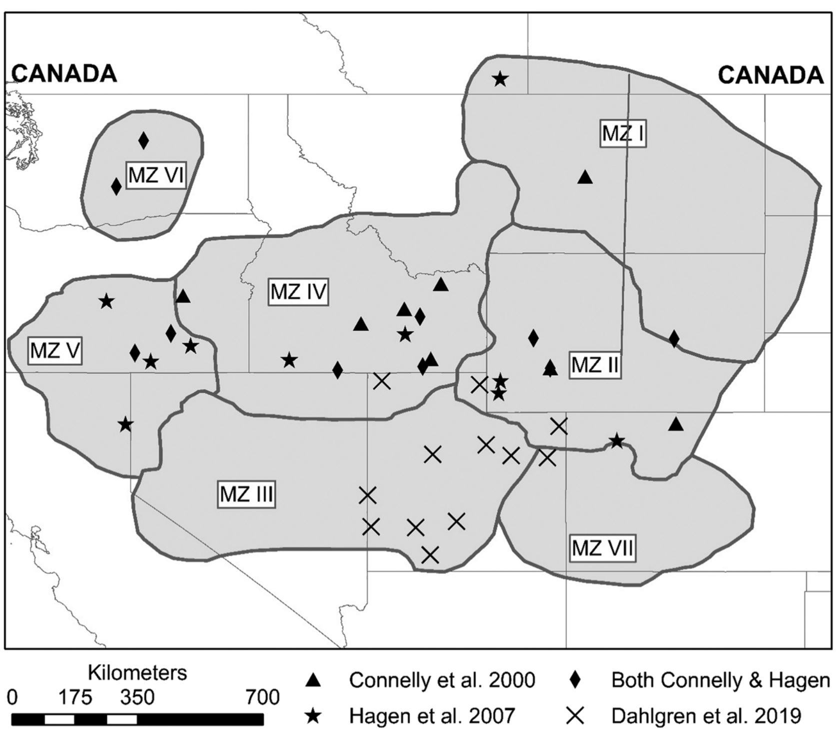

Figure 1. Locations of specific study sites within the western United States, taken from study area descriptions, where vegetation data were collected to develop sage-grouse habitat guidelines in Connelly et al. (2000), Hagen et al. (2007), and our efforts herein (i.e., Dahlgren et al. 2019. The "Both Connelly & Hagen" category identifies studies that were used in both Connelly et al. (2000) and Hagen et al. (2007). The borders of western states are in light grey and each sage-grouse management zone (MZ), as delineated by Stiver et al. (2006), is shaded in grey and outlined in dark grey.

northern range of the species; thus, unintentionally, information on the habitat conditions located throughout the southern Great Basin and desert shrub regions is lacking (Fig. 1; Messmer 2013, Dahlgren et al. 2016). Connelly et al. (2000) urged managers to exercise caution in applying the guidelines as a range-wide standard because of these limitations. They further recommended that more research would be needed to describe differences in sage-grouse habitat conditions within specific populations. Despite this warning, the Connelly et al. (2000) guidelines have largely been applied across the species' range regardless of the diversity in sagebrush communities and the ecological site potential of these communities (Boyd et al. 2014).

As an alternative to Connelly et al. (2000), we combined microsite habitat vegetation parameters from radiomarked sage-grouse nest and brood locations with state-wide spatially continuous vegetation, climatic, and elevation data in a cluster analysis to develop empirically based habitat guidelines that encompass the range of ecological and environmental variation across Utah. Specifically, our objectives were to 1) develop a process for establishing habitat guidelines using empirical techniques, 2) assess factors that influence the diversity in habitat conditions among populations, and 3) provide an example of habitat guidelines developed from the habitats where said guidelines would be applied.

STUDY AREA

We compiled data used from 13 study areas in Utah from 1998 to 2013. These study areas represented most of the sage-grouse populations in Utah (Fig. 2; Dahlgren et al. 2016). Populations in northern Utah inhabited sagebrush-steppe, whereas populations in central and southern Utah primarily used sagebrush semidesert (West 1983). Both were shrub-dominated sagebrush systems differentiated by an increased herbaceous component in higher latitude sagebrush-steppe systems compared with lower latitude sagebrush semidesert. Sagebrush communities also varied by elevation within the same area.

Four floristic provinces (i.e., sage-grouse management zones) intersected Utah's sagebrush landscapes: namely, Snake River Plain, Wyoming Basins, Colorado Plateau, and Southern Great Basin (Stiver et al. 2006). Sagebrush communities occurred in elevations from approximately 1,300 to 3,000 m throughout Utah, and generally, big sagebrush (*A. tridentata*) varieties dominated most occupied landscapes, with Wyoming (*A. t. wyomingensis*), basin (*A. t. tridentata*), and mountain (*A. t. vaseyana*) big sagebrush at lower, mid, and high elevations, respectively. Shallow soils supported inclusions of low (*A. arbuscula*) and black (*A. nova*) sagebrush. Silver sagebrush (*A. cana*) was present at high-elevation mesic areas and there was limited distribution of three-tip sagebrush (*A. tripartita*) in northern Utah. Annual precipitation ranged and averaged 17–32 cm and 26 cm, 21–37 cm and 30 cm, and 30–70 cm and 43 cm, in low-elevation Wyoming big sagebrush, intermediate areas such as basin big sagebrush, and mountain big sagebrush communities, respectively, in Utah (Goodrich et al. 1999). Most precipitation generally came in the form of snow during the winter, although late summer monsoons were common throughout Utah. Growing season

