




Research Article

Are Sage-Grouse Fine-Scale Specialists or Shrub-Steppe Generalists?

JOSEPH T. SMITH ¹, *Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*

BRADY W. ALLRED, *College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*


CHAD S. BOYD, *U.S. Department of Agriculture Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA*

JOHN C. CARLSON, *U.S. Department of Interior Bureau of Land Management, Billings, MT 59101, USA*

KIRK W. DAVIES, *U.S. Department of Agriculture Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA*

CHRISTIAN A. HAGEN, *Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA*

DAVID E. NAUGLE, *Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*

ANDREW C. OLSEN , *Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA*

JASON D. TACK, *U.S. Department of Interior Fish and Wildlife Service, Habitat and Population Evaluation Team, Missoula, MT 59812, USA*

ABSTRACT Sage-grouse (*Centrocercus* spp.) are influencing rapidly evolving land management policy in the western United States. Management objectives for fine-scale vegetation characteristics (e.g., grass height >18 cm) have been adopted by land management agencies based on resource selection or relationships with fitness proxies reported among numerous habitat studies. Some managers, however, have questioned the appropriateness of these objectives. Moreover, it remains untested whether habitat–fitness relationships documented at fine scales (i.e., among individual nests within a study area) also apply at scales of management units (e.g., pastures or grazing allotments), which are many orders of magnitude larger. We employed meta-analyses of studies published from 1991 to 2019 to help resolve the role of fine-scale vegetation structure in nest site selection and nest success across the geographic range of greater sage-grouse (*C. urophasianus*) and evaluate the validity of established habitat management objectives. Specifically, we incorporated effects of study design and functional responses to resource availability in meta-regression models linking vegetation structure to nest site selection, and used a novel meta-analytic approach to simultaneously model vegetation structure and its relationship to nest success. Our approach tested habitat relationships at a range-wide extent and a grain size closely matching scales at which agencies make management decisions. We found moderate, but context-dependent, effects of shrub characteristics and weak effects of herbaceous vegetation on nest site selection. None of the tested vegetation characteristics were related to variation in nest success, suggesting nesting habitat–fitness relationships have been inappropriately extrapolated in developing range-wide habitat management objectives. Our findings reveal surprising flexibility in habitat use for a species often depicted as having very particular fine-scale habitat requirements, and cast doubt on the practice of adopting precise management objectives for vegetation structure based on findings of individual small-scale field studies. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

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Rangeland ecosystems of North America are beset by persistent and pervasive anthropogenic land-use and land cover change. Agents of change include woodland expansion (Briggs et al. 2005, Romme et al. 2009), positive feedbacks between exotic annual grasses and wildfire (D'Antonio and Vitousek 1992), energy and infrastructure development (Allred et al. 2015), cropland conversion (Lark et al. 2015),

and residential development (Hansen et al. 2002, Galvin and Ellis 2008). These broad-scale threats continue to erode ecosystem services and habitat for sensitive species despite extensive documentation of effects and existing regulatory frameworks, leading some to question the adequacy of conservation and management paradigms for rangelands and their inhabitants (Briske et al. 2003, Boyd et al. 2014).

Sage-grouse (*Centrocercus* spp.) are intensively studied species influencing rangeland management policy in the western United States. As sensitive and charismatic sagebrush (*Artemisia* spp.) obligates, sage-grouse have become a primary focal point for conservation and management of sagebrush rangelands, which are among the most imperiled

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¹E-mail: joe.smith@umontana.edu

ecosystems in North America (Noss et al. 1995). Sometimes called landscape species because of their large area requirements and use of diverse seasonal habitats throughout their life-cycle (Knick and Connelly 2011), sage-grouse populations are sensitive to disturbances at large spatial scales (Aldridge et al. 2008, Naugle et al. 2011, Baruch-Mordo et al. 2013, Smith et al. 2016). Nevertheless, fine-scale metrics (e.g., food, cover) remain a cornerstone of habitat management even as broad-scale threats continue to diminish usable space (Guthery 1997). Misalignment between the focal scale of management and ultimate causes of population declines has contributed to the failure to recover other species (e.g., northern bobwhite quail [*Colinus virginiana*]; Williams et al. 2004). Thus, a better understanding of the importance of fine-scale habitat attributes will help managers effectively prioritize limited resources.

Habitat management guidelines for sage-grouse were built upon a foundation of decades of research examining links between vegetation structure measured at fine grain sizes (mostly <1 ha) and individual-level fitness proxies (Fig. 1). In the most-cited publication on sage-grouse to date, Connelly et al. (2000) informally synthesized available studies to develop vegetation management objectives that have been widely incorporated into documents guiding management of federally administered lands in the United States (Stiver et al. 2015, U.S. Fish and Wildlife Service 2015). These objectives include heights and percent cover of major vegetation functional groups for breeding, brood-rearing, and winter habitats (Connelly et al. 2000:977). However, recognizing the inherent heterogeneity of sagebrush ecosystems, managers have questioned the feasibility and efficacy of these objectives (Schultz 2004, Davies et al. 2006, Dahlgren and Thacker 2019).

Scale is central to 2 primary criticisms of vegetation management objectives. First, these objectives represent an effort to summarize findings of studies conducted across a geographic range characterized by marked spatial and temporal heterogeneity in vegetation composition and structure. Behavioral plasticity or local adaptation may preclude generalization of habitat relationships across a species' range (Morrison 2012). If habitat relationships are largely idiosyncratic, range-wide targets for optimal fine-scale habitat structure may be inappropriate in many

local circumstances. Second, inference from fine-scale habitat studies may be wholly inadequate to predict outcomes of large-scale management manipulations on vital rates of populations (Bro et al. 2004). With few exceptions (Smith and Beck 2018, Smith et al. 2018b), effects of extensive vegetation manipulation on sage-grouse demography are poorly studied. Habitat management guidelines and monitoring assessments thus rest on the assumption that fine-scale habitat relationships scale up to predict effects of manipulating vegetation at management scales (e.g., pastures, ranches, allotments; Fig. 1). This is a precarious assumption given that scale-dependence is a pervasive quality of ecological patterns, including habitat relationships (Wiens 1989, Rettie and Messier 2000, Bissonette 2013).

Our motivation was to clarify relationships between fine-scale vegetation structure and sage-grouse resource selection and demography and test whether patterns from which widely used management objectives were derived apply at management-relevant scales. Focusing specifically on nesting habitat, we approached this by conducting meta-analyses of nesting studies from across the range of greater sage-grouse (*C. urophasianus*). We limited our analysis to nesting habitat because, as the most thoroughly studied seasonal habitat, many studies with similar protocols and reporting comparable data were available. Furthermore, nest success is among the most important factors influencing population growth in sage-grouse (Taylor et al. 2012, Dahlgren et al. 2016) and hence a common management target (Doherty et al. 2014, Severson et al. 2017, Smith et al. 2018b). The scale of our analysis is novel for this species and confers several advantages. First, the extent of our analysis spans the species' geographic range and, therefore, encompasses a gradient of vegetation characteristics appropriate for testing management guidelines applied at the species level (Morrison 2012). Second, nesting studies are conducted over areas ranging from approximately 100 km² to several thousand square kilometers (median reported study area size among studies in this meta-analysis was 1,250 km²), which is a grain size comparable to management units in this region (Fig. 1).

Our first objective was to quantify selection for nest site characteristics, expanding on an earlier meta-analysis of sage-grouse nesting habitat selection (Hagen et al. 2007).

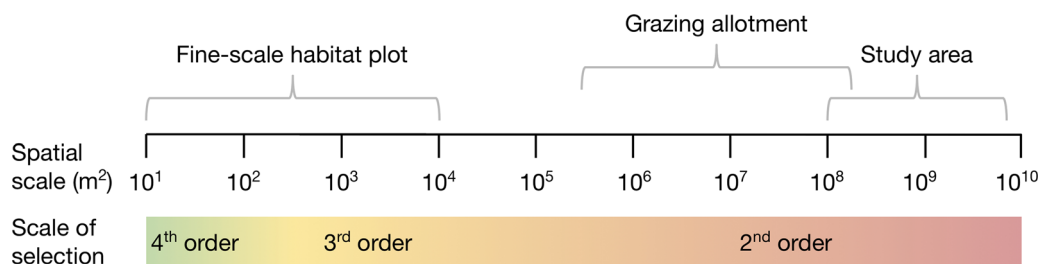


Figure 1. The grain sizes of plots used to quantify vegetation structure at sage-grouse nest sites correspond to Johnson's (1980) definition of third and fourth orders of habitat. Inference from fine-grain studies has strongly influenced management of vegetation at much larger spatial scales. For example, the 19,537 Bureau of Land Management grazing allotments in the United States occupied by greater sage-grouse are characteristic of the grain size at which management assessments and decisions are made. Because habitat relationships are often scale-dependent, relationships between average vegetation structure and demographic rates among studies in North America from 1991–2019 may reveal more about the likely effects of management than inference from individual-level, fine-grain studies.

