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Evaluating Greater Sage-Grouse Seasonal Space Use Relative to Leks: Implications for Surface Use Designations in Sagebrush Ecosystems

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ABSTRACT The development of anthropogenic structures, especially those related to energy resources, in sagebrush ecosystems is an important concern among developers, conservationists, and land managers in relation to greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations. Sage-grouse are dependent on sagebrush ecosystems to meet their seasonal life-phase requirements, and research indicates that anthropogenic structures can adversely affect sage-grouse populations. Land management agencies have attempted to reduce the negative effects of anthropogenic development by assigning surface use (SU) designations, such as no surface occupancy, to areas around leks (breeding grounds). However, rationale for the size of these areas is often challenged. To help inform this issue, we used a spatial analysis of sage-grouse utilization distributions (UDs) to quantify seasonal (spring, summer and fall, winter) sage-grouse space use in relation to leks. We sampled UDs from 193 sage-grouse (11,878 telemetry locations) across 4 subpopulations within the Bi-State Distinct Population Segment (DPS, bordering California and Nevada) during 2003–2009. We quantified the volume of each UD (vUD) within a range of areas that varied in size and were centered on leks, up to a distance of 30 km from leks. We also quantified the percentage of nests within those areas. We then estimated the diminishing gains of vUD as area increased and produced continuous response curves that allow for flexibility in land management decisions. We found nearly 90% of the total vUD (all seasons combined) was contained within 5 km of leks, and we identified variation in vUD for a given distance related to season and migratory status. Five kilometers also represented the 95th percentile of the distribution of nesting distances. Because diminishing gains of vUD was not substantial until distances exceeded 8 km, managers should consider the theoretical optimal distances for SU designation between 5.0 km and 7.5 km, depending on migratory status. Although these results represent space use for sage-grouse within the Bi-State DPS, our results likely have broad relevance to other areas with similar landscape characteristics and patterns of space use. © 2013 The Wildlife Society.

KEY WORDS anthropogenic structures, *Centrocercus urophasianus*, energy development, no surface occupancy, sage-grouse, space use, surface use, utilization distribution.

Development of anthropogenic structures in the western United States has increased substantially within sagebrush (*Artemisia* spp.) steppe ecosystems, and is likely to continue at a rapid pace as exploitation of domestic energy sources continues to grow (Naugle and Copeland 2011). Large portions of the western United States have limited power transmission capabilities to support this growth. Therefore, utility-scale transmission lines will likely be needed to provide conduits for many renewable and non-renewable energy development projects. A common goal among wildlife managers, land administrators, and developers is to minimize the adverse effects of such anthropogenic

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structures on wildlife populations, an objective that requires an in-depth understanding of species' space use.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) have been decreasing in distribution since Euro-American settlement of western North America (Schroeder et al. 2004). Most population declines have been estimated at 17–92% in recent decades (Connelly et al. 2004). Sage-grouse depend on healthy sagebrush-steppe ecosystems, and the availability of sagebrush habitat at relatively large spatial scales is necessary to fulfill life history requirements and ensure population viability (Connelly et al. 2011*b*). Sage-grouse have been referred to as an umbrella, or surrogate, species because management for sage-grouse populations benefits those of other species of conservation concern, particularly those functioning at smaller spatial scales (Rowland et al. 2006, Hanser and Knick 2011).

Sage-grouse populations may be affected by increased prevalence of anthropogenic structures in sagebrush habitats (Johnson et al. 2011, Wisdom et al. 2011). Research suggests that infrastructure associated with anthropogenic development may have adverse effects on sage-grouse populations. Such effects include avoidance of leks near structures (Lyon and Anderson 2003, Holloran 2005), decreased adult survival rates (Kaiser 2006, Aldridge and Boyce 2007), decreased nest survival (Braun 1998), lower lek attendance (Harju et al. 2010), loss of habitat (Connelly et al. 2000, Walker et al. 2007), increased avian predation (Ellis 1984, Braun 1998), displacement of nests (Braun et al. 2002), and increased mortality from fence collision (Stevens et al. 2012). Collisions with meteorological towers have also been observed (Coates et al. 2011).

To help prevent such adverse effects to sage-grouse and other wildlife, federal land management agencies may identify areas of importance and place 1 or more restrictions on land uses within those areas. For example, the Bureau of Land Management (BLM) can designate closed, withdrawn, avoidance, exclusion, or restricted use areas to protect or conserve certain resource values, including important wildlife habitat. Beyond these designations, a suite of stipulations such as surface use (SU) designations (e.g., no surface occupancy) can be applied to particular resource uses or activities on public lands (BLM 2012). No surface occupancy is used to protect sensitive surface resource values by prohibiting the physical presence of gas and oil extraction, as well as associated infrastructure, on the surface of public lands (2007 BLM Information Bulletin No. WY-2007-029). Other types of stipulations (e.g., avoidance areas and restricted areas) are used for non-fluid mineral land use planning.

Leks are traditional breeding grounds for sage-grouse (Patterson 1952) and often used as focal points to assign SU designations, largely because females often nest in close proximity to them (Fedy et al. 2012). However, setting specific area thresholds (i.e., the amount of area surrounding a lek to be protected) for SU designation is often challenging. Although recommendations for area thresholds exist (Manville 2004), they are frequently disputed because they are often based on expert knowledge rather than strong empirical evidence. Scientifically defensible information on space use of sage-grouse relative to lek locations will inform the establishment of SU designations and provide information needed to consider sage-grouse space requirements during all life phases in decision making processes. Animal location data derived from telemetry-based monitoring, combined with Geographic Information Systems (GIS) and recent advances in statistical procedures, can provide powerful empirically based support tools for these types of management decisions.

Evaluating animal space use surrounding specific landscape features is complicated by the fact that continuous monitoring of individuals is almost never possible. Direct observation or triangulations of radio-marked individuals can be used to assess animal locations at specific points in time, but inferences made from these data are limited because animal locations outside of monitoring intervals are typically unknown (Millspaugh and Marzluff 2001). For this reason, researchers often calculate utilization distributions (UDs), which estimate animal space use based on the distribution and density of known locations (Worton 1989). UDs are useful tools for evaluating sage-grouse space use because they allow for estimation of the probability of use by individual sage-grouse seasonally and year-round, while accounting for the imperfect monitoring effort that is ubiquitous among radio-telemetry studies. They also enable quantification of the relative intensity of use by a population of sage-grouse that would be encompassed by SU areas of varying size, thus providing an important decision support tool.