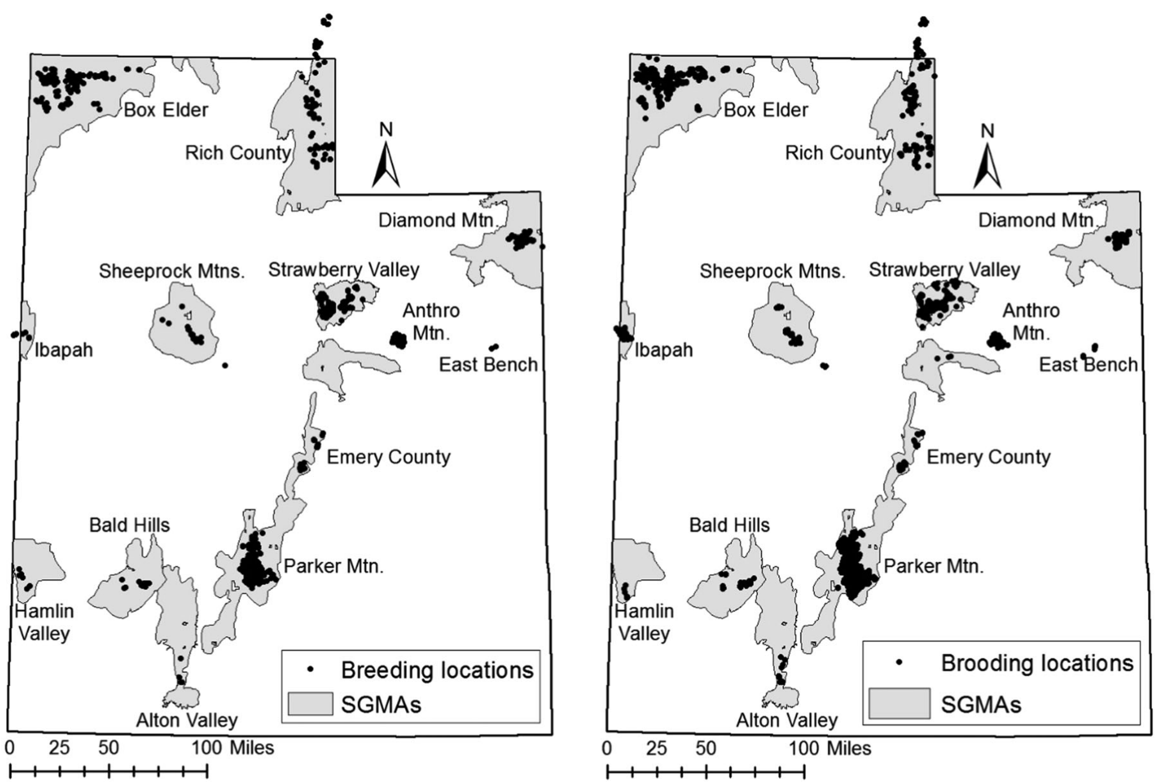

Figure 2. Greater sage-grouse study areas with Sage-Grouse Management Areas (SGMAs) delineated in Utah, USA, 1998–2013, where vegetation data were collected to develop habitat guidelines.

generally began in late March or early April and extended through August and sometimes into September. In any given year, ambient temperatures in sagebrush communities reached approximately −23° C or lower and up to or beyond 38° C.

Beck et al. (2003) used historical records to compare historic and current distribution of sage-grouse within Utah. Dahlgren et al. (2016) refined the current distributions using known sage-grouse locations obtained through long-term radiotelemetry studies. Most of the sage-grouse populations in the state were relatively small and inhabit isolated and remote landscapes. The largest sage-grouse populations in the state are associated with larger, contiguous sagebrush landscapes (Dahlgren et al. 2016).

Our study area locations in Utah occurred within several designations used to delineate and prioritize sage-grouse habitats (Fig. 2). The State of Utah delineated Sage-Grouse Management Areas (SGMA) encompassing approximately 95% of sage-grouse populations in Utah (State of Utah 2013, Dahlgren et al. 2016). The BLM and USFS delineated Priority (PHMA) and General (GHMA) Habitat Management Areas for sage-grouse habitats in Utah (BLM 2015, USFS 2015). Federal and state conservation plans use SGMAs, PHMAs, and GHMAs as priority areas, which differ slightly in the hectares encompassed and exhibit a high percentage of overlap. When referring to SGMAs, PHMAs, and GHMAs collectively, we simply use 'priority areas' hereafter.

METHODS

Sage-Grouse Telemetry Database

We used 1,001 sage-grouse nest and 5,809 brood locations recorded by researchers using very-high-frequency (VHF) radiotelemetry necklace-style radiotransmitters from 1998 to 2013 to describe habitat-use areas and microsite habitat vegetation parameters in Utah (Dahlgren et al. 2016). We measured habitat vegetation variables at sage-grouse use sites following standard procedures presented by Connelly et al. (2003). Institutional Animal Care and Use Committee permit numbers from Utah State University were 2322, 2411, 2419, 2560, 1451, 2189, 942, 942R, 1194, 1404, 1332, and from Brigham Young University were 100302, 110301, 050301, 080402.

Vegetation, Climate, and Elevation Data

We recorded habitat variables of shrub, forb, and perennial grass percent cover and height at nest and brood sites. We censored perennial grass height values associated with unsuccessful nests from our analysis because of the potential for sampling bias, reducing our sample size from $n = 1,001$ nests to $n = 546$ successful nests (Gibson et al. 2016, Smith et al. 2017). Vegetation surveys consisted of 4 transects, one in each cardinal direction or a random starting bearing and then the other transects at successive 90° intervals, centered on the nest bowl or brood site (Connelly et al. 2003). Nest and brood site transects were each 15 and 12 m in length, respectively (Connelly et al. 2003). We temporally spaced brood-site vegetation surveys ≥1 week apart and conducted them at radiomarked brood locations. We used a line-intercept method to determine percent shrub canopy cover and the Daubenmire frame (i.e., 50 cm × 20 cm) technique to estimate species composition (percent cover and height) of forbs and perennial grasses (Daubenmire 1959, Connelly et al. 2003). We placed frames along each nest-survey transect at 3-m intervals for both nest and brood sites, with 5 and 4 frames, respectively. We measured plant height for shrubs, forbs, and grasses with a ruler and used droop height for grasses and forbs.

We focused on 7 vegetation variables available in the VHF sage-grouse location database that would be most applicable to management (Connelly et al. 2000). These included percent shrub cover, shrub height, sagebrush cover, forb cover, forb height, perennial grass cover, perennial grass height, and percent sagebrush composition. We determined sagebrush cover by multiplying shrub cover and percent sagebrush composition. Multiple shrub species are commonly present within sage-grouse habitat, so we included percent sagebrush composition of the overall shrub canopy cover.

We obtained landscape-level vegetation, climatic, and topographic cover values from publically available spatial data sets, which were consistent throughout our study period. We described climatic conditions at 800-m spatial resolution by the average annual temperature, precipitation, and minimum and maximum temperatures, over the period 1981–2010, as measured by the PRISM Climate Group (http://prism.oregonstate.edu/). We obtained elevation and vegetation data from the Landfire project (www.landfire.gov).

Fedy et al. (2014) identified 0.6–100.0 ha as a patch scale suitable for summarizing habitat characteristics biologically relevant to sage-grouse. We were explicitly interested in specific vegetation characteristics such as cover and height of plants, so we identified a patch scale toward the lower end of the scales identified by Fedy et al. (2014). As such, we tabulated Landfire's Existing Vegetation Type (EVT) 1.3.0 codes for the nearest 100 vegetation pixels around each telemetry and grid point location, which implies a buffer distance of approximately 175 m or an area of about 9.6 ha. Landfire data began in 2001, updated in 2008 and then every 2 years following; therefore, we matched data by year as closely as possible to Landfire updates. The EVT classifications reflect ecological systems, and are the finest thematic resolution of land-cover data in the LANDFIRE suite of products (Comer et al. 2003). To spatially project the model output across Utah, we also recorded climate and elevation values, and tabulated vegetation classes, at a grid of regularly spaced points with 1-km spacing across all locations within priority areas and any sage-grouse location that fell outside of those boundaries but within 20 km of those areas.