Capitalizing on the proliferation of sage-grouse nesting habitat studies during the intervening decade, we tested several potential sources of variation in strength of selection for nest site characteristics among studies. These included elements of study design and behavioral responses to variation in ecological context. Because selection for critical resources should appear stronger where the availability of those resources is low (i.e., functional response; Mysterud and Ims 1998, Matthiopoulos et al. 2011), testing for relationships between selection strength and availability should help identify particularly important nest site characteristics. Our second objective was to test for relationships between fine-scale vegetation structure and nest success rates among studies to identify variables likely to influence sage-grouse productivity if manipulated over large areas via management. Finally, we sought to quantify the agreement between fine-scale nest site habitat structure among studied populations and the objectives proposed in Connelly et al. (2000) and widely used by land management agencies.

METHODS

Literature Review

We searched Web of Science, ProQuest Dissertations, and Google Scholar for published studies, theses, dissertations, and reports. Our search keywords included sage-grouse, nest or nesting, selection or success or survival, and habitat or vegetation. We also reviewed cited literature from previous sage-grouse habitat and vital-rate reviews, including Connelly et al. (2000), Hagen et al. (2007), and Taylor et al. (2012). Finally, we contacted principal investigators of several recent or ongoing nesting studies to request unreported summary statistics. We included only studies that reported means and standard errors or standard deviations of ≥ 1 of the following vegetation structural characteristics at nest sites and, where provided, available sites: percent cover of shrubs, percent cover of sagebrush, percent cover of grasses, percent cover of forbs, height of shrubs, height of live grasses, and height of residual or senesced grasses. If grass height was reported without distinguishing between live and senesced, we considered it a measurement of live grasses because measurements were of the tallest portion of a plant and heights of live grasses almost always exceeded those of senesced grasses. When vegetation cover variables were reported as sub-categories of the variables we examined (e.g., percent cover of short, medium height, and tall shrubs; Gregg 1991), we calculated means and standard deviations of the sums of the sub-categories to derive the desired variable. When statistics were reported separately for different groups of nests (e.g., successful vs. failed or nests in different substrates or vegetation types), we calculated pooled means and standard deviations. We recorded several methodological variables, including the size of vegetation plots and methods used to estimate height and percent cover of herbaceous vegetation. When available, we recorded estimates of nest success, the number of monitored nests, type of transmitter used on monitored females, typical nest monitoring interval (e.g.,

daily, weekly), and nesting period to which the nest success estimate pertained (laying, incubation, or both).

Bayesian Meta-Analytical Approach

We used Bayesian methods to estimate parameters while accounting for variable sample sizes, study designs, and heterogeneity in ecological context among studies that might affect responses. We used a multi-level modeling approach, employing global regression coefficients and hyperparameters to model variation in responses among studies and study units (i.e., data from different sites or years reported in the same study). We used reported estimates and their uncertainties to estimate latent (unobserved) population parameters at each study unit i , $i = 1, \dots, N$. Because a number of unreported factors can introduce measurement-related errors into estimates of vegetation cover or height, we included study unit- and variable-specific measurement error terms to model this variation. We fit models with Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer 2003) via the rjags (Plummer 2016) package in R (R Development Core Team 2014). We report medians and 95% highest posterior density intervals of MCMC samples of posterior distributions for parameters of interest. The JAGS model code is available online in Supporting Information.

Nest Site Selection

Our primary objectives in analyzing nest site selection studies were to estimate strength of selection for vegetation characteristics and identify functional responses to availability. Rather than restrict our analysis to studies reporting estimated coefficients from resource selection models (e.g., resource selection functions), we used Hedges' g' (Hedges 1981) as a common measure of selection that allowed us to incorporate information from any study reporting distributions of vegetation characteristics among a sample of nests and a sample of availability. Briefly, Hedges' g' expresses the difference between the estimated means of 2 groups in units of their weighted, pooled standard deviation (Hedges 1981). In our study, g' indicates the difference between the means of vegetation characteristics at use samples (nest sites) and availability samples (random sites). In this context, $g' > 0$ is consistent with selection and $g' < 0$ avoidance.

A previous meta-analysis of sage-grouse nest site selection assumed strength of selection arose from a common distribution (Hagen et al. 2007). We took advantage of the larger number of studies now available to test potential sources of variation in g'_i . In particular, we tested for a linear relationship between g'_i and mean availability (X_i^A), representing a hypothesized functional response in which strength of selection depends on availability. We also estimated effects of 2 elements of study design we hypothesized could affect the magnitude of g'_i . First, we considered an effect for paired study designs where the availability sample was spatially constrained to within an easily traversed distance (usually 100–500 m) of used sites (paired = 1 if constrained; otherwise, paired = 0). This could affect the differences between available and used sites because of hierarchical resource selection or spatial autocorrelation in

vegetation structure. Second, studies measure vegetation using various grain sizes (i.e., the diameter or width of the vegetation plot centered at the point of interest), ranging from 2–60 m (median = 10) for herbaceous vegetation variables and from 2–100 m (median = 30) for shrub variables. Therefore, we grouped studies into 2 categories indicating those where vegetation was measured at grain sizes >20 m (large grain = 1) or a smaller grain size (large grain = 0).

We fit a separate model for each recorded vegetation metric, using reported means, \bar{x}^U and \bar{x}^A , at use (U) and availability (A) samples to estimate latent true means, X^U and X^A , of the vegetation characteristics at each i study unit:

$$\bar{x}_i^U \sim N(X_i^U + \epsilon_i, \text{SE}(\bar{x}_i^U))$$

$$\bar{x}_i^A \sim N(X_i^A + \epsilon_i, \text{SE}(\bar{x}_i^A)),$$

where $\text{SE}(\bar{x}_i^U)$ and $\text{SE}(\bar{x}_i^A)$ are the reported standard errors associated with \bar{x}_i^U and \bar{x}_i^A , respectively, and ϵ_i is an additive measurement error term accounting for various unreported sources of heterogeneity such as observer effects or phenological stage of vegetation. We assumed ϵ_i was equal among used and availability samples within a study unit, and normally distributed with mean 0 and standard deviation σ^ϵ .

We assumed availability at each study unit, X_i^A , arose from a log-normal distribution with a global mean, μ^A , and standard deviation, σ^A :

$$\ln(X_i^A) \sim N(\mu^A, \sigma^A),$$

and use was related to availability via the standardized difference g' , which we scaled by the pooled standard deviation $s(x)^{\text{pooled}}$ among use and availability samples:

$$X_i^U = g'_i s(x)^{\text{pooled}} + X_i^A$$

$$s(x)^{\text{pooled}} = \sqrt{\frac{(n_i^U - 1)s(x)_i^U + (n_i^A - 1)s(x)_i^A}{n_i^U + n_i^A - 2}},$$

where n_i^U and n_i^A are sample sizes of use and availability samples and $s(x)_i^U$ and $s(x)_i^A$ are the reported standard deviations at use and availability samples.

We modeled variation in g'_i with a linear model including an intercept and effects of estimated availability X_i^A (i.e., a functional response), paired sampling design, and large (>20 m) measurement grain, and random effects for study (α_j) and study unit (γ_i):

$$g'_i = \beta_0 + \beta_1 X_i^A + \beta_2 \text{paired}_i + \beta_3 \text{large grain}_i + \alpha_{j[i]} + \gamma_i$$

$$\alpha_j \sim N(0, \sigma^\alpha), \text{ for } j = 1, \dots, J,$$

$$\gamma_i \sim N(0, \sigma^\gamma).$$

We placed compact but relatively uninformative $U(-5,5)$ and $U(0,5)$ priors on global (log-scale) means (μ^A) and standard deviations (σ^A). We experienced difficulty with

MCMC convergence when we placed a vague uniform prior on the standard deviation among measurement errors (σ^ϵ) so we fixed σ^ϵ equal to 10% of the overall mean of \bar{x}^A among included study units. We felt it was reasonable to expect measurement errors would fall within this distribution. Reasonable values of g' were in the range of -3 to 3 so we placed $U(-5,5)$ priors on regression coefficients and $U(0,5)$ priors on σ^α and σ^γ . JAGS code is available online in Supporting Information. Inference was based on 20,000 MCMC samples, 10,000 each from 2 independent chains, after discarding 251,000 burn-in samples from each chain.