Our study objectives were to evaluate seasonal space use of sage-grouse, and relate these seasonal use areas to leks to inform appropriate area thresholds for SU designations. We identified thresholds for SU designation intended to limit overlap between areas of development and those used by sage-grouse, rather than quantifying the effects of anthropogenic development, which has been described elsewhere (e.g., Lyon and Anderson 2003, Walker et al. 2007, Doherty et al. 2008). We conducted these analyses from data collected in the southwestern area of the species' range for the Bi-State Distinct Population Segment (DPS). The Bi-State DPS was recently designated by the United States Fish and Wildlife Service as a candidate for protection under the Endangered Species Act of 1973 (U.S. Department of the Interior 2010), largely because these sage-grouse are genetically distinct (Benedict et al. 2003, Oyler-McCance et al. 2005) and geographically isolated (Benedict et al. 2003, Casazza et al. 2011). Consequently, sage-grouse in the Bi-State DPS are currently evaluated separately from other greater sage-grouse populations range-wide for listing decisions. Although energy exploration and development are not considered the primary threats to sage-grouse populations within the Bi-State DPS, plans for renewable energy development exist, and other forms of human land use (e.g., urban expansion) are a concern within this portion of their range. Nevertheless, energy development and other anthropogenic factors are a concern for sage-grouse range-wide and this study can contribute to range-wide decisions.

STUDY AREA

We collected sage-grouse data at 4 study sites within a 2,800-km^2 region of Mono County, California (119°11′1.94″N 38°6′30.80″W), which lies on the eastern side of the Sierra Nevada Mountains adjacent to the Nevada border. Mono County contains the majority of sage-grouse subpopulations within the Bi-State DPS. Through the course of this study we did not observe interchange of sage-grouse between study sites. These sites differed slightly in dominant landscape features. The sage-grouse subpopulations within these sites did not make up the entire population of sage-grouse within the Bi-State DPS but provided a reliable representation of the population. The study areas were topographically diverse and several mountain ranges separated the northern and southern ends. Elevations ranged from 1,660 m to 3,770 m. Vegetation types across sites were generally similar and predominantly consisted of big sagebrush (*Artemisia tridentata* spp.) interspersed with low sagebrush (*A. arbuscula*). Native bunchgrasses and perennial forbs dominated the understory vegetation. Cheatgrass (*Bromus tectorum*) was present but uncommon and singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) woodlands were relatively common at elevations of 1,850–3,000 m.

METHODS

Field Techniques

We captured sage-grouse using spotlighting techniques at night (Giesen et al. 1982, Wakkinen et al. 1992) during March–April and October–November over a 7-year period from 2003 to 2009. We determined sex of sage-grouse based on physical characteristics (Dalke et al. 1963), and fit each bird with a 21-g necklace-style radio-transmitter (Advanced Telemetry Systems, Isanti, MN) that emitted very high frequency (VHF) signals. Transmitters included an activity sensor to identify mortality (Sveum et al. 1998). We attempted to locate each sage-grouse to within 30 m $\geq$2 times per week during spring months and $\geq$1 during fall and winter using handheld Yagi antennas and radio receivers (Advanced Telemetry Systems). We used a hand-held Global Positioning System (GPS) to record Universal Transverse Mercator (UTM) coordinates (datum NAD83, UTM zone 11) of sage-grouse locations. During the spring, we monitored females for nesting activities and recorded nest locations using methods described by Kolada et al. (2009).

Data Analysis

We conducted a 2-part data analysis using the sage-grouse radio location data. The first analysis focused on quantifying seasonal space use of sage-grouse with respect to leks across subpopulations, sexes, and seasons, and evaluating their space use within different area thresholds (i.e., circular polygons centered at leks). The second analysis focused on examining biological sources of variation in space use with respect to leks.

Analysis I, space use relative to leks.—We used sage-grouse location data to estimate UDs for 3 distinct seasons based on sage-grouse phenology, spring (breeding and nesting; 1 Mar–30 Jun), summer and fall (brood-rearing; 1 Jul–31 Oct), and winter (1 Nov–28 Feb). UDs in this study were represented by probability density functions (PDFs) that define space use using fixed kernel density estimators (Silverman 1986). The kernel estimator is a non-parametric analysis that places no constraint on the shape of the UD and, thus, resulted in a spatially explicit surface grid (specified 30-m cell size) depicting the probability of sage-grouse occurrence, given the input location data. A parameter h controls the bandwidth of the kernel function, and we estimated the appropriate h for each individual grouse and season using a smoothed cross-validation technique (SCV; Hall et al. 1992). The smoothed technique is a generalization of the least-squares cross-validation technique (LSCV; Duong 2007). The LSCV technique is used to estimate h by minimizing the integrated least squares error between the true and the estimated distributions across a range of bandwidth values (Gitzen and Millspaugh 2003). The SCV technique has advantages over LSCV, such as allowing for pre-smoothing of the difference between a PDF value at a known location (data point) and a value from an estimated PDF at the same location after the data point is omitted (Wand and Jones 1995). Smoothed cross-validation is recommended to estimate the most appropriate h based on relocation data (Duong 2007).

In choosing the most appropriate h for these data, we carried out preliminary analyses by subsampling the data and investigating performance of multiple bandwidth estimators, including LSCV, SCV, and likelihood-based techniques (Horne and Garton 2006). First, we visually inspected the UDs and found that cross-validation techniques better represented these data than the likelihood-based technique. We further investigated a subsample of data by exploring differences between SCV and LSCV and found that the SCV technique outperformed LSCV. Therefore, we chose SCV as the final estimator for all data sets. We computed bandwidth estimation and PDFs using Geospatial Modeling Environment (Beyer 2012).

We adjusted for the irregular sampling intervals among sage-grouse by implementing a weighting technique in the SCV processing stage. Without weighting the individual locations, the reliability of the PDF is reduced (Katajisto and Moilanen 2006). For example, relocation points that were closely spaced often represent areas where sampling was most intensive, and these areas would have received too much weight in a standard kernel analysis (Katajisto and Moilanen 2006). We assigned lower weights to points that were closely spaced because these points are more autocorrelated (Katajisto and Moilanen 2006). For each seasonal UD, grid cell values summed to 1 across the entire grid.