Cluster Development and Analysis

Our analysis of the sage-grouse VHF telemetry data ($n = 2,179$ radiomarked individuals) of nest and brood locations to develop habitat clusters included 1) random forest (RF) clustering (Shi and Horvath 2006) to classify k clusters in the telemetry data, for values of k ranging from 2 to 6; 2) spatial projection of cluster classes to locations statewide by fitting a second RF trained on cluster labels identified in step 1; 3) assessment of cluster significance by summarizing and statistically comparing habitat measurements (e.g., shrub, forb, and perennial grass canopy cover and height, etc.) among clusters; and 4) selecting the optimal number of k clusters based on the cluster stability and significance assessed in steps 2 and 3. We assessed the stability of the clusters using the Jaccard coefficient (Hennig 2007). We then generated habitat guidelines based on distributions of habitat characteristics across clusters. We implemented all analyses in Program R (R Core Team 2016).

Random Forest Clustering

A major input of clustering methods is a measure of Euclidean distance among observations. To spatially group sage-grouse telemetry locations, we used an unsupervised RF because of its ability to handle variables measured on differing scales and ability to capture nonlinear responses and interaction effects in the data (Breiman 2001). A RF is a collection of individual classification trees, each of which is trained on random subsets of the data and predictors. The RF predictions are made by aggregating predictions across the individual trees. When used as an unsupervised classifier, RF attempts to separate observed data from a synthetic data set created by sampling from the univariate distributions from observed data. The RF procedure generates a measure of proximity between 2 samples based on the proportion of trees in the forest that placed them in the same terminal node (Breiman 2001).

To generate a spatially balanced representation of sage-grouse space use in Utah, we used a sample of available telemetry locations drawn such that not more than one data point, selected randomly if more than one occurred, was represented per 1-km^2 region across the state. We fit an unsupervised RF to the resulting sample of 1.425 data points and defined a dissimilarity matrix as the square root of one minus the proximity matrix (Kaufman and Rousseeuw 1990).

We used partitioning around medoids (PAM; Kaufman and Rousseeuw 1987) to identify clusters of similar covariates in the dissimilarity matrix. The PAM assigns observations to clusters based on minimizing the distance from each observation to a centroid, or medoid, which is constrained to be one of the observed data points. This produced interpretable cluster centroids that were guaranteed to be members of the training data set. The PAM is more robust to outliers and noise compared with the widely used k-means algorithm because it minimizes a sum of pairwise dissimilarities rather than squared distances (Hartigan and Wong 1979).

We assessed the stability of the PAM clustering solutions using the Jaccard similarity coefficient on 30 bootstrap samples of the nest and brood data (Hennig 2007). The Jaccard similarity coefficient compares the similarity of 2 sets of data by dividing the size of the intersection of the sets by the size of the union of sets. Generally, a valid, stable cluster should exhibit a Jaccard coefficient of >0.75; values from 0.6 to 0.75 indicate patterns in the data, but exactly which points should belong to which cluster is doubtful and Jaccard values <0.6 should not be trusted (Hennig 2007). We used the *clusterboot* function in the "fpc" package in R to estimate the average bootstrapped Jaccard values for each cluster (Hennig 2015).

Spatial Projection of Clusters

We spatially projected results of the clustering technique using a supervised random forest model trained to predict PAM cluster labels at telemetry locations, using the suite of vegetation, climatic, and elevation variables. We then predicted cluster labels at all locations within 20 km of any priority area or telemetry location in the database using a raster data set with 1-km spatial resolution.

We tested the sufficiency of this spatial extent by finding the proportion of occupied lek locations it contained. Lek locations can be used as surrogates for available breeding habitat. The Utah Division of Wildlife Resources (UDWR) provided the 1998–2013 sage-grouse lek location data (UDWR, unpublished data). As a final step, we passed a 3×3-pixel modal moving window over the raster surface to remove the salt-and-pepper effect that arises from individual pixels surrounded by neighbors of a differing class. This resulted in a more spatially consistent, less fragmented map of habitat clusters.

Assessing Cluster Significance

To assess cluster significance, we compared habitat characteristics measured at radiomarked nest and brood sites across cluster values extracted from the smoothed raster surface. We used pairwise Wilcoxon rank-sum tests, utilizing a Holm P-value adjustment to control for Type I error risk, to determine whether median nest and brood site habitat characteristics differed across clusters. We set $\alpha = 0.05$.

Habitat Guidelines

We selected an optimal number of clusters based on the stability, significance, and projection onto geographic space of the clusters. We used a nonparametric ensemble classifier, random forests (Breiman 2001), a clustering algorithm, and partitioning around medoids (Kaufman and Rousseeuw 1987) to identify distinct sage-grouse breeding and late brood-rearing habitat characteristics across and within priority areas (State of Utah 2013, BLM 2015). We used the distributions of the 8 field variables/cluster to develop habitat guidelines for Utah. We used the 20th percentile of each variable per cluster as the lowest threshold for habitat guidelines within each cluster, such that 80% of sage-grouse radiomarked locations per cluster reflected use of habitat vegetation conditions that exceeded the low threshold of the guideline. We then generated a set of guidelines for breeding and late brood-rearing habitat across 3 clusters that can be used as habitat standards that reflect the selection of sage-grouse in Utah.

RESULTS

Cluster Stability

Cluster partitions exhibited greater stability for lower numbers of k (Table S1; available online). Across 30 bootstrap iterations, the average minimum Jaccard similarity coefficient value for $k = 2$ was 0.88, and the mean was 0.92, indicating 2 highly stable clusters. When $k = 3$, the average minimum Jaccard was 0.79, and the mean was 0.85, again indicating stable clusters. However, at $k = 4$, bootstrapped Jaccard values were 0.56, 0.74, 0.74, and 0.79, indicating that 2 of the 4 clusters were capturing spurious patterns in the data. The average bootstrapped Jaccard values for $k = 4$, 5, and 6 were 0.71, 0.62, and 0.79, respectively, indicating that on average, the clustering solution captured relatively stable patterns in the data, although less stable than the $k = 2$ or $k = 3$ solutions.

Pairwise comparisons of 8 field variables in the nest data using Wilcoxon rank-sum tests indicated a negative relationship between the number of clusters and rate of significant pairwise differences (Table S2; available online). For values of k from 2 through 6, 75%, 79%, 60%, 58%, and 44% of all pairwise comparisons differed, respectively. Habitat variables exhibited a generally declining rate of differences with increases in k. Pairwise comparisons using the brood data show a similar decreasing relationship between k and rate of pairwise differences (Table S3; available online). For values of k from 2 through 6 in the brood data, 100%, 92%, 69%, 71%, and 63% of all pairwise comparisons differed, respectively.