Nest Success

To assess relationships between nest success and vegetation characteristics, we fit 2 meta-regression models with nest success (S) as the dependent variable. In the first model, we used average vegetation characteristics at nests as predictors (i.e., use model), and in the second model we used the same characteristics measured at available sites (i.e., availability model). We chose to fit the second model for 2 reasons. First, samples of availability are most directly relevant to managers, who often do not have the benefit of marked individuals and known nest sites and instead must judge habitat quality based on a representative sample of potential nesting habitat. Second, if use was found to be relatively invariant across a gradient of availability, then availability data might contain information about effects of vegetation structure on nest success that use data alone would lack.

We first standardized study unit-level estimates of S (\hat{s}_i) to reflect the probability of a nest surviving a 37-day laying and incubation period using methods of Johnson and Klett (1985). We assumed incubation was initiated 1.5 monitoring intervals (F ; the typical number of days between monitoring events) before nests were discovered to estimate the average exposure period (E ; in days) of successful nests for each study. Incubation averages 27 days (Blomberg et al. 2015), so the exposure period $E_i = 27 - 1.5F_i$. We then calculated daily survival rate during incubation: $\text{DSR}_i^{\text{incubation}} = \hat{s}_i^{1/E_i}$. We found only 2 studies that attempted to estimate daily survival rate separately for laying and incubation. Walker (2008) reported DSR was slightly higher, whereas Gibson et al. (2015) reported DSR was slightly lower, during laying than during incubation. Therefore, we assumed daily survival during laying, which averages 10 days (Blomberg et al. 2015), was equal to daily survival during incubation. We calculated an adjusted estimate of the probability of a nest surviving from the beginning of laying to hatch: $\hat{s}'_i = \text{DSR}_i^{37}$. We did not adjust estimates of nest success that already included the laying and incubation periods (i.e., $\hat{s}'_i = \hat{s}_i$), and set E_i to 27 days for studies that estimated nest success for the whole incubation period. We excluded studies that used poncho-type transmitters (Amstrup 1980) because they are highly visible and may increase probability of detection by predators or alter the relationship between concealment and predation risk (Taylor et al. 2012). Preliminary analysis confirmed that standardized estimates of nest success were significantly lower among study units in which poncho-type transmitters were used.

Because different subsets of the 6 tested vegetation variables were measured or reported among studies with estimates of nest success (range = 2–6, median = 4), we estimated parameters of a global-level (i.e., range-wide) multivariate log-normal distribution to help estimate the complete latent vector of true means of all 6 vegetation characteristics (X_i) at each study unit. These study unit-level latent parameters are, therefore, estimated with information about the distributions of, and correlations among, vegetation characteristics across the range in addition to the reported study unit-level data. This approach allowed us to include all studies with estimates of nest success regardless of the particular subset of reported vegetation variables and explicitly accounts for the sampling and measurement error in the independent variables.

We modeled nest success as a binomial process using integer outcomes trials and successes comparable across i study units:

$$\text{successes}_i \sim \text{Binomial}(\text{trials}_i, S_i),$$

where trials_i was the total number of nests used to estimate reported \hat{s}'_i , and successes_i was derived as the product $\hat{s}'_i \times \text{trials}_i$ rounded to the nearest integer. This obviated the need to incorporate estimates of variance from each study unit, which were frequently unavailable (e.g., for studies supplying only apparent nest success), because the variance of a binomial random variable depends only on probability of success and number of trials.

We modeled variation in nest success S_i with a regression model of the form:

$$\text{logit}(S_i) = \beta_0 + \beta X_i + \alpha_{j[i]} + \gamma_i.$$

We included group-level effects to account for unmeasured variables at the study level (e.g., observer effects):

$$\alpha_j \sim N(0, \sigma^\alpha)$$

and study unit level (e.g., weather, predator abundance or community composition, age structure, average body condition) that could affect nest success independent of effects of vegetation:

$$\gamma_i \sim N(0, \sigma^\gamma).$$

We modeled reported means of vegetation characteristics (\bar{x}_{ik}) as arising from latent means X_{ik} , which were unobservable because of sampling and measurement error:

$$\bar{x}_{ik} \sim N(X_{ik} + \epsilon_{ik}, \text{SE}(\bar{x})_{ik}),$$

where $\text{SE}(\bar{x})_{ik}$ is the reported standard error, and ϵ_{ik} is an additive measurement error term accounting for unreported sources of heterogeneity such as observer effects or phenological stage of vegetation. We assumed measurement errors (ϵ_{ik}) were normally distributed with mean 0 and standard deviation σ_ϵ^k , on which we placed U(0,10) priors. We estimated vectors of latent means of vegetation characteristics (X_i) using a multivariate log-normal distribution,

$$\ln(X_i) \sim \text{MVN}(\boldsymbol{\mu}, \boldsymbol{\Sigma}).$$

Because of collinearity among predictors (some $|r| > 0.7$), we used Bayesian variable selection with indicator variables (Kuo and Mallick 1997) to simultaneously identify the most supported subset of predictors and estimate their effects (Mutshinda et al. 2013, Ghosh and Ghattas 2015). Regression coefficients ($\boldsymbol{\beta}$) were the product of vectors of independent binary indicator variables (\mathbf{I}) and continuous effect size parameters ($\boldsymbol{\theta}$): $\boldsymbol{\beta} = \mathbf{I}\boldsymbol{\theta}$. We calculated posterior model probabilities and Bayes factors from the posterior distribution of \mathbf{I} to express the relative evidence for each candidate model.

We placed a N(0,1.6) prior on β_0 , resulting in an approximately U(0,1) prior on the probability scale. We placed independent Bernoulli(0.5) priors on indicators. We held total model uncertainty constant across candidate models by scaling the prior on effect sizes ($\boldsymbol{\theta}$) by the total number of variables in the model at each step in the MCMC chain (Link and Barker 2006; see JAGS code in Supporting Information). We placed U(0,10) priors on standard deviations of study and study unit-level effects (σ^α and σ^γ). We used a scaled inverse-Wishart prior (Gelman and Hill 2006) on parameters $\boldsymbol{\mu}$ and $\boldsymbol{\Sigma}$ of the global multivariate normal distribution. This relaxed constraints imposed on the standard deviations and correlations of a multivariate normal distribution by a standard inverse-Wishart prior, and involved estimating independent scaling parameters (ξ_k) for each variable and an unscaled variance-covariance matrix (\mathbf{Q}) to derive the elements of the mean vector $\boldsymbol{\mu}$, variance-covariance matrix $\boldsymbol{\Sigma}$, and correlation matrix $\boldsymbol{\rho}$. We placed flat priors on each scaling parameter,

$$\xi_k \sim U(0,100)$$

and an inverse-Wishart prior with degrees of freedom = $K + 1$ and scale = \mathbf{I} (the $K \times K$ identity matrix) on the unscaled variance-covariance matrix,

$$\mathbf{Q} \sim \text{Inv-Wishart}_{K+1}(\mathbf{I}).$$

The variance-covariance matrix $\boldsymbol{\Sigma}$ was then derived as:

$$\boldsymbol{\Sigma} = \text{Diag}(\boldsymbol{\xi})\mathbf{Q}\text{Diag}(\boldsymbol{\xi}).$$

We derived elements of the mean vector ($\boldsymbol{\mu}$) by multiplying a vector of unscaled (raw) mean parameters ($\boldsymbol{\mu}^{\text{raw}}$) by the vector of scaling parameters $\boldsymbol{\xi}$. We placed vague normal priors on the raw mean parameters,

$$\boldsymbol{\mu}_k^{\text{raw}} \sim N(0,100).$$

We derived standard deviations from the scale parameters and elements of the unscaled variance-covariance matrix,

$$\sigma_k = \xi_k \sqrt{Q_{kk}}$$

and correlations,

$$\rho_{kl} = \boldsymbol{\Sigma}_{kl} / (\sigma_k \sigma_l) \text{ (Gelman and Hill 2006)}.$$

Variation in vegetation measurement methods among studies posed a potential source of error in our meta-regressions.

Therefore, we conducted a sensitivity analysis to explore the potential effect of bias associated with variation in methods for measuring grass height (Appendix A) and, using simulations, developed correction factors to standardize canopy cover estimates prior to model fitting (Appendix B). JAGS code is available online in Supporting Information. Inference from nest success models was based on 100,000 MCMC samples, 50,000 each from 2 independent chains, after discarding 1,010,000 burn-in samples from each chain.