In addition to space use as defined by UDs, we also evaluated the distribution of discrete nesting locations with respect to distance to leks. Although nesting locations were, by definition, contained within nesting season UDs, we conducted this additional analysis because factors associated with nesting are often a focal point of sage-grouse conservation and merit a more in-depth analysis. As such,

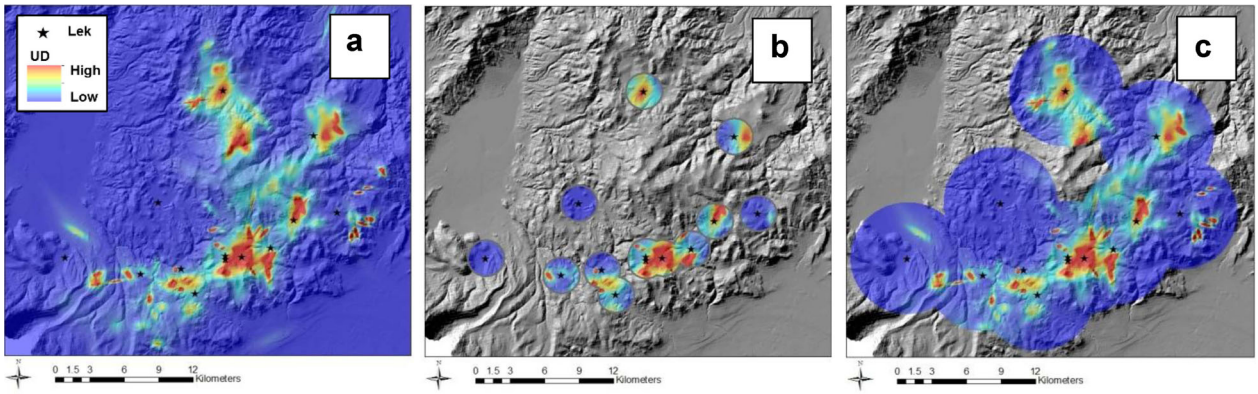

Figure 1. Illustration of a greater sage-grouse population level utilization distribution (UD; calculated from weighted individual UDs) at 1 of the 4 subareas (Bodie Hills) in the Bi-State Distinct Population Segment in Mono County, California, 2002–2009 (a). We calculated volume of UD at each 30-m increment radiating outward from lek locations to a maximum distance of 30 km. We show graphical representations of vUDs at the 3-km (b) and 6-km distances (c).

we sought to provide a more specific assessment of sage-grouse space use during this particular life stage. Furthermore, nesting season UDs reflect use of areas by sage-grouse during the nesting period, which would contain pre- and post-nesting areas in addition to nest locations. Thus, nesting season UDs are not exclusive to nesting female sage-grouse and represent a more general classification of space use during the breeding season.

Kernel density estimation is subjected to error based on sample size (Seaman et al. 1999) and, in this study, sample sizes varied between individuals. Therefore, in preparation for the next step of the analysis, we developed a weighting factor (see Appendix A) that accounted for error in population-level inferences from individual UDs derived from location data that varied in sample size (Fig. A1). Although we derived most UDs from sample sizes that met reported recommendations for kernel density estimation using LSCV techniques (Seaman et al. 1999), we applied a respective weight to UDs derived from location data with <40 samples (Fig. A2). The seasonal UD with the fewest samples in this analysis consisted of 10 radio-telemetry locations. A weighting technique was appropriate for these analyses because we conducted inferences at the population level. Furthermore, we did not use the probability density distributions to generate isopleths (e.g., 95% home ranges or 50% core areas), which can be sensitive to sample size (Seaman et al. 1999). Instead, the weighting factor minimized surface-wide uncertainty (error) associated with individual UDs with lower sample sizes in calculating population level estimates.

During the second step, we calculated population-level estimates based on the individually weighted UDs. We sequentially increased the area threshold by increasing the distance using 30-m increments radiating outward from lek locations to a maximum distance of 30 km and calculated the volume of UD (vUD) that was contained within varying area thresholds (i.e., circular buffers). We limited our maximum threshold area to a distance of 30 km because this was the distance required to capture the entire vUD for all seasons. When multiple leks were within 30 km of each other, we allowed area thresholds to merge with each other. We implemented the weighting factor based on the UD sample size (Fig. A2) at each 30-m incremental distance by 1) multiplying vUD by the corresponding weighting factor, 2) summing these values across all individuals, and 3) dividing by the sum of the weights (see Fig. 1 for examples). We carried out this process for individuals grouped by migratory status (migratory vs. non-migratory), season, and sex. We assigned migratory status to subpopulations where sage-grouse appeared to make seasonal movements based on a lack of overlap in 50% vUDs among breeding and winter use areas. By this definition, the 2 migratory subpopulations were Bodie Hills and Parker Meadows of the 4 subpopulations considered in this study. We conducted the spatial analyses using Program R (package: raster; R Development Core Team 2008, Hijmans and van Etten 2010), Python (van Rossm and Drake 1995), and ModelBuilder (ArcGIS 10.0; Environmental Systems Research Institute, Redlands, CA).

We developed 2 population-level response curves to evaluate sage-grouse space use as area thresholds increased incrementally from leks. The first response curve evaluated vUD with each 30-m incremental increase in distance and the second represented a benefit–cost value index, defined as vUD divided by area encompassed by each given threshold value. We rescaled the value index between 0 and 1 and used this metric to observe the increasing, leveling, and diminishing gains of vUD as threshold area increased. Specifically, this benefit–cost index allows for an evaluation of vUD at each 30-m incremental increase while accounting for increasing area (i.e., vUD benefit vs. area costs). We used each of these curves to identify a range of optimal thresholds for SU-designated areas based on sage-grouse space use. We conducted a similar assessment for nest locations, although here we calculated the percentile of the distribution of distances from nests to nearest lek within each 30-m incremental increase in area threshold.

Analysis II, sources of variation in vUD.—In a post hoc analysis, we examined sources of biological variation in vUD at 2 specified scales (3 km and 6 km) to further inform SU designation for circumstances when wildlife and land

Table 1. Number of utilization distributions calculated for greater sage-grouse monitored using radio-telemetry by season, sex, and site within the Bi-State Distinct Population Segment in Mono County, California, during 2002–2009. Values in parentheses represent number of radio-telemetry relocations.

	Female			Male			
Site[a]	Spring	Summer and fall	Winter	Spring	Summer and fall	Winter	Total
Bodie Hills	57 (1,764)	51 (1,513)	27 (387)	7 (150)	4 (98)	7 (110)	153 (4,022)
Sweetwater	23 (795)	17 (607)	9 (132)	7 (139)	4 (79)	0	60 (1,752)
Parker Meadows	13 (507)	10 (368)	6 (128)	4 (76)	3 (105)	3 (58)	39 (1,242)
Long Valley	54 (2,139)	51 (1,940)	25 (498)	6 (145)	5 (101)	2 (39)	143 (4,862)
Total[b]	147 (5,205)	129 (4,428)	67 (1,145)	24 (510)	16 (383)	12 (207)	395 (11,878)

[a] Bodie Hills and Parker Meadows represent migratory subpopulations, whereas Sweetwater Mountains and Long Valley represent non-migratory subpopulations.