Clusters based on distributions of elevation and 8 habitat variables measured at nest and brood sites effectively separated differences in elevation and habitat variables for $k = 3$ (Figs. 3, 4). Visual assessment of the density curves shows general agreement with the findings of the pairwise Wilcoxon tests.

Spatial Projection of Clusters

We assigned names to the $k = 3$ clusters based on their elevation or location spatially projected across the state of Utah (Fig. 5). The *Low* cluster covers lower elevation areas (~1,200–2,200 m) in the state, consisting primarily of Wyoming big sagebrush communities, with some basin big sagebrush included. The *Wasatch* cluster covers mid- to high-elevation areas (~2,200–3,000 m) consisting primarily of basin (mid-elevation) and mountain big sagebrush (high elevation), as well as other mesic and higher elevation vegetation communities. The *Parker* cluster occurred primarily on the high-elevation (~2,300–2,800 m) plateau of Parker Mountain in south-central Utah, and was dominated by black sagebrush communities (Figs. 2, 5). Habitat cluster extents, selected to encompass all areas within 20 km of a priority area or telemetry location, were sufficient to encompass all 356 occupied leks in UDWR data. The *Low* cluster contained 242 occupied leks, the

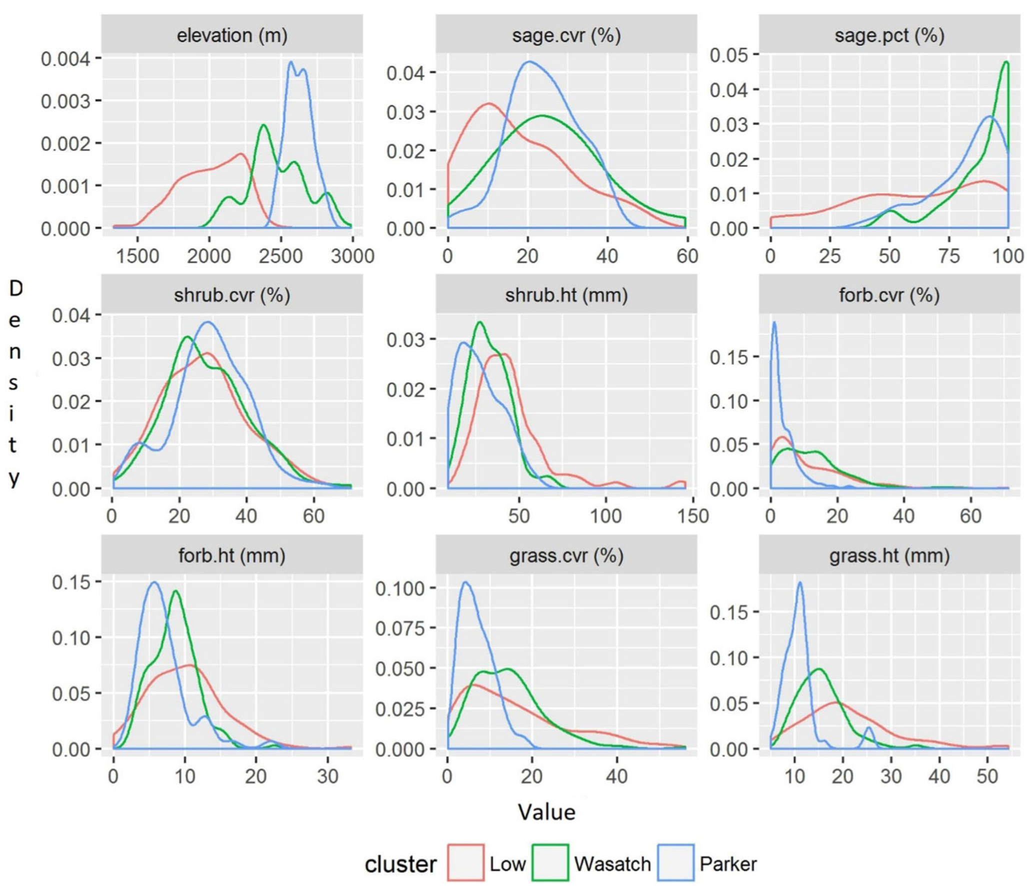

Figure 3. Distributions of vegetation variables across $k = 3$ clusters in greater sage-grouse breeding habitat, Utah, USA, 1998–2013. cvr = cover, pct = percentage, and ht = height.

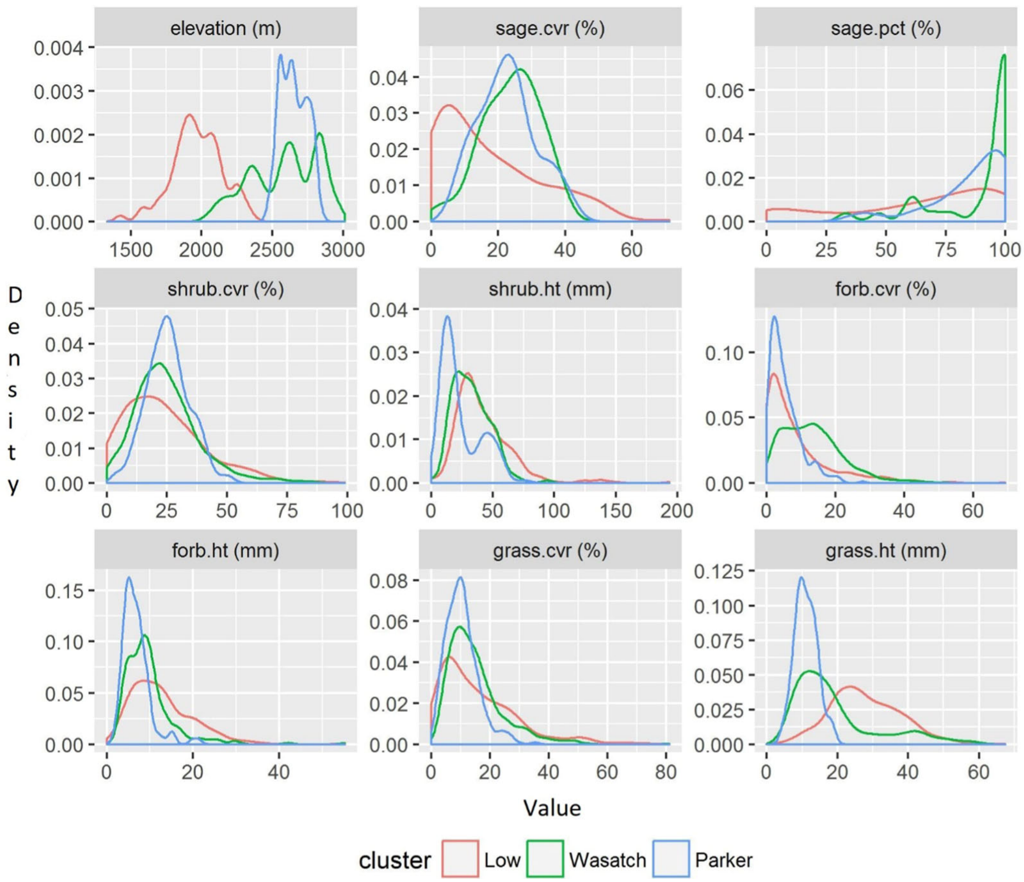

Figure 4. Distributions of vegetation variables across $k = 3$ clusters in greater sage-grouse late brood-rearing habitat, Utah, USA, 1998–2013. cvr = cover, pct = percentage, and ht = height.