Assessment of Objectives

To compare the published management objectives in Connelly et al. (2000: table 3) and Stiver et al. (2015: table 5 and form S-3) to the multivariate distribution of vegetation structure among study areas, we derived the following variables from our nest success models. For each iteration l of the MCMC chain, we reclassified the $N \times K$ matrix of latent true means of vegetation structural characteristics (X^l) into a binary matrix (G^l), indicating whether each variable fell within the most permissive range prescribed in the objectives (i.e., sagebrush cover 15–25%, shrub height 30–80 cm, grass cover >10%, forb cover >5%, residual or live grass height >18 cm [the objectives do not discriminate between live and residual grass]). We then summed G^l by row to derive a vector of length N indicating the estimated number of objectives met at each study unit (M^l , integer from 0–5). Finally, we reclassified M^l to a binary breeding habitat suitability vector (1 if $M_i^l = 5$, else 0), and took the mean across study units to arrive at an estimate of the proportion of N study units deemed fully suitable by the guidelines. We report the median and 95% credible interval (CRI) of this derived variable for use and availability models, and provide histograms of the estimated number of objectives met among study units.

RESULTS

Our search yielded 43 studies meeting our criteria for inclusion (Fig. 2; Tables S1–S9, available online in Supporting Information), including 25 theses or dissertations, 13 peer-reviewed articles, and 5 government reports. We contacted the authors of several studies that reported relevant statistics but pooled data from >1 study area separated by >25 km and were subsequently provided the unpooled statistics from 2 of those studies (Doherty 2008, Kirol et al. 2012). We excluded 10 study units from 5 studies from the nest success meta-analyses because the investigators used poncho transmitters (Gregg 1991, Fischer 1994, Hanf et al. 1994, Apa 1998, Sveum et al. 1998). The final dataset included studies from all 11 states in the United States and 2 Canadian provinces occupied by greater sage-grouse, and all 7 management zones (Fig. 2).

Nest Site Selection

Gelman diagnostics (<1.1) and visual examination of posterior distributions indicated adequate mixing and convergence among MCMC chains for all variables. Model estimates of latent parameters X^U and X^A were strongly correlated ($r \geq 0.98$) with reported means \bar{x}^U and

\bar{x}^A for all vegetation characteristics. Selection for all vegetation characteristics tended to be positive (Fig. 3; Fig. S1, available online in Supporting Information), and the strongest selection was for sagebrush cover, total shrub cover, and shrub height (Table 1). A functional response was strongly supported only for sagebrush cover ($\beta_1 = -0.03$, 95% CRI = -0.04 to -0.02), total shrub cover ($\beta_1 = -0.02$, 95% CRI = -0.03 to -0.01), and shrub height ($\beta_1 = -0.01$, 95% CRI = -0.02 to 0.00). A functional response to availability was weakly supported for live grass height ($\beta_1 = -0.01$, 95% CRI = -0.03 to 0.01). Across nearly all tested variables, selection appeared stronger when available sites were sampled using a random (study area-wide) sampling scheme ($\beta_2 < 0$; Table 1), with live and residual grass heights the exceptions to this trend. However, credible intervals for β_2 overlapped zero for all variables (Table 1). Estimated coefficients of the forb cover model indicated there may be weak selection for nesting areas with greater forb cover but that this effect diminishes or even reverses at smaller spatial scales captured with paired availability sampling. Grain size had less influence on strength of selection; point estimates of β_3 were mostly negative, suggesting studies measuring vegetation characteristics within 20 m of the point of interest better differentiate nests from available points, but credible intervals for β_3 widely overlapped zero for all variables (Table 1). This is consistent with previous research reporting strong cross-scale correlations ($r \geq 0.8$) for vegetation characteristics measured around sage-grouse nests (Gibson 2015).

Nest Success

Standardized estimates of nest success (\hat{s}') ranged from 0.10 to 1.0 ($\bar{x} = 0.36$; Table S2). Ninety study units from $J = 35$ studies were included in the use model, and 77 study units from $J = 28$ studies were included in the availability model. Gelman diagnostics (<1.1) and visual examination of posterior distributions indicated adequate mixing and convergence among MCMC chains for all parameters for use and availability models.

For the use model, the posterior mean inclusion probability, $P(I_k = 1)$, of all vegetation variables was <0.5 and the model containing only the intercept and random effects received strong support with a Bayes factor (BF) of 6.60 (Table 2). The second-ranked model (BF = 2.63) included a weak negative effect of forb cover ($\beta_3 = -0.09$, 95% CRI = -0.28 to 0.10) and the third-ranked model (BF = 1.99) included a weak negative effect of live grass height ($\beta_5 = -0.07$, 95% CRI = -0.25 to 0.12) on nest success. Conditioned on the top model, the intercept ($\beta_0 = -0.71$, 95% CRI = -0.92 to -0.51) indicated global average nest success for a 37-day exposure period was 0.33 (95% CRI = 0.29 – 0.38). Study-level variation ($\sigma^\alpha = 0.42$, 95% CRI = 0.21 to 0.64) was similar to study unit-level variation ($\sigma^\gamma = 0.43$, 95% CRI = 0.29 to 0.57), consistent with the fact that these groupings were often redundant because many studies (22 of 35) contributed only a single nest success observation.

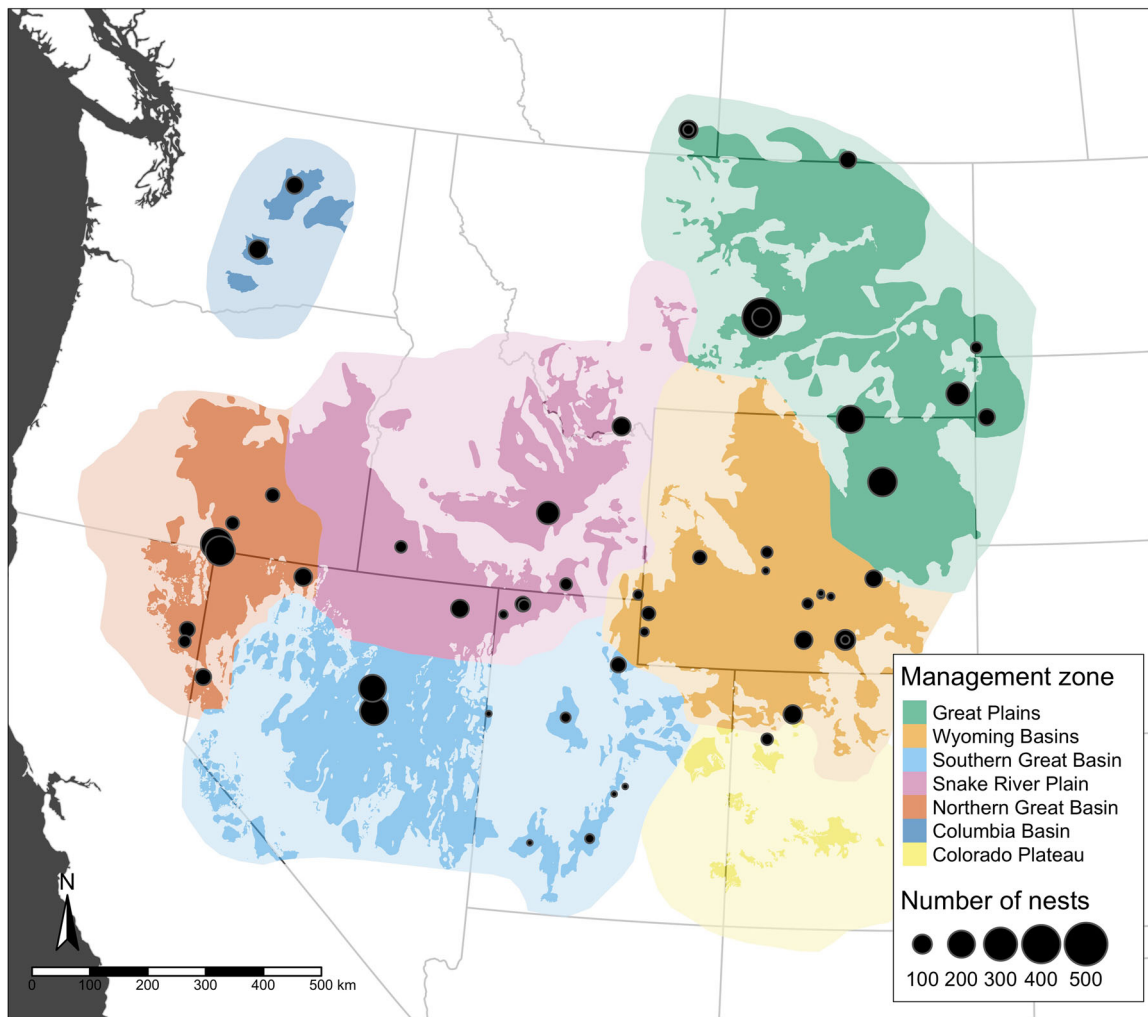


Figure 2. Sage-grouse nesting studies across North America included in meta-analyses of the effects of vegetation characteristics on nest site selection and nest success based on studies from 1991–2019. Colored polygons represent sage-grouse management zones (Stiver et al. 2006), with the estimated current range of greater and Gunnison (*Centrocercus minimus*) sage-grouse depicted by darker shading (Schroeder et al. 2004).