[b] The total number of sage-grouse monitored in this study was 193. The same individuals often represented different seasons, but no individual sage-grouse were observed moving between subpopulations.

managers have some knowledge of their sage-grouse populations. We chose these scales based on the relatively high amount of variation in vUD (3 km), as well as an observed plateau in vUD (6 km) from observations during analysis I. We used linear mixed-effects models (Faraway 2006, Gillies et al. 2006, Zuur et al. 2009), which allowed us to specify random effects that accounted for variation that might otherwise confound parameter estimates for fixed effects. The matrix model notation took the form:

$$\text{vUD} = X\beta + Zu + \varepsilon$$

where X is a matrix containing the fixed effects regressors (sex, season, migratory status), β is a vector of fixed effects that represents the effect sizes associated with those predictors, Z is a matrix of random effects regressors, u represents a single vector of independent random effects (year and individual sage-grouse), and ε represents a normally distributed random error term. In other words, we modeled vUD as a function of sex, season, and migratory status, while specifying year and individual sage-grouse as random intercepts to account for within-year and within-subject correlation structures, respectively. We developed models that included individual fixed effects (sex, season, migratory status), as well as a model that evaluated an interaction between season and migratory status. To account for unequal sample sizes among UDs, we specified the calculated weighting factor (Appendix A) for each value of vUD and included it in the model. We derived estimates of model parameters using Program R (package: lme4; R Development Core Team 2008, Bates 2010).

We evaluated evidence of support for models using Akaike's Information Criterion (AIC) with second-order bias correction ($_c$; Burnham and Anderson 2002), and evaluated uncertainty among models using AIC_c differences (ΔAIC_c), where we considered models with $\Delta\text{AIC}_c < 2.0$ to be competitive. To limit Type I error, we assigned the number of effective degrees of freedom to the individual level (i.e., individual female) and not the observation level (relocation). We calculated model probabilities (w; Anderson 2008) and reported evidence ratios ($\text{ER} = w_{\text{model } i}/w_{\text{model } j}$) comparing the most parsimonious model with other models in the set (Anderson 2008). We report values as means ± standard error.

RESULTS

Analysis I, Space Use Relative to Leks

We collected 11,878 radio-telemetry locations from 193 sage-grouse across 4 study sites during 2003–2009 (Table 1). The average number of locations per sage-grouse was 62.3 ± 3.2, with an average sampling interval between locations of 4.7 days ± 0.09. Not all sage-grouse monitored within the year were represented in every season because of mortalities and limitations in the number of locations per individual in some seasons. We developed 395 seasonal UDs (Table 1). We derived the majority of UDs (87%) from female sage-grouse, but 52 UDs derived from males permitted us to investigate differences between sexes. We located 194 nests during our study, with an average of 48.5 ± 13.7 nests per subpopulation.

We found substantial variation between individual vUD as we increased the threshold area surrounding lek locations (Fig. 2a). Ninety percent of the weighted averaged vUD was contained within 5.16 km (95% CI = 4.65–5.52 km), 75% of vUD was within 2.79 km (95% CI = 2.58–3.03), and 50% was within 1.56 km (95% CI = 1.50–1.65) of leks (Fig. 2a). Nearly the entire vUD (99%) for our sample of sage-grouse was contained within 10.6 km of leks representing year-round space use.

We identified a local peak in the value index (benefit–cost) at a distance of approximately 3 km from leks (Fig. 2b), with another slight increase beginning at 5 km and peaking at 7.5–8.0 km. Overall, this response curve illustrated diminishing gains beginning at approximately 8 km (Fig. 2b), suggesting that beyond this distance, additional incremental increases did not result in appreciable increases in the amount of sage-grouse space use contained within threshold areas. The minimum distance that captures most of the vUD (i.e., 90%) and provides a relatively high value index is approximately 5 km (Fig. 2a and b).

The average distance from nest to lek across all study sites was 1.9 ± 0.1 km. The 95th percentile of nest distribution occurred within 5 km of a lek, the 75th percentile was within 2.2 km, and the 50th was within 1.5 km (Fig. 3). The maximum nest to lek distance we observed during the study was 8.2 km.

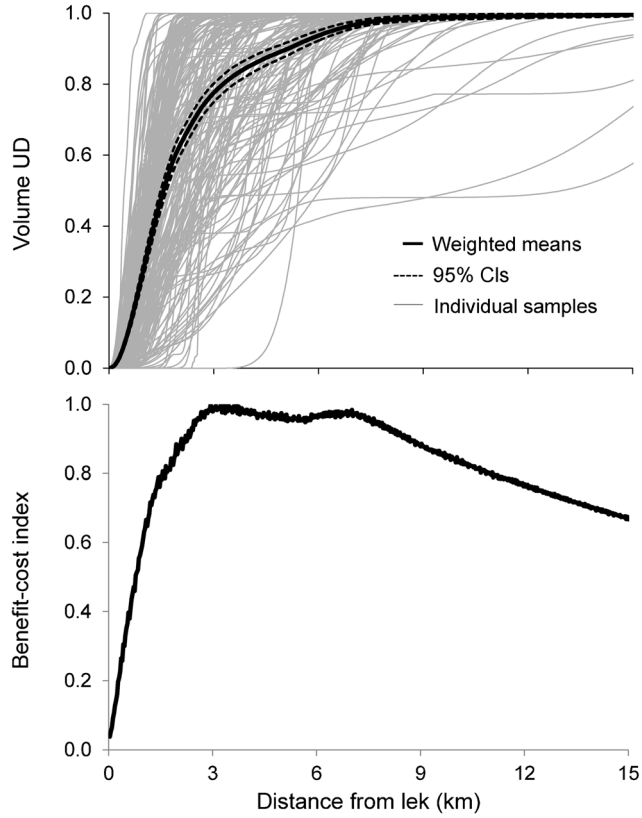

Figure 2. Response curves for (a) volume of utilization distribution (vUD) and (b) benefit–cost index (vUD/area within the threshold) for greater sage-grouse. The benefit–cost index was rescaled to 0–1. We collected these data in the Bi-State Distinct Population Segment in Mono County, California, during 2002–2009.