Wasatch cluster contained 77, and the *Parker* cluster contained 37 occupied leks. All 3 clusters contain breeding, summer, and winter seasonal habitat use for sage-grouse populations.

Selection of Optimal Number of Clusters

We selected $k = 3$ to represent clusters of sage-grouse breeding and late brood-rearing habitats across the state. With 3 clusters, 79% and 92% of pairwise comparisons of the field variables differed in the nest and brood data, respectively (Tables S2 and S3). Cluster stability was high as assessed using the Jaccard coefficient, with a minimum bootstrapped Jaccard value of 0.79 and a mean of 0.85. Although the $k = 2$ solution had more desirable Jaccard and pairwise Wilcoxon results than the $k = 3$ solution, we opted to use the larger k-value to avoid selecting an overly coarse cluster solution (Figure S1; available online).

Habitat Guidelines

We selected percentiles for distributions of the 8 field variables by cluster for breeding and late brood-rearing data (Tables 1 and 2). We used our selection of the 20th percentile of these distributions as the lowest criteria values of potential habitat for breeding and late brood-rearing guidelines. We rounded up the 20th percentile values to the nearest integer (Table 3). Two clusters encompassed most of Utah's sage-grouse habitats (Table 4).

DISCUSSION

Our guidelines provided distinctive values based on the relatively high variability in characteristics of sage-grouse habitat in Utah. To date, Braun et al. (1977), Connelly et al. (2000), and Hagen et al. (2007) are the only published guidelines that have been provided specific values for evaluating sage-grouse habitat. Connelly et al. (2000) was expressly developed as an update and expansion of Braun et al. (1977) by accessing published literature, theses, and dissertations. Hagen et al. (2007) refined these guidelines using means and standard errors of vegetation sampling data at microsites (i.e., generally ≤30 m transects) from previously published studies (Connelly et al. 2003). There are ≥3 potential issues with these earlier approaches: 1) a lack of capturing variation in habitat due to an unintended bias in study site locations from reviewed literature; 2) a lack of capturing variation in vegetation characteristics that comprise habitat due to a focus on average conditions rather than variation in habitat characteristics; and 3) there remains a disparity in spatial scale between data collected at microsites selected by sage-grouse used to develop guidelines and application of those guidelines to assess broad

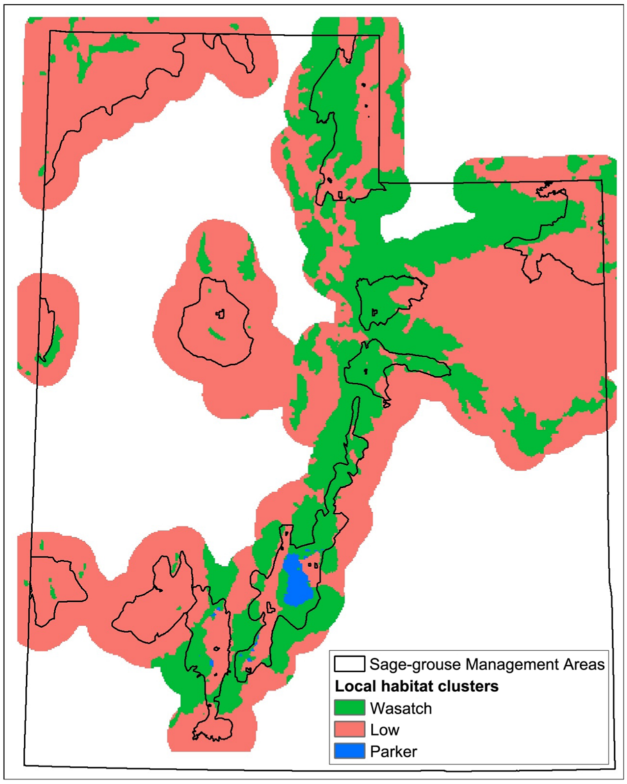

Figure 5. Spatial projection of $k = 3$ clusters of greater sage-grouse breeding habitat, Utah, USA, 1998–2013.

landscapes (Duarte 1991, Benedetti-Cecchi 2003, Boyd et al. 2014). Using past guidelines to assess habitat across landscape scales is further complicated because sage-grouse have been shown to select nest and brood sites with vegetation parameters different from random sites within the same area, thus resulting in highly selected vegetation characteristics potentially influencing broad landscape-scale assessments (Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Holloran et al. 2005).

We attempted to address these issues by developing guidelines based on original data generated from the same habitat where the guidelines would be applied. We attempted to account for ecological variability across that state by utilizing the 20th percentile in vegetation conditions to set minimum values, thus characterizing our guidelines according to habitat variation, rather than means, for sage-grouse nest and brood sites. We similarly used data from microsite sampling of selected habitat; therefore, our approach did not fully compensate for the disparity in spatial scale between vegetation sampling and guideline application. However, by connecting vegetation measurements from microsites to spatially explicit land-cover data, we were better able to account for the variation in habitat characteristics across broad spatial scales and thus provide a more representative approach for evaluating sage-grouse breeding and brooding habitat. Associated with our seasonal habitat guidelines, we were also able to use nest hatch dates to

Table 1. Summary of habitat characteristics for breeding greater sage-grouse in Utah, USA, 1998–2013. Number of breeding telemetry locations per cluster: Wasatch (W): 468; Low (L): 357; and Parker (P): 179.