The availability model yielded qualitatively similar results but with slightly more model uncertainty (Table 2). Posterior mean inclusion probabilities of all vegetation effects were <0.50 . The top-ranked intercept-only model ($BF = 5.52$) received more than twice the weight of the second-ranked model ($BF = 2.52$), which included a slight positive effect of sagebrush cover on nest success ($\beta_1 = 0.12$, 95% CRI = -0.14 to 0.40). The third ranked model ($BF = 2.24$) included a weak negative effect of live grass height ($\beta_5 = -0.10$, 95% CRI = -0.30 to 0.12). The top-ranked model intercept ($\beta_0 = -0.76$, 95% CRI = -1.0 to -0.49), study-level standard deviation ($\sigma^\alpha = 0.47$, 95% CRI = 0.23 to 0.73), and study unit-level standard deviation ($\sigma^\gamma = 0.43$, 95% CRI = 0.28 to 0.58) were similar to the use model.

Among studies, there were strong correlations between sagebrush cover and shrub height ($\rho = 0.80$), grass and forb cover ($\rho = 0.70$), and heights of live and residual grasses ($\rho = 0.70$) at nest sites. Grass cover and residual grass height were moderately correlated ($\rho = 0.61$), and shrub

characteristics were moderately to weakly negatively correlated with most herbaceous vegetation characteristics (Table 3). Correlations among vegetation characteristics at available sites were generally similar to correlations at used sites (Table 3).

Correcting grass heights to account for differences in measurement methods did not change inference with regard to the effect of grass height on nest success. The intercept-only model retained the most support for both use and availability models and the direction of coefficients for grass height remained negative among lower-ranked models (Appendix A).

Assessment of Objectives

Mean vegetation structure at nest sites was estimated to meet all 5 breeding habitat objectives from Connelly et al. (2000:977) in 11.1% (95% CRI = 5.5 to 16.6%) of 90 study units (Fig. 5A). Mean vegetation structure at available sites met all 5 objectives in an estimated 5.2% (95% CRI = 0.0 to 10.3%) of 77 study units (Fig. 5B). Consistent with the lack of

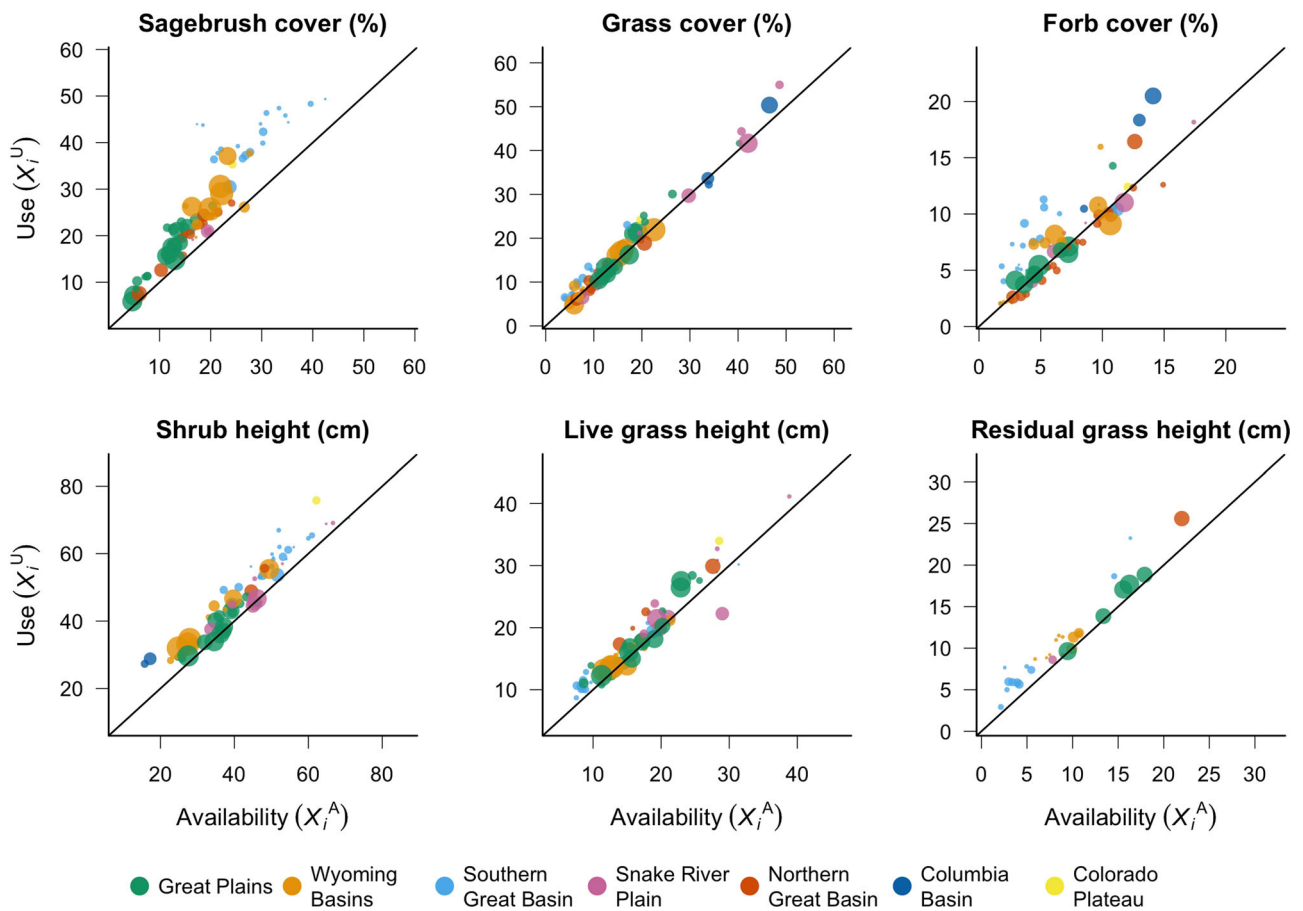


Figure 3. Mean percent cover and height of vegetation functional groups at greater sage-grouse nest sites relative to availability across North America based on studies from 1991–2019. Colors correspond to sage-grouse management zones (Stiver et al. 2006), and point size is proportional to sample size (number of nests). A 1:1 slope is indicated by solid black lines.

association between nest success and any of the tested vegetation variables (Figs. S1 and S2), there was no apparent relationship between nest success and the number of guidelines met at nests or available sites (Fig. 5).

DISCUSSION

Consistent with a view of sage-grouse nesting habitat as essentially homogeneous environments where predation risk is unpredictable (Gerber et al. 2019), and in stark contrast to the degree of specialization implied in management objectives, we show that nesting sage-grouse are fine-scale habitat generalists, selecting slightly shrubbier but otherwise unremarkable patches of vegetation without consequences for nest success. By highlighting the variability among successfully exploited nesting habitats across their range, our results challenge the validity of widely adopted habitat management objectives. Among the most striking results was the strong correlation between available and selected nest sites (Fig. 3). Throughout their geographic range, sage-grouse select nest sites nearly indistinguishable from the surrounding landscape. On average, only half a standard deviation differentiated shrub structure at nest sites from available sites (Fig. S1). For herbaceous vegetation characteristics, differences were even smaller.

Use-availability differences, including the metric used herein (Hedges' g' ; Fig. S1), should be viewed as hypothesis-generating patterns and, ideally, interpreted in conjunction with inference on demographic performance. Previous habitat syntheses have overemphasized univariate differences between use and availability, interpreting them as evidence of fitness consequences that influence patterns of selection (Connelly et al. 2000, 2011; Braun et al. 2005). Such interpretations, however, may be confounded by even weak, within-study correlations among vegetation or abiotic variables (e.g., topographic position, aspect, or soil attributes). For example, heights of live and residual grass were positively correlated ($0.15 < r < 0.25$; J. T. Smith, University of Montana, unpublished data) with sagebrush cover and shrub height in central Montana (Smith et al. 2018a). Where similar correlations exist, apparent selection for taller grasses could be an artifact of true selection for shrub structure. Studies employing multiple regression model-based methods less susceptible to confounding variables provide equivocal support for selection of greater herbaceous vegetation height or cover. Positive selection is supported in several of these studies (Aldridge 2005, Holloran et al. 2005, Tack 2009, Gibson et al. 2016) but unsupported in many others (Aldridge and Brigham 2002, Kolada et al. 2009, Doherty et al. 2010, Lockyer et al. 2015, Dinkins et al. 2016).