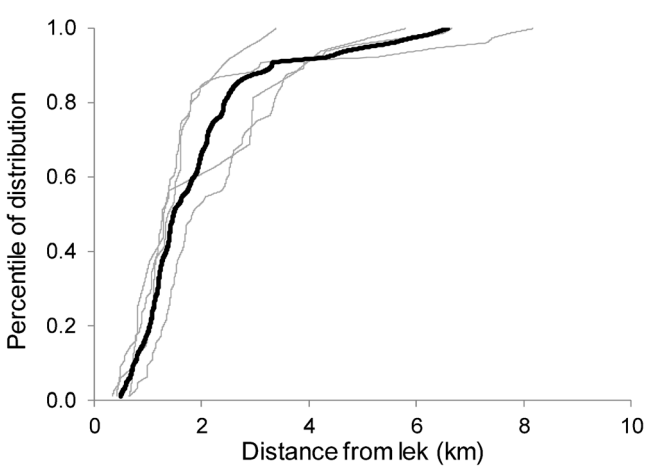

Figure 3. Response curve for the percentile of distribution of greater sage-grouse nests encompassed by increasing area thresholds centered at lek sites. Black line depicts a weighted average response curve at the population level and light gray lines represent subpopulations. We collected these data in the Bi-State Distinct Population Segment in Mono County, California, during 2002–2009.

Table 2. Evaluation of mixed-effects generalized linear models of volume of utilization distribution (vUD) for greater sage-grouse using covariates of migratory status, season, and sex. K = number of model parameters; LL = model log-likelihood; ΔAIC_c = difference (Δ) in Akaike's Information Criterion (AIC) with second order bias correction ($_c$) between the model of interest and the most parsimonious model of the model set (Anderson 2008); w = the model probability (Anderson 2008). We collected these data in the Bi-State Distinct Population Segment in Mono County, California, during 2002–2009.

Distance to lek	Model[a]	K	−2LL	ΔAIC_c	w
3 km	Migration × season	8	3.3	0.0	1.00
	Migration + season	6	21.6	13.9	0.00
	Migration	4	37.5	25.6	0.00
	Migration + sex	5	37.3	27.5	0.00
	Season	5	63.5	53.7	0.00
	Season + sex	6	63.5	55.8	0.00
	Null	3	81.1	67.1	0.00
	Sex	4	81.0	69.1	0.00
6 km	Migration × season	8	−558.3	0.0	0.96
	Migration + season	6	−551.1	7.1	0.03
	Season	5	−546.7	11.6	0.00
	Season + sex	6	−545.3	13.0	0.00
	Migration	4	−506.8	51.4	0.00
	Sex + migration	5	−505.6	52.7	0.00
	Null	3	−500.5	57.7	0.00
	Sex	4	−499.3	58.9	0.00

[a] Mixed models consisted of values of vUD at 3-km and 6-km distances as response variables and cross random effects (intercepts) for year and individual sage-grouse (i.e., repeated observations). Model selection notation follows Burnham and Anderson (2002).

Analysis II, Sources of Variation in vUD

At both 3-km and 6-km scales, vUD was best explained by an interaction between season and migratory status (Table 2). At 3 km, migratory subpopulations during the winter season resulted in the lowest vUD (0.54; 95% CI = 0.47–0.61), whereas the highest were associated with non-migratory subpopulations during summer (0.90; 95% CI = 0.85–0.94; Fig. 4a). Similarly at 6 km, vUD was lowest for migratory subpopulations during the winter (0.76; 95% CI = 0.69–0.82), whereas non-migratory subpopulations during summer had the highest vUD (0.98; 95% CI = 0.96–0.99; Fig. 4b). At 3 km, the most parsimonious model consisted of an interaction between season and migratory status and was 1,040 times more likely to explain variation in vUD than a model with an additive effect between these covariates based on evidence ratios (Anderson 2008). Differences in vUD related to sex were not supported by these data at either scale. The response curve with the lowest values for vUD per iteration represented a migratory subpopulation during the winter, whereas the greatest values represented non-migratory sage-grouse during the spring and summer (Fig. 5). For migratory subpopulations across all seasons, the rate of increase slowed substantially at approximately 7.5 km (Fig. 5), and area thresholds at this distance captured >90% of the vUD.

DISCUSSION

This study provides empirical findings on seasonal space use of sage-grouse in relation to their lek sites, and can be used as a decision support tool to help guide management actions. These findings are based on sage-grouse space use data and

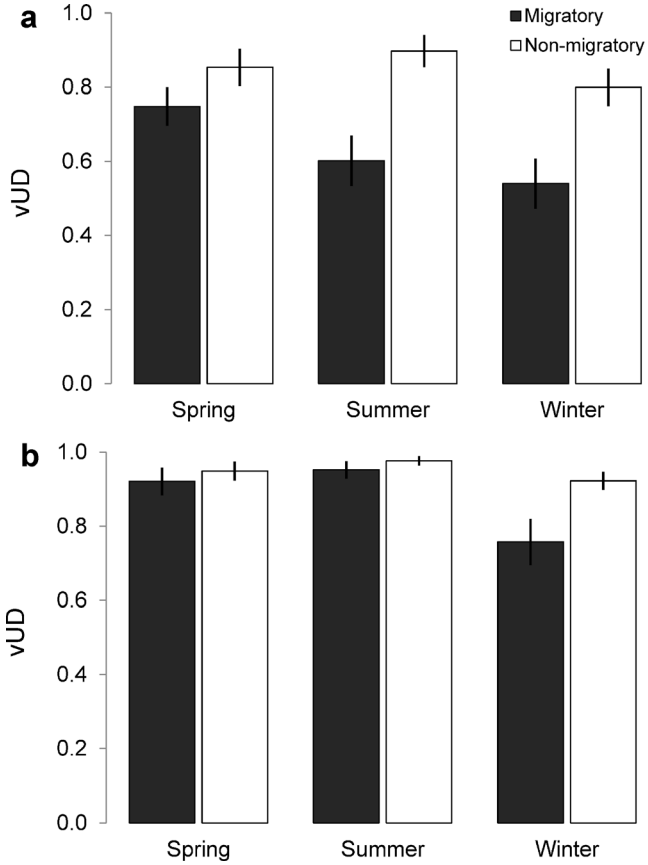

Figure 4. Volume of utilization distribution (vUD) for greater sage-grouse by migratory status and season at (a) 3-km and (b) 6-km distances from leks. We collected these data in the Bi-State Distinct Population Segment in Mono County, California, during 2002–2009.