Variable	Cluster	n[a]	diff[b]	q5[c]	q10[c]	q15[c]	q20[c]	q30[c]	q50[c]
Shrub cover (%)	Wasatch	199	[none]	8.97	13.56	16.64	18.96	21.32	26.37
	Low	193	[none]	7.79	12.33	14.53	16.26	19.94	27.55
	Parker	127	[none]	7.16	11.69	19.48	21.52	24.14	29.17
Shrub height (cm)	Wasatch	150	L,P	15.98	18.62	21.03	22.44	25.74	31.00
	Low	177	W,P	20.47	26.19	27.44	29.65	33.01	41.30
	Parker	54	W,L	12.38	13.06	13.90	14.31	18.77	25.34
Sagebrush composition (%)	Wasatch	32	L,P	59.78	73.23	78.91	82.54	86.90	98.39
	Low	82	W,P	1.84	21.39	33.14	35.97	45.38	67.86
	Parker	40	W,L	52.09	56.91	67.53	70.70	78.37	88.03
Sagebrush cover (%)	Wasatch	32	L	6.71	10.18	11.96	13.38	19.25	23.70
	Low	82	W,P	0.43	2.96	4.59	6.82	9.51	14.36
	Parker	40	L	13.11	14.92	16.22	17.23	19.07	23.34
Perennial grass cover (%)	Wasatch	198	P	3.97	5.47	6.15	7.42	8.92	13.50
	Low	192	P	2.53	3.07	3.76	4.50	7.00	12.55
	Parker	127	W,L	2.14	2.54	2.79	3.31	4.35	6.12
Perennial grass height (cm)	Wasatch	87	L,P	8.94	10.09	10.62	11.65	13.24	15.58
	Low	95	W,P	9.33	11.74	12.31	14.35	16.57	20.30
	Parker	36	W,L	7.06	7.77	8.03	8.75	9.56	11.23
Forb cover (%)	Wasatch	219	L,P	0.90	1.33	2.70	3.99	5.99	10.75
	Low	192	W,P	0.21	0.81	1.31	1.82	3.08	6.25
	Parker	127	W,L	0.18	0.30	0.44	0.65	0.88	1.60
Forb height (cm)	Wasatch	150	L,P	3.81	4.32	4.97	5.61	6.75	8.43
	Low	172	W,P	2.52	4.10	4.63	5.60	6.84	9.56
	Parker	54	W,L	3.09	3.86	4.22	4.33	4.74	6.29

[a] n = no. of telemetry locations with observations of variable.
[b] diff = clusters with differing median values by first letter, based on pairwise Wilcoxon test at $\alpha = 0.05$ with Holm P-value correction.
[c] q5 ⋯ q50 = quantiles of observations.

Table 2. Summary of habitat characteristics for late brood-rearing greater sage-grouse in Utah, USA, 1998–2013. Number of brood telemetry locations per cluster: Wasatch (W): 3,348; Low (L): 1,685; and Parker (P): 809.

Variable	Cluster	n[a]	diff[b]	q5[c]	q10[c]	q15[c]	q20[c]	q30[c]	q50[c]
Shrub cover (%)	Wasatch	882	L,P	5.36	9.86	12.10	16.32	17.10	23.04
	Low	547	W,P	0.17	4.96	7.03	9.41	12.77	21.10
	Parker	302	W,L	11.13	14.57	16.67	18.11	20.93	24.91
Shrub height (cm)	Wasatch	300	L,P	12.64	15.16	17.30	19.27	22.71	31.21
	Low	352	W,P	17.08	20.02	23.02	25.10	29.21	35.91
	Parker	112	W,L	8.60	9.36	10.29	10.98	12.34	16.33
Sagebrush composition (%)	Wasatch	30	L,P	52.75	60.68	64.93	76.18	94.16	99.63
	Low	209	W,P	0.00	3.98	16.45	27.67	51.73	74.59
	Parker	27	W,L	49.67	63.38	72.20	76.07	83.44	91.82
Sagebrush cover (%)	Wasatch	21	L	12.75	13.38	14.07	14.89	19.72	24.62
	Low	191	W,P	0.00	0.38	1.82	3.38	5.50	12.98
	Parker	27	L	10.15	11.46	12.86	15.05	18.24	22.32
Perennial grass cover (%)	Wasatch	877	P	4.50	5.50	6.85	7.64	9.49	12.88
	Low	548	P	1.69	3.36	4.20	5.00	6.81	12.50
	Parker	302	W,L	2.87	4.14	5.02	5.64	7.50	9.88
Perennial grass height (cm)	Wasatch	300	L,P	7.14	8.11	8.87	9.90	11.73	15.33
	Low	363	W,P	11.98	16.42	18.71	19.80	21.89	26.30
	Parker	112	W,L	6.47	7.36	7.91	8.53	9.29	10.8
Forb cover (%)	Wasatch	877	L,P	2.19	2.97	3.90	5.21	7.69	12.38
	Low	546	W,P	0.20	0.50	0.90	1.31	2.31	5.19
	Parker	302	W,L	0.69	1.00	1.31	1.57	2.25	3.92
Forb height (cm)	Wasatch	300	L,P	3.82	4.29	4.80	5.33	6.40	8.66
	Low	344	W,P	3.83	5.03	5.74	6.69	7.99	11.54
	Parker	112	W,L	3.24	3.72	4.16	4.35	5.00	6.27

[a] n = no. of telemetry locations with observations of variable.
[b] diff = indicates clusters with significantly differing median values by first letter, based on pairwise Wilcoxon test at $\alpha = 0.05$ with Holm P-value correction.
[c] q5 ⋯ q50 = quantiles of observations.

Table 3. A comparison of guideline values for sage-grouse breeding and late brood-rearing among Connelly et al. (2000), Hagen et al. (2007), and Dahlgren et al. (2019, this study; guidelines presented herein). Connelly et al. (2000) reported separate guidelines for arid and mesic habitat types and included sagebrush height and canopy cover, but did not address other shrub components and combined grass and forb recommendations. Hagen et al. (2007) reported 95% confidence intervals (i.e., lower and upper confidence limits [CL]) for their data and did not provide threshold limits similar to Connelly et al. (2000) and Dahlgren et al. (2019, this study). Hagen et al. (2007) did not report shrub or forb height values, but they did consider grass height. We reported overall shrub cover, percent sagebrush composition within the shrub community, and separate recommendations for grasses and forbs.

			Connelly et al. 2000		Hagen et al. 2007		Dahlgren et al. (2019)		
			Arid	Mesic	Lower CL	Upper CL	Wasatch	Low	Parker
Breeding	Height (cm)	Sagebrush	30–80	40–80					
		Shrub					≥23[a]	≥30[a]	≥15[a]
		Grass–forb	>18	>18					
		Grass			17.4	22.2	≥12[a]	≥15[a]	≥9[a]
		Forb					≥6[a]	≥6[a]	≥5[a]
	% Cover	Sagebrush	15–25	15–25	19.9	23.9	≥14[a]	≥7[a]	≥18
		Shrub			20.4	30.0	≥19[a]	≥17[a]	≥22
		Grass–forb	≥15	≥25					
		Grass			4.5	9.0	≥8	≥5	≥4[a]
		Forb			2.1	6.0	≥4	≥2	≥1[a]
	Sagebrush composition (%)						≥83	≥36	≥71
Brooding	Height (cm)	Sagebrush	40–80	40–80					
		Shrub					≥20[a]	≥26[a]	≥11[a]
		Grass–forb	variable	variable					
		Grass			15.1	23.2	≥10[a]	≥20	≥9[a]
		Forb					≥6	≥8	≥5
	% Cover	Sagebrush	10–25	10–25	8.4	19.9	≥15	≥4[a]	≥16
		Shrub			7.5[b]	22.8[b]	≥17	≥10	≥19
		Grass–forb	≥15	≥15					
		Grass			5.8	17.1	≥8	≥5[a]	≥6
		Forb			2.9	14.1	≥6	≥2[a]	≥2[a]
	Sagebrush composition (%)						≥77	≥28	≥77

[a] Represents value differences in our guidelines versus Connelly et al. (2000) and Hagen et al. (2007).
[b] This represents the upper and lower CLs for early and late brooding periods and no combined estimate was provided.