Table 1. Parameter estimates (posterior medians) and highest posterior density 95% credible intervals (in parentheses) of meta-regression models of effects of fine-scale vegetation structure on nest site selection in greater sage-grouse, based on studies from across their geographic range in North America, 1991–2019. Parameters include an intercept (β_0), effects of availability (β_1), paired sampling design (β_2), and grain size (β_3); standard deviations for study- (σ^2) and study unit-level (σ^r) random effects; and the range-wide mean (μ^A) and standard deviation (σ^A) of availability (log scale) of each vegetation variable.

Variable	β_0	β_1	β_2	β_3	σ^2	σ^r	μ^A	σ^A
Shrub cover (%)	1.01 (0.67 – 1.39)	-0.02 (-0.03 – -0.01)	-0.21 (-0.47 – 0.06)	-0.02 (-0.31 – 0.26)	0.32 (0.16 – 0.49)	0.16 (0.02 – 0.28)	2.94 (2.81 – 3.06)	0.49 (0.40 – 0.60)
Sagebrush cover (%)	1.14 (0.80 – 1.53)	-0.03 (-0.04 – -0.02)	-0.20 (-0.46 – 0.07)	-0.16 (-0.38 – 0.08)	0.32 (0.20 – 0.47)	0.07 (0.00 – 0.16)	2.81 (2.68 – 2.92)	0.51 (0.41 – 0.61)
Grass cover (%)	0.09 (-0.09 – 0.29)	0.00 (-0.01 – 0.01)	-0.01 (-0.22 – 0.21)	-0.03 (-0.20 – 0.14)	0.20 (0.11 – 0.32)	0.08 (0.00 – 0.19)	2.46 (2.32 – 2.62)	0.63 (0.52 – 0.75)
Forb cover (%)	0.16 (-0.07 – 0.39)	0.00 (-0.03 – 0.02)	-0.11 (-0.34 – 0.12)	0.07 (-0.15 – 0.29)	0.19 (0.09 – 0.30)	0.19 (0.10 – 0.28)	1.69 (1.53 – 1.85)	0.64 (0.52 – 0.77)
Shrub height (cm)	0.90 (0.52 – 1.28)	-0.01 (-0.02 – 0.00)	-0.12 (-0.34 – 0.09)	-0.03 (-0.26 – 0.21)	0.22 (0.11 – 0.36)	0.11 (0.00 – 0.21)	3.66 (3.56 – 3.77)	0.36 (0.28 – 0.45)
Live grass height (cm)	0.45 (0.08 – 0.83)	-0.01 (-0.03 – 0.01)	0.13 (-0.12 – 0.38)	-0.09 (-0.34 – 0.15)	0.26 (0.07 – 0.43)	0.22 (0.11 – 0.35)	2.71 (2.60 – 2.81)	0.43 (0.35 – 0.51)
Residual grass height (cm)	0.34 (-0.10 – 0.77)	0.00 (-0.03 – 0.03)	0.07 (-0.52 – 0.61)	-0.16 (-0.88 – 0.54)	0.24 (0.00 – 0.60)	0.16 (0.00 – 0.32)	1.99 (1.70 – 2.27)	0.70 (0.49 – 0.98)

Commonly, habitat studies sample only a small and biologically arbitrary subset of the species over a short period of time, and are therefore unlikely to produce knowledge of habitat relationships universally applicable to a species (Morrison 2012, McKellar et al. 2014, Van Horne and Wiens 2015). That none of the fine-scale vegetation metrics identified in breeding habitat management guidelines scaled up to predict range-wide variation in nest success should perhaps be unsurprising given the disagreement about such relationships in the literature. The lack of association between vegetation structure and nest success at a range-wide scale does not imply local relationships do not exist. Rather, it confirms what an objective survey of the literature suggests, i.e., local relationships are variable and idiosyncratic, such that range-wide benchmarks for suitable breeding habitat are of doubtful utility.

Effective management of ecosystems upon which sensitive species rely requires knowledge of system dynamics and responses to management actions spanning spatial and temporal scales. Reductionist approaches yielding relationships among constituent parts, typified by fine-scale, individual-level habitat studies, are necessary but insufficient to gain such an understanding (Kessler et al. 1992, Bennetts et al. 1998, Bro et al. 2004). Rather, reliable knowledge of how management affects populations requires data at a scale that matches the question. This could include large-scale management experiments or observational studies of actual management actions (Walters and Holling 1990). Fortunately, such investigations are increasingly common (Monroe et al. 2017, Smith and Beck 2018, Smith et al. 2018b, Olsen 2019). For example, recent management studies have affirmed the effectiveness of watershed-scale restoration of conifer-invaded sagebrush rangelands (Severson et al. 2017, Olsen 2019) but have failed to demonstrate clear benefits of managing fine-scale vegetation structure, e.g., via grazing management (Smith et al. 2018b) or other treatments (Smith and Beck 2018) intended to increase herbaceous understory cover.

Managers, who are charged with multiple, often competing goals with limited resources, may be justifiably frustrated when scientific guidance proves a poor fit for local conditions. Available vegetation failed to meet the accepted definition of suitable breeding habitat in 95% of reviewed studies, leaving little doubt that many managers will find these targets difficult, if not impossible, to achieve (Fig. 4). Some variables (e.g., shrub height) are essentially unmanageable, whereas others (e.g., grass height, forb cover) exhibit considerable natural fluctuation in response to weather. With few tools available to achieve them, ambitious habitat management targets may predetermine a particular management action and limit managers' flexibility to respond appropriately to other local issues or management goals. Lacking evidence that meeting these objectives provides demographic benefits to the target species (Fig. 5), effort and resources spent pursuing them may be more judiciously directed toward maintaining vegetation conditions that promote resistance to ecosystem-scale threats such as exotic annual grass invasion and woodland expansion and resilience to disturbances such as fire and

Table 2. Model ranks, posterior model weights, and Bayes factors for the 10 highest-ranked meta-regression models of effects of fine-scale vegetation structure on greater sage-grouse nest success across their geographic range in North America, 1991–2019.

Model (sign of coefficient)		Posterior model weight ^a	Relative model weight	Bayes factor ^b
Use	Intercept-only	0.095	1.00	6.60
	Forb cover (–)	0.040	0.42	2.63
	Sagebrush cover (–)	0.031	0.32	1.99
	Live grass height (–)	0.030	0.32	1.96
	Grass cover (–)	0.029	0.31	1.93
	Shrub height (–)	0.027	0.28	1.73
	Residual grass height (–)	0.026	0.28	1.70
	Grass cover (–) + live grass height (–) + residual grass height (+)	0.024	0.26	1.58
	Live grass height (–) + residual grass height (+)	0.023	0.24	1.49
	Forb cover (–) + residual grass height (+)	0.022	0.23	1.42
Availability	Intercept-only	0.081	1.00	5.52
	Sagebrush cover (+)	0.038	0.48	2.52
	Live grass height (–)	0.034	0.43	2.24
	Residual grass height (–)	0.032	0.39	2.06
	Grass cover (–)	0.025	0.32	1.67
	Live grass height (–) + residual grass height (–)	0.023	0.28	1.48
	Forb cover (–)	0.023	0.28	1.47
	Shrub height (–)	0.022	0.28	1.43
	Sagebrush cover (+) + shrub height (–)	0.022	0.27	1.40
	Sagebrush cover (+) + residual grass height (–)	0.022	0.26	1.36

^a Prior inclusion probability for each of $k=6$ candidate variables was 0.5, so each of 2^k possible models had a prior probability of 0.5^6 or $1/64$.

^b The Bayes factor is the ratio of posterior odds to prior odds.

drought. Established and emerging tools are available to aid managers in these efforts (Pellant et al. 2005, Chambers et al. 2017).