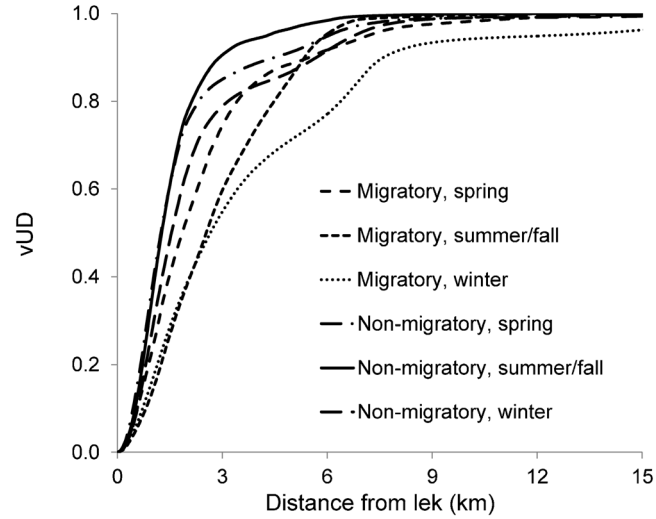

Figure 5. Response curves of volume of utilization distribution (vUD) for sage-grouse grouped by migratory status and season as a function of distance to leks. We collected these data in the Bi-State Distinct Population Segment in Mono County, California, during 2002–2009.

are intended to provide information that can be used to avoid or minimize the impacts of anthropogenic development on sage-grouse populations. Specifically, these data help inform optimal sizes of SU designation. Fedy et al. (2012) provided a somewhat similar assessment in Wyoming based on movements of sage-grouse between seasonal use areas. Those analyses were used to evaluate the core regions concept (Doherty et al. 2011), which identified sage-grouse priority areas using 6.4-km buffers and an abundance-weighted kernel method to prioritize leks with greater abundance of males. Fedy et al. (2012) determined that females nested within 75% core regions, and that 15% of summer locations and 35% of winter locations fell outside of core region boundaries. The analysis described here expands on the concepts introduced by Fedy et al. (2012) by characterizing seasonal space use of sage-grouse as a continuous function of distance from leks (Fig. 2a). This approach also allows for a benefit–cost analysis for identifying distances as a function of where gains of vUD begin diminishing while accounting for size of SU designation (Fig. 2b). In this sense, managers can evaluate the relative utility of alternative SU designation scenarios, because we present results as continuous response curves.

Centering SU designations at lek sites is likely ideal for multiple reasons. Leks are detectable using ground and air surveys, meaning that given sufficient survey effort, classifying the majority of leks in a given landscape is possible. Leks are also generally considered hubs for nesting (Fig. 3; Autenrieth 1985, Connelly et al. 2004), and our results show that with an appropriate threshold size and several important assumptions (discussed below), lek sites provide an appropriate focal point for SU designations that encompass the majority of areas critical for all sage-grouse life phases. Based on our findings, SU designations of areas up to 7.5 km from leks year-round will encompass nearly all seasonal space used by sage-grouse. For example, the first peak in the value index at 3 km (Fig. 2b) likely represented a large volume of spring and summer vUD of migratory and non-migratory populations. The second peak of the value index at approximately 6 km likely reflected increased winter use, especially of those populations that were migratory (Fig. 5). Finally, the majority of vUD ($\geq$90%) was contained within 7.5 km, even for those populations that were migratory during the winter months (Fig. 5). The value index exhibited diminishing gains beyond 8 km.

In situations where SU designations are not sufficiently large, areas used by sage-grouse during the breeding season (i.e., leks) may be protected, but populations may ultimately be affected by anthropogenic development during other life phases (Doherty et al. 2008). For example, female adult survival has a major influence on sage-grouse population growth rates (Taylor et al. 2012), in part because selective pressures produced stability in female survival relative to other vital rates (Blomberg et al. 2013). Reductions in female survival would therefore be expected to have a disproportionally large impact on sage-grouse population growth (Sæther and Bakke 2000). In eastern Nevada, monthly survival rates of female sage-grouse were shown to be high and stable during the winter months (Blomberg et al. 2013), suggesting that observed stability in annual survival was influenced, in part, by low mortality during winter. Other authors have suggested that winter habitat is critical to

meeting sage-grouse seasonal requirements for population viability and persistence (Beck and Braun 1980, Connelly et al. 2000, Lyon 2000). In a more recent study, sage-grouse were shown to avoid areas with anthropogenic development that consisted of otherwise suitable vegetation during winter (Doherty et al. 2008). Wintering areas are largely unknown for most populations, and in most cases are located farther from leks than other seasonal use areas (Fig. 5; Fedy et al. 2012). Given that winter survival is a potentially influential driver of population growth, ensuring SU designations are sufficiently large to include winter habitat will reduce the potential for population-level impacts from anthropogenic development. Seasonal-only SU stipulations (e.g., restricting construction timing or operating periods to occur only outside of the season of use by sage-grouse) may still have adverse effects in subsequent seasons. For example, anthropogenic development in wintering areas during the spring could adversely affect sage-grouse use of the area during the winter, especially if habitat alteration occurred or anthropogenic structures remain. Using the composite response curves from this analysis helps address this issue because they consist of information on space use across all seasons.

The goal of our study was not to estimate effects of anthropogenic structures on sage-grouse populations, but instead to identify a range of distances from the lek sites for SU designation that would limit overlap between development and sage-grouse space use. Nevertheless, our study was not without assumptions and constraints. First, we assumed that our sample of marked sage-grouse from Mono County was representative of the Bi-State population as a whole, and we did not systematically include or exclude sage-grouse from the sample based on their proximity to leks. For example, if our sampling did not capture female sage-grouse that nested at greater distances from leks, we may have underestimated the amount of nesting season UD that was encompassed by a given area threshold. We believe this assumption was largely met because our sample of marked sage-grouse was relatively large, included migratory and non-migratory populations, and spanned a relatively long time interval. Furthermore, we marked individual sage-grouse from multiple distinct areas to prevent biases associated with 1 area. Within those areas, sage-grouse were radio-marked at random to represent an unbiased population sample. Second, we assumed all lek sites were known. Although using a lek-centered method to execute protection stipulations has its logistical advantages and can be relatively cost-effective, this method will only provide an appropriate tool in areas where nearly all lek locations are known. If this assumption is violated, the estimated vUD occurring within a given distance of the nearest lek can be biased, although the biases will likely be negligible if nearly all the leks are known. However, unknown leks will not receive SU designations from a lek-centered method, reducing the total designation area that may otherwise be used by sage-grouse populations. In recent years, the Nevada Department of Wildlife (NDOW) and California Department of Fish and Wildlife (CDFW) have executed extensive aerial surveys for unknown leks in the Bi-State DPS (NDOW and CDFW, unpublished data), and based on this effort we are confident that nearly all leks in the region were captured in our analysis, with the Pine Nut Mountains being a potential exception. However, we stress that any lek-based approach to identifying protected areas shares this critical assumption. Finally, this method may only partially account for dispersal. For example, sage-grouse may make long-distance movements that exceed the SU designation to breeding sites in other populations. Identifying and including areas that maintain population connectivity may be essential to population viability.