Table 4. Area (km^2) for Wasatch, Low, and Parker habitat clusters within and outside of the State of Utah's, USA, Sage-Grouse Management Areas (SGMA) by land ownership type for U.S. Forest Service (USFS), Bureau of Land Management (BLM), Utah's School Institutional Trust Lands (STILA), and private lands in Utah.

	USFS		BLM		SITLA		Private	
Cluster	SGMA	Other	SGMA	Other	SGMA	Other	SGMA	Other
Wasatch	4,031	1,347	916	1,088	457	759	3,729	4,534
Low	1,065	3,266	10,049	21,451	1,471	3,902	6,972	17,269
Parker	41	0	321	0	291	0	4	0
Total	5,137	4,613	11,286	22,539	2,219	4,661	10,705	21,803

establish seasonal periods for nesting (1 Apr to 29 Jun), early brood-rearing (8 May to 20 Jul), and late brood-rearing (5 Jun to 17 Aug) for populations within Utah (Fig. S1; available online).

Our approach was particularly relevant for sage-grouse populations in the Southern Great Basin Management Zone (MZ), which included most of Utah, Nevada, and the Bi-State area of Nevada and California (Connelly et al. 2000, Stiver 2006, Hagen et al. 2007, Doherty et al. 2016; Fig. 1). Previous habitat guidelines have not incorporated data from this MZ. As such, guidelines relevant to Utah's populations are critical for accurately assessing habitat within the state because some local sagebrush communities have likely been providing habitat, but may not have the ecological potential to achieve habitat conditions recommended in other more northern latitude productive regions (Connelly et al. 2000, Boyd et al. 2014). Moreover, Connelly et al. (2000) concluded that if information on sage-grouse habitat becomes available for a specific area, it should be incorporated into habitat assessments for that population.

Our recommendations for herbaceous components (i.e., perennial grass and forb cover and height) for breeding or late brood-rearing designations were lower than previously published guidelines (Connelly et al. 2000, Hagen et al. 2007). Although our forb and perennial grass cover recommendations were slightly lower than values reported in Hagen et al. (2007), they were considerably lower than those reported by Connelly et al. (2000). This was most evident for the *Low* and *Parker* clusters even after we combined perennial grass and forb cover values for comparison with herbaceous values published in Connelly et al. (2000). Much of Utah's occupied sage-grouse habitat occurs within the sagebrush semidesert biome, which can be characterized by low herbaceous vegetation productivity (West 1983, Doherty et al. 2016). Therefore, we suggest that our lower herbaceous cover and height recommendations are more representative of the ecological potential within sagebrush communities used by Utah's sage-grouse populations during our study (Boyd et al. 2014). Past publications have duly placed emphasis on the importance of herbaceous components within sage-grouse habitat (Connelly et al. 2000, Crawford et al. 2004). However, some characteristics, such as perennial grass height, may have been overemphasized when considering sage-grouse breeding habitat (Gibson et al. 2016, Smith et al. 2017).

Past research has shown that perennial grass height was positively correlated with sage-grouse nest survival (Gregg et al. 1994, Holloran et al. 2005, Doherty et al. 2014). However, an inherent bias was recently identified in analysis within past publications (Gibson et al. 2016, Smith et al. 2017). Both Gibson et al. (2016) and Smith et al. (2017) demonstrated that the positive correlation of grass height and nest survival was explained by grass phenology during the nesting period (i.e., successful nests inherently had more time for grass growth than unsuccessful nests, rather than successful nests having taller grasses associated with them compared with equivalent sampling of unsuccessful nests). Although the positive correlation between grass height and nest survival has been largely discredited, we realize that perennial grass height may remain an important characteristic within sage-grouse habitat and emphasize that perennial grasses remain integral to, and provide the resilience needed for, recovery and long-term persistence of sagebrush communities as sage-grouse habitat (Crawford et al. 2004, Thacker et al. 2008).

Although sage-grouse use both grasses and forbs for cover, forbs are particularly important, being directly consumed as well as indirectly providing habitat for associated arthropods that are critical for chicks to meet posthatch protein requirements for growth (Drut et al. 1994). Forbs and perennial grasses have shown similar response to some management actions, but they may be managed separately based on type of livestock used for grazing and specific methods of sagebrush management (Beck and Peek 2005, Dahlgren et al. 2006, Dumont et al. 2007). Therefore, we argue perennial grass and forb characteristics should have separate guideline recommendations as shown by Hagen et al. (2007).

To our knowledge, our guidelines are the first to provide separate shrub and sagebrush canopy cover recommendations and incorporate shrub species composition for sage-grouse. Our shrub canopy cover recommendations for all 3 clusters generally agreed with other published guidelines, but a discrepancy in sagebrush canopy cover did occur within our *Low* cluster (Connelly et al. 2000, Hagen et al. 2007). This difference was due to lower percent sagebrush composition in shrub communities in the *Low* cluster. Our *Low* cluster primarily consisted of Wyoming big sagebrush communities and their transition zone to salt-desert shrublands, which can have a high diversity of nonsagebrush shrub species (West 1983, Davies et al. 2006). Although sagebrush canopy cover was lower, the *Low* cluster had similar total shrub canopy-cover values to the other 2 clusters and past guidelines, underscoring the importance of shrub cover when assessing sage-grouse habitat.

Although nonsagebrush shrub species were components of sage-grouse use locations throughout Utah, especially within our *Low* cluster, we emphasize that sagebrush species remained the key defining characteristic of sage-grouse habitat within all of our clusters. Conservation measures should focus on maintaining sagebrush on the landscape and sagebrush canopy cover within specific habitat types, especially within the *Low* cluster (Aldridge et al. 2008, Wisdom et al. 2011).