One-size-fits-all management prescriptions may have unintended detrimental effects on ecosystems (e.g., by undermining the role of heterogeneity in giving rise to diversity; Hiers et al. 2016). Sage-grouse have been forwarded as surrogates for conservation of sagebrush-associated fauna because they are sensitive to anthropogenic disturbance and require large and diverse landscapes to carry out their life cycle (Dobkin 1995). At broad scales, high overlap between sage-grouse and other sagebrush-associated species supports their potential effectiveness as an umbrella species (Rowland et al. 2005, Hanser and Knick 2011, Runge et al. 2019). The coverage of the sage-grouse conservation umbrella, however, is largely a function of the heterogeneity represented across their diverse seasonal habitats (Hanser and Knick 2011). At scales finer than annual home ranges (i.e., third- and fourth-order; Fig. 1), habitat preferences diverge and overlap with sympatric species declines (Wiens et al. 1987, Timmer et al. 2019). If a desired outcome of management is to extend benefits to the widest possible variety of co-occurring species,

heterogeneity at multiple scales should be an explicit management goal (Fuhlendorf et al. 2017). Precise fine-scale habitat objectives instead direct managers' attention toward eliminating undesired variation, with homogenization of vegetation structure a probable consequence.

MANAGEMENT IMPLICATIONS

We emphasize the importance of matching range-wide sage-grouse habitat management policies and guidelines with habitat attributes that can be empirically shown to influence sage-grouse occupancy and demographic performance at broad spatial scales. Our findings suggest common metrics of vegetation structure have no consistent relationship with nest success, an influential demographic rate for which management is commonly targeted, across the species' range. Nest success is, however, only 1 of several important factors influencing sage-grouse population dynamics. Generally, our results suggest managers should be skeptical of recommendations that extrapolate habitat relationships beyond their original spatial scale or ecological context. These should be treated as hypotheses in need of testing before widespread adoption.

Table 3. Parameter estimates (posterior medians) of a multivariate log-normal distribution describing the range-wide means (μ), standard deviations (σ), and correlations (ρ) among 6 commonly reported vegetation characteristics at used (above diagonal) and available (below diagonal) greater sage-grouse nest sites across their range in North America, based on studies from 1991–2019.

Variable	Use		Availability		ρ					
	μ	σ	μ	σ	Sagebrush cover	Grass cover	Forb cover	Shrub height	Live grass height	Residual grass height
Sagebrush cover	3.11	0.42	2.85	0.39						
Grass cover	2.46	0.62	2.27	0.69	–0.59					
Forb cover	1.82	0.70	1.62	0.72	–0.46	0.80				
Shrub height	3.72	0.30	3.62	0.34	0.74	–0.25	–0.18			
Live grass height	2.79	0.38	2.66	0.42	–0.57	0.40	0.44	–0.47		0.70
Residual grass height	2.47	0.60	2.24	0.64	–0.43	0.55	0.53	–0.21	0.80	

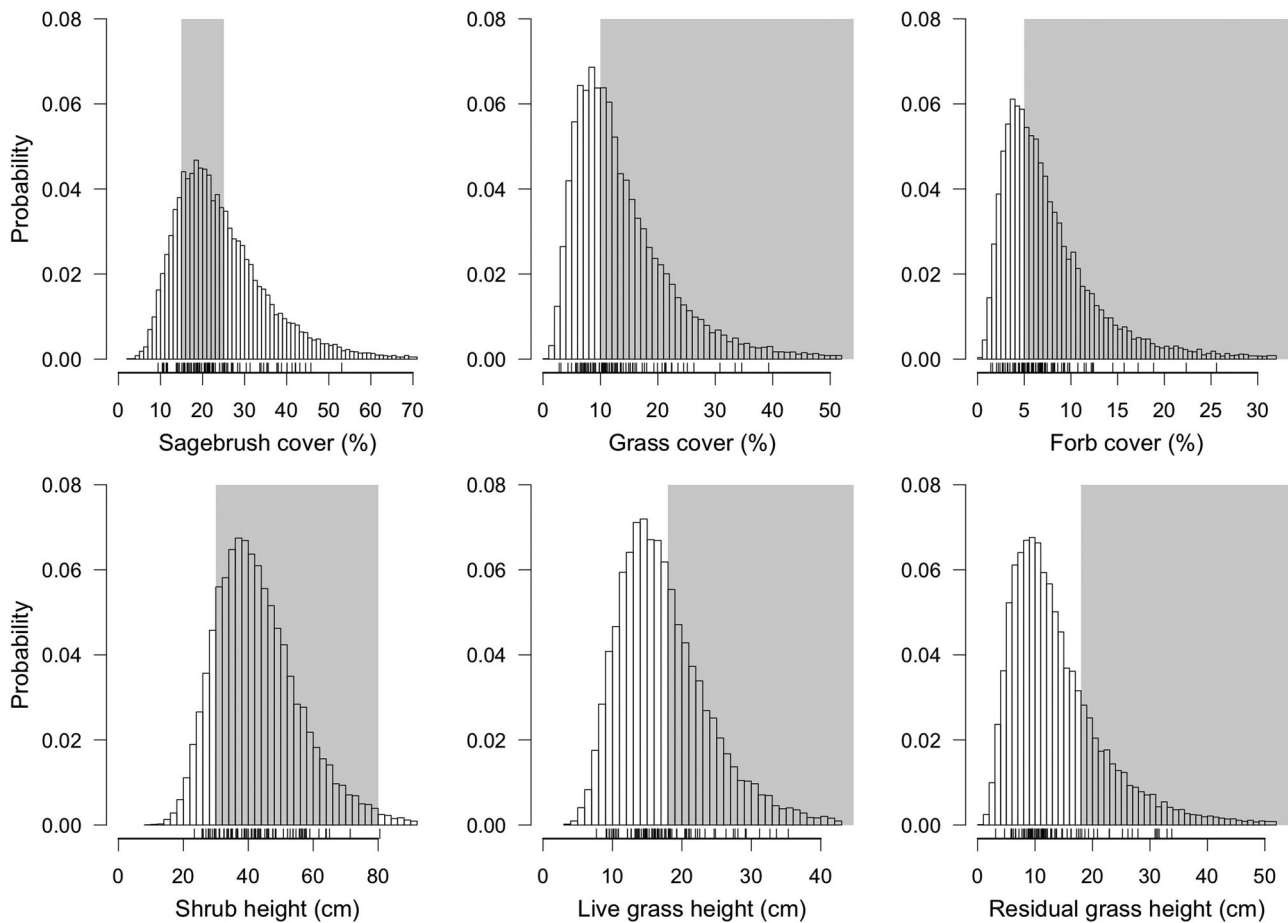


Figure 4. Distribution of 20,000 draws from a multivariate log-normal distribution characterizing average structural characteristics of dominant vegetation functional groups at greater sage-grouse nests (histograms), where we estimated the mean vector and variance-covariance matrix with data from 39 studies conducted across their range in North America from 1991–2019. In rug plots along the horizontal axis, ticks are positioned at the estimated means at each of 90 study units. Shaded regions represent objectives for breeding habitat according to habitat management guidelines (Connelly et al. 2000: table 3). Only 11% of nesting habitat across the range is estimated to meet all objectives. None of these vegetation characteristics explained variation in nest success.

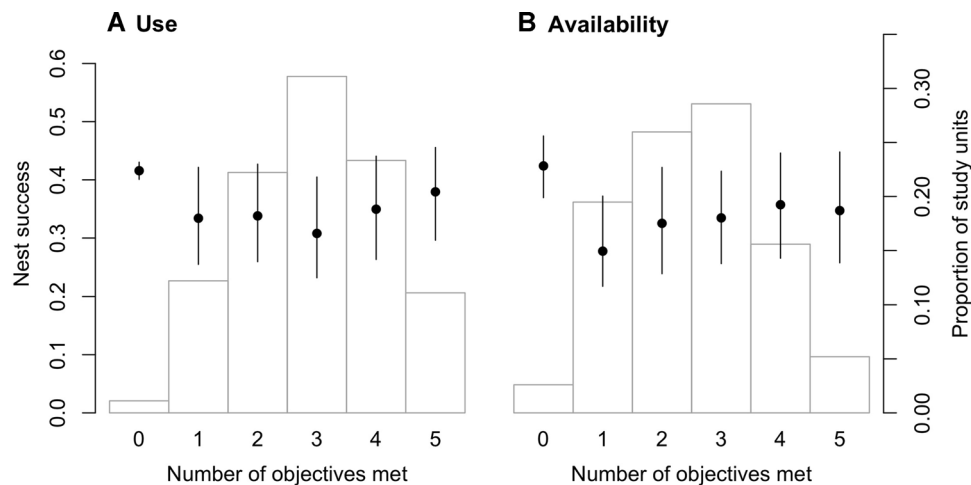


Figure 5. Proportion of study units (histograms) meeting varying numbers of fine-scale vegetation objectives in commonly used management guidelines for greater sage-grouse across their geographic range in North America based on studies from 1991–2019 and estimated nest success (points and error bars indicate median and interquartile range) among those study units. Objectives include 1) sagebrush cover 15–25%, 2) shrub height 30–80 cm, 3) grass cover >10%, 4) forb cover >5%, and 5) residual or live grass height >18 cm. Study units were binned based on the number of objectives achieved at nest sites (A) or random sites quantifying availability (B). Nest success did not increase with greater compliance with these objectives.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A. GRASS HEIGHT SENSITIVITY ANALYSIS

Slight differences in methods can significantly affect measurements of vegetation structure (Di Stefano et al. 2018). Reviewed studies variously reported measuring either 1) the tallest grass plant(s) within a predetermined area (e.g., a quadrat; hereafter tallest grass method) or 2) the grass plant nearest a predetermined point (e.g., a mark along a transect; hereafter nearest grass method). This methodological variation introduces noise into grass height variables that could obscure their influence on nest success. We explored the potential effect of this variation on our inference by identifying studies using the nearest grass method, determining the average percent difference between grass heights in these studies and grass heights from other studies with a linear mixed effects model on log-transformed measurements of grass height with a random effect for study, using the estimated coefficient from the fitted model as a correction factor to adjust grass heights from studies that used the nearest grass method, and refitting the meta-regression model. We did not alter grass heights from studies that did not report grass measurement method because they were statistically indistinguishable from studies that reported using the tallest grass method (Fig. A1).