The number of males that attend individual leks (lek size) may also be valuable in establishing sizes of SU designations. This consideration is important because impacts to larger leks likely influence population viability rates at larger spatial scales than those to smaller leks. Research that incorporates lek size as a component to inform area thresholds for SU designation may provide more flexibility in the decision-making process.

Reported information on the effects of anthropogenic development and other disturbances surrounding leks on sage-grouse vital rates studied elsewhere is consistent with the distance-based area thresholds we identified during this study. For example, in Wyoming, non-renewable energy development (i.e., gas and oil) was shown to have negative impacts on sage-grouse lek attendance within 3.2 km of lek sites (Walker et al. 2007) and breeding populations were reduced when drilling activity occurred within 5 km of leks (Holloran 2005). Furthermore, within the northeastern portion of their range, activities on and around well sites have been observed to negatively affect sage-grouse lek attendance up to 4.8 km from leks (Harju et al. 2010), perhaps as a result of increased noise pollution (Blickley et al. 2012) and/or sage-grouse perception of increased predation threat. One study focused on the importance of considering wintering areas in SU designations, and concluded sage-grouse avoid areas where anthropogenic structures occur within a 4-km^2 area (Doherty et al. 2008). Furthermore a recent study in eastern Nevada indicated that per-capita recruitment and survival of males were reduced when exotic grassland impacts occurred within a 5-km radius of a lek, but were not influenced for other leks in the study landscape without similar lek-level impacts (Blomberg et al. 2012). These results highlight the importance of habitat conditions surrounding leks on the dynamics of sage-grouse breeding at those leks. The findings by Blomberg et al. (2012) related to the 5-km lek radius are consistent with the threshold levels we identified during our study.

Indirect adverse effects, which include reduced population vital rates that are influenced by changes in predator composition, may also be reduced using a 5–7.5-km area threshold. For example, common ravens (*Corvus corax*), an effective predator of sage-grouse nests (Coates et al. 2008), are more likely to occur in areas with increased anthropogenic structures (Knight and Kawashima 1993, Howe 2011). Sage-grouse nest survival decreases with greater numbers of common ravens (Coates and Delahanty 2010), and ravens are

associated with tall anthropogenic structures at >6-km^2 spatial scales (Howe 2011). In our analysis, we found that 95% of nests were located within 5 km of a lek. This value is consistent with distances reported from other studies (reviewed by Connelly et al. 2011*a*); however, many studies of greater sage-grouse nesting have not reported lek-to-nest distances. Given our results, SU designations that extend 5–7.5 km from all known lek locations are likely to limit both direct and indirect adverse effects to sage-grouse nesting associated with anthropogenic disturbance.

The total area currently used for SU designation to benefit sage-grouse varies both among and within land management agencies. For example, in portions of sage-grouse range, agencies currently implement distances from leks for SU stipulations as low as 0.4 km and 1 km (0.25 miles and 0.6 miles, respectively, Connelly et al. 2000). These stipulations were assigned to prevent abandonment of displaying grounds, reduced reproductive success, and adverse habitat loss. Distances of 0.4 km and 1 km, in the context of our study, represented 5% and 28% of the total vUD, respectively. Given our results, and those of other researchers (Fedy et al. 2012), such stipulations are insufficient to protect sage-grouse populations because they largely fail to protect adequate habitat critical to life stages outside the breeding period, such as nesting, summer and fall, and winter habitats. These stipulations would be considered especially deficient for populations that exhibit large seasonal movements, such as the migratory populations we monitored in the Parker Meadows and Bodie Hills. In these 2 populations, the 0.4-km and 1-km distances encompassed 4% and 18% of annual vUD, respectively.

In this study, for each 30-m increase in distance from leks we did not observe an increase in total area as a squared function of distance (e.g., area $= \pi r^2$, where r is distance from lek), as one might expect. Instead, the juxtaposition of leks influenced the relationship between total area and distance. Leks were located within 30 km of each other and as distance increased, areas were merged together, which slowed the rate of increasing total area. The relationship between distance and threshold area was nearly linear and the average distance between leks in the Bi-State DPS was 8.7 km $\pm$ 5.2 (SD).

To the extent that conditions in the Bi-State DPS are somewhat representative of conditions experienced by other sage-grouse populations, these response curves can be generalized to other populations. These sage-grouse likely share similar seasonal movement patterns with others among the western portion of their range. However, some populations in the northeastern portion of their range appear to show differences. For example, average distance between leks and winter areas (migratory and non-migratory) was 3.2 km in the Bi-State DPS, whereas only 50% of interseasonal movement distances (e.g., between nest to winter site) were $\leq$10 km in Wyoming (Fedy et al. 2012). Where telemetry data are available or can be readily obtained, we suggest this approach be replicated to inform site-specific relationships and recommend adjustments as needed. Additionally, multiple studies using this approach could help inform general SU designations for areas with leks for which no telemetry data are available. Before such information exist, the variation in vUD curves found in this study (Fig. 2) may serve as a baseline that represents space-use patterns elsewhere, especially those occurring in areas with similar landscape characteristics to those found in the Bi-State DPS.

MANAGEMENT IMPLICATIONS

The UD estimates and response curves we have described here allow wildlife and land managers flexibility in decision-making regarding sage-grouse regulatory mechanisms and the potential assignment of SU designations. For example, managers may decide that a SU designation should consist of an area threshold that contains 90% of the vUD rather than 99% based on the results of the diminishing gains analysis. With additional knowledge that a population is migratory, an alternative curve derived from data of migratory populations that will better reflect the behavior of their local population could be used in the decision making process. If the goal is to choose a SU designation distance with a relatively high value index while capturing most of the vUD (i.e., 90%), then these data suggest the minimum distance should be approximately 5 km (Fig. 2a and b). Thus, we have identified a theoretical optimal distance in relation to leks at approximately 5 km, and we highlight that our results suggest that this is the appropriate minimal threshold for SU designations for most populations. However, if populations are considered migratory, then managers should consider increasing the distance to explicitly account for all seasonal use areas, specifically distant wintering areas. Under this scenario, a 7.5-km SU designation may be most appropriate. Nonetheless, the response curves we present here may help establish SU designations based on case-specific considerations.