Our shrub height guidelines were generally shorter than previous studies, although our shrub height recommendation in *Low* cluster breeding habitat was comparable to Connelly et al. (2000). Additionally, comparing breeding with late brood-rearing recommendations in Connelly et al. (2000) shrub–sagebrush height stayed the same or was higher in late brood-rearing; however, our recommendations decreased from breeding to late brood-rearing habitat in all 3 clusters. Notably, shrub height for the *Parker* cluster was appreciably lower than *Low* and *Wasatch* clusters, as well as past guidelines. This was likely due to the *Parker* landscape being dominated by black sagebrush communities (Dulfon 2016). Musil (2011) described sage-grouse breeding habitat characteristics within dwarf sagebrush communities in Idaho, including black sagebrush, using similar sampling methods to ours. Musil (2011) reported shrub heights $\geq$10 cm taller than our minimum recommendations. Black sagebrush communities can have considerable variation in heights and the *Parker* cluster had extremely low black sagebrush throughout much of the area (Dulfon 2016). However, similar to Musil (2011), nest success in the *Parker* area, where approximately half of our nests were located in black sagebrush–dominated communities, was equivalent to or greater than range-wide averages (Taylor et al. 2012, Dahlgren et al. 2016).

Our approach to developing sage-grouse habitat guidelines was focused within Utah's jurisdictional boundaries. We believe this was appropriate and justifiable because of how both state and federal conservation plans currently use state boundaries for application of conservation measures (BLM 2015, Western Association of Fish and Wildlife Agencies [WAFWA] 2015, Utah Public Land Policy Coordination Office 2019). Although range-wide sage-grouse conservation assessments have generally adopted an ecoregional approach within the species' range, state-based planning and application has likely continued within conservation plans because sage-grouse have not been federally listed and remain a state-trust species (Stiver et al. 2006, 2015; WAFWA 2015).

Ecoregions, or MZs, were delineated based on large-scale floristic provinces, grouping sage-grouse populations across the species' range into 7 MZs (Stiver et al. 2006, 2015; Doherty et al. 2016). More MZs occur in Utah than any other state with extant sage-grouse populations, although the majority of Utah's sage-grouse populations occur within the Southern Great Basin MZ. Our analyses began with large-scale sagebrush types within Landfire and then linked sagebrush types to site-specific vegetation measurements across all 4 MZs; therefore, we speculated that our cluster analyses might group habitat by differences in floristic provinces. However, this was not the case, because elevation proved to be the overriding factor distinguishing our clusters. In other words, site-specific habitat characteristics tended to be much more alike at similar elevations across ecoregions compared with sites within an ecoregion. We also found that the *Parker* cluster, which is wholly contained within the Southern Great Basic Ecoregion, had unique habitat characteristics even compared with other habitats within this ecoregion. We did not develop habitat guidelines based on ecoregions because of our results. However, if range-wide efforts to develop empirically based sage-grouse habitat guidelines occur in the future, we would anticipate an ecoregional approach. Although we would readily support such an endeavor, we caution that our results indicated other factors (e.g., elevation and area-specific vegetation characteristics) need to be considered so that guidelines might appropriately reflect the variation in sagebrush habitat, potentially at smaller scales than ecoregions or MZs.

In our guidelines, we only provide the lower limit for each recommended habitat value and did not provide any recommendations for maximum habitat values, similar to others (Connelly et al. 2000, Hagen et al. 2007). Based on the distribution of data from known nest and brood sites, we did not necessarily identify any recorded habitat values that were so great they might not be considered habitat for sage-grouse. This does not imply that sagebrush communities always provide habitat and are beneficial to sage-grouse, even if certain habitat category values (e.g., sagebrush cover and height) may be too high or dense in some areas to provide optimal conditions. Dahlgren et al. (2006) documented effective management techniques to reduce shrub canopy cover in high-elevation mountain big sagebrush communities that may be limiting the understory in late brood-rearing habitat. Managers should have flexibility in their approach to managing sagebrush communities, with the caveat that habitat should at least meet the recommended guidelines for their area. We recommend caution when managing sagebrush communities, especially when methods include the reduction of shrub canopy cover. For example, sagebrush canopy reduction in Wyoming big sagebrush most often resulted in habitat characteristics that did not meet minimum guidelines, even after several years of posttreatment recovery, and could have been detrimental to the associated sage-grouse populations (Hess and Beck 2012).

Annual and spatial variation in plant communities, especially in more arid systems such as sagebrush, is a common phenomenon (Chambers et al. 2014). We did not attempt to explicitly account for annual variation in habitat conditions. Rather, we assumed that the longevity of our data (i.e., 1998–2013) and the spatial extent across the majority of Utah's sage-grouse populations accounted for both types of variation and captured the range of habitat conditions available to sage-grouse.

We have provided an alternative case study approach in which available data from Utah's sage-grouse populations were used within a quantitative framework to develop spatially explicit habitat guidelines for Utah's populations. Our results provide an alternative, quantitative approach to establish achievable habitat objectives for managers to implement. We acknowledge that our approach and results may not be appropriate for other sage-grouse populations or wildlife species. However, sage-grouse have received considerable research attention in recent decades across their range and most studies have used similar methodologies as we did for collecting habitat characteristics (Connelly et al. 2003). However, drawbacks to our approach include some inherent subjectivity required to determine the number of clusters when using random forest analyses. Additionally, our choice of the 20th percentile to define minimum habitat requirements was based on comparisons with previously published guidelines and our professional opinion, and thus, may be viewed as subjective. The most desirable process for developing habitat guidelines would incorporate a relationship of habitat characteristics to population vital rates; however, microsite habitat characteristics have only indirectly been shown to relate to vital rates, while the influence of other factors, such as large-scale habitat continuity (i.e., percent of the landscape dominated by sagebrush), movements, predator community dynamics, among others have been shown to be more directly related to sage-grouse vital rates and need to be accounted for prior to assessing the relationship of population dynamics to microsite vegetation characteristics of sage-grouse habitat (Beck et al. 2006, Aldridge et al. 2008, Wisdom et al. 2011, Knick et al. 2013, Dinkins et al. 2014).

MANAGEMENT IMPLICATIONS

Our analysis included site-specific sage-grouse habitat-use data for Utah, so our recommendations represent a refinement of previous habitat guidelines for a subset of the species' occupied range. Our suggested guidelines for breeding and brooding habitat can be incorporated into the development and implementation of conservation strategies designed for Utah's sage-grouse populations and potentially nearby areas with similar sagebrush communities. Habitat sampling methods have been fairly consistent across the distribution of sage-grouse and multiple research and monitoring projects. Therefore, our approach to developing habitat guidelines can be used by those with large data sets of vegetation measurements at sage-grouse seasonal use locations to develop more representative habitat guidelines for specific areas. We believe such an approach would better capture the variation of habitat characteristics used by sage-grouse range-wide and lead to improved monitoring and assessment of seasonal habitat types as conservation of sage-grouse continues into the future.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Cluster stability assessments using the Jaccard similarity coefficient, greater sage-grouse breeding habitat, 1998–2013, in Utah, USA.

Table S2. Proportion of pairwise comparisons of fourth-order habitat characteristics in nest data that exhibited significant differences at a 95% confidence level.

Table S3. Proportion of pairwise comparisons of fourth-order habitat characteristics in brood data that exhibited significant differences at a 95% confidence level.

Figure S1. Nest end dates (density) by Julian date.