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Appendix A: A weighting factor for utilization distributions for population level inference based on telemetry sample sizes

The purpose of this 3-step analysis was to develop a weighting factor that reflects uncertainty in individual-level utilization distributions (UDs) based on sample size limitations. We first randomly selected a subset of 10 bird/season UDs from sage-grouse from those that we had collected 35–40 radio-telemetry locations. We chose this sample size as a cutoff value for 2 reasons. This value represented an upper limit to the number of relocations we were logistically capable of obtaining for any 1 bird/season UD and because these values exceeded the 30 observations that have been recommended elsewhere based on least-squares techniques (Seaman et al. 1999). We calculated the UD for each of the 10 sage-grouse using the full number of samples by season (UD_k, $k = 1, \ldots, 10$). We then randomly selected relocations from each of those sage-grouse for all possible sample sizes ($3, \ldots, J-1$) using an iterative process, where J was the maximum number of locations (ranging from 35 to 40). This procedure resulted in 33–38 UDs based on the subsampled datasets for each of the 10 sage-grouse ranging from 35 to 40 locations. We generated all UDs using Geospatial Modeling Environment (Beyer 2012).

During the second step, we calculated the within-individual variance associated with each sample size. We compared the UDs derived from the subsampled datasets (UD_{jk}), where j represents subsample sizes for individual k, to those derived from the full sample (UD_k) by summing the squared errors across all 30 m × 30 m cells, expressed as:

$$y_{jk} = ||\mathrm{UD}_{jk} - \mathrm{UD}_k||^2$$

Double vertical bars represent the Euclidean norm of the difference in values between subsampled and full sample UD arranged into a vector, and the y_{jk} represents surface-wide variance at each subsample. Because the relationship may take a curvilinear form, we used an exponential decay function, expressed as:

$$y = \beta e^{-n/\alpha}$$

where n was the sample size of the subset. We estimated the parameters of β and α by fitting a linear regression to the log of y_{jk} model, expressed as:

$$\log y_{jk} = b_0 + b_1 j$$

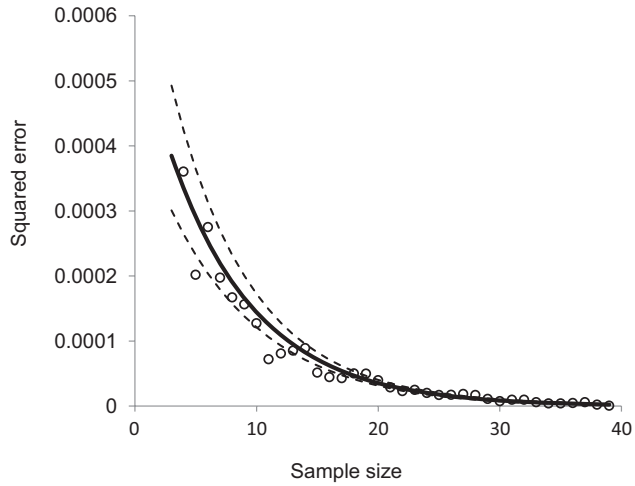

Figure A1. Averaged squared error for 388 seasonal utilization distributions as a function of radio-telemetry sample size derived from individual greater sage-grouse in Mono County, California during 2002–2009. Solid line represents predicted squared error based on best-fit exponential decay function. Dashed lines represent the 95% confidence intervals.

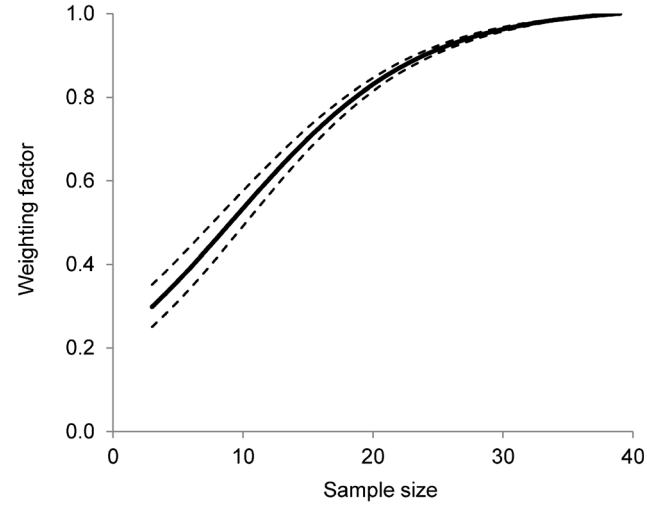

Figure A2. A sample size weighting factor applied to individual seasonal utilization distributions used to calculate population-level estimates of space use by greater sage-grouse in Mono County, California during 2002–2009. Dashed lines represent 95% confidence intervals.

where $\alpha = -1/b_1$ and $\beta = e^{b_0}$ and j represents the predictor variable sample size. We used the estimated parameters from this model to predict within-individual sum of squared error (surface-wide variance, y) based on different sample sizes ($3, \ldots, J-1$; Fig. A1), which we computed as:

$$y = e^{-7.44} \times e^{-n/7.14}$$

During step 2, we calculated the between-individual sample variance among the full sampled UD_k. We overlapped the full sampled UDs (35–40 relocations) and calculated the variance at each grid cell. We then totaled the variances across all grid cells to obtain a surface-wide between-individual variance (s^2), which we then added to the surface-wide within-individual variance to estimate total variance, which is expressed as:

$$V_k = e^{-7.44} \times e^{-n/7.14} + s^2$$

where $s^2 = 0.00016$. During step 3, we used the total variance to develop a weighting factor (w_k) for each UD by calculating the inverse of V_k (Casella and Berger 1990) and rescaling between 0 and 1, which is expressed as:

$$w_k = \frac{1/V_k}{\max_i(1/V_i)}$$

The purpose of the weighting factor was to minimize error (variance) in the population-level UD based on differences in sample size (the predicted curve expressing the relationship between w and sample size is shown in Fig. A2). Utilization distributions comprised of $\geq$40 locations received a weight of 1, whereas those with fewer relocations received less weight (<1). For example, a volume of UD (vUD) comprised of 20 relocations can be multiplied by a weighting factor of 0.83 (receiving less weight) based on the equations above. We conducted the grid analyses using Program R (package: raster; Hijmans and van Etten 2010, R Development Core Team 2008).