On average, live grass heights among studies using the nearest grass method were 78.3% of live grass heights from studies using the tallest grass method ($\beta_{\text{nearest}} = -0.24 \pm 0.12$ [SE]). Only 3 studies using the tallest grass method reported residual grass heights. We felt this was insufficient to estimate a separate measurement effect size, so we assumed the effect would be similar and used the same correction factor to adjust residual grass heights from those studies.

These adjustments had no effect on the most supported use model; the intercept-only model still received the majority of support with a Bayes factor of 7.35. The second-ranked model, which received weak support with a Bayes factor of 2.80, contained a negative effect of forb cover on nest success ($\beta = -0.09$, 95% CRI = -0.25 to 0.08), and the third ranked model, with a Bayes factor of 2.26, indicated a negative effect of sagebrush cover ($\beta = -0.05$, 95% CRI = -0.25 to 0.15). Bayes factors of all other models were <2 .

Results were similar for the availability model. After adjustment of grass heights, the intercept-only model remained the most supported with a Bayes factor of 5.75. A model with a positive effect of sagebrush cover ($\beta = 0.14$, 95% CRI = -0.08 to 0.37) ranked second with a Bayes factor of 2.90, and a model with a negative effect of live grass height ($\beta = -0.11$, 95% CRI = -0.31 to 0.08) ranked third with a Bayes factor of 2.54. The fourth ranked model, with a Bayes factor of 2.06, included a negative effect of residual grass height ($\beta = -0.08$, 95% CRI = -0.30 to 0.12). Bayes factors of all other models were <2 .

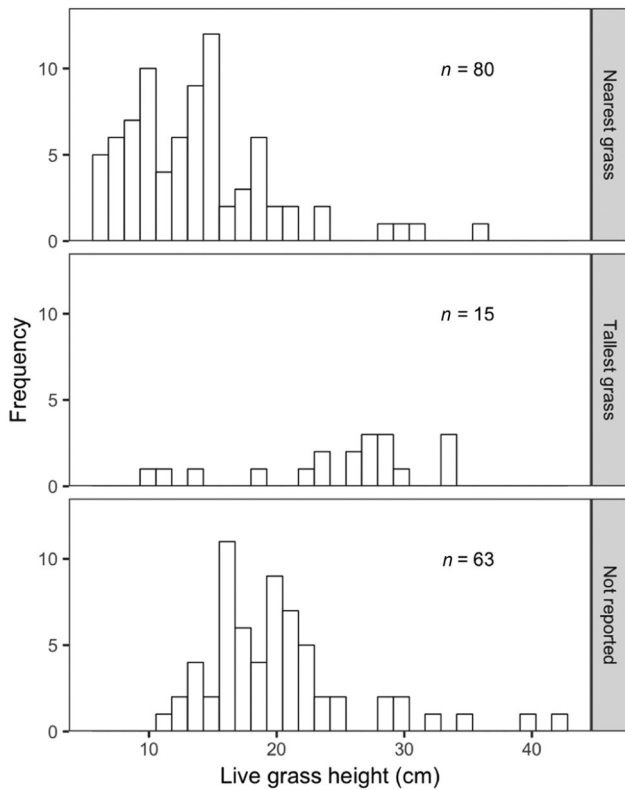


Figure A1. Mean live grass height at greater sage-grouse nests among 158 study units from 34 studies conducted across their range in North America from 1991–2019, by measurement method.

Correcting grass heights to account for methodological differences did not appreciably change inference with regard to the effect of grass height on nest success. Model rankings were similar to rankings using uncorrected values for both the use and availability models, and the direction of effects was unchanged. Therefore, it appears exceedingly unlikely that true positive associations were simply obscured by noise introduced by variable methods of measuring height of grasses.

APPENDIX B. CORRECTION OF GRASS AND FORB COVER ESTIMATES USING VARIOUS METHODS

Among studies reporting cover of herbaceous vegetation (grasses and forbs), most used visual estimation aided by 20 × 50-cm quadrats as described in Daubenmire (1959; Daubenmire's method). Daubenmire's method involves estimating cover of each species or functional group of interest within the quadrat to 1 of 6 cover classes: 1 = (0–5%], 2 = (5–25%], 3 = (25–50%], 4 = (50–75%], 5 = (75–95%], and 6 = (95–100%]. The midpoints between the lower and upper bounds of cover classes (e.g., 0.25%, 15%, 37.5%) recorded within several sampled quadrats at each plot are averaged to estimate average cover at the plot. Though fast and repeatable, Daubenmire's method overestimates cover of species or functional groups with sparse cover (Floyd and Anderson 1987). The method assumes true cover is uniformly distributed around the midpoints of cover classes. If, however, values below the midpoint of cover classes are more

common than values above the midpoint, Daubenmire's method will produce positively biased estimates.

Several reviewed studies used narrower cover classes such as the nearest 5% (Burnett 2013) or 1% (Smith et al. 2018b; Olsen 2019). Another (Schroff et al. 2018) used the line-point intercept method to estimate cover, which tends to produce higher estimates of cover than either Daubenmire's method (Thacker et al. 2015) or visual estimation to the nearest 1% (Symstad et al. 2008). Finally, one study used the line intercept method (Canfield 1941) to estimate cover (Fischer 1994). Thus, to allow direct comparison among studies, we sought to standardize cover estimates to be consistent with a single method.

We performed simulations to quantify the expected bias associated with each visual estimation method relative to true cover. For a range of mean cover values (μ) from 1–60% in increments of 1%, we simulated estimating cover using the 3 visual estimation techniques described above as follows. First, we fit a linear model to estimate the relationship between reported sample means, \bar{x} , and sample standard deviations, $s(x)$, of grass cover from the reviewed studies (Fig. B1). A square-root transformation of \bar{x} produced the best linear fit. We used the coefficients from this fitted model to determine the appropriate standard deviation (σ) for each simulated value of μ .

For values of $\mu < 40\%$, we found a beta distribution was best able to reproduce a realistic distribution of cover, so we converted from percent to proportion and reparametrized μ and σ to the beta shape parameters a and b :

$$a = \left(\frac{1 - \mu}{\sigma^2} - \frac{1}{\mu} \right) \mu^2$$

$$b = a \left(\frac{1}{\mu} - 1 \right)$$

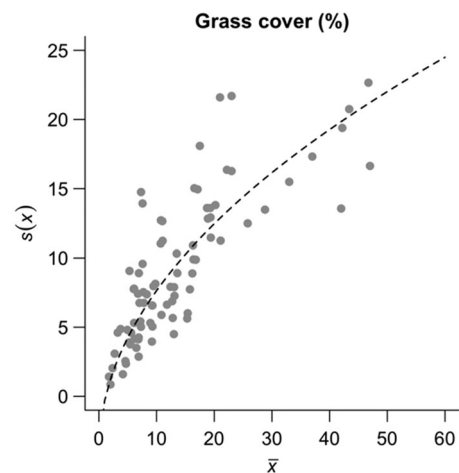


Figure B1. We fit a linear model relating the sample standard deviation $s(x)$ to the square root of the sample mean \bar{x} of percent cover of grasses among $n = 84$ study units reporting grass cover in available sage-grouse nesting habitat across the species' range in North America, 1991–2019. We then used this model to simulate replicate samples of herbaceous cover from populations with true means ranging from 1% to 60% to characterize bias associated with different visual estimation methods.

For values of $\mu \geq 40\%$ we drew values from a truncated normal distribution $N(\mu, \sigma) T(0, 100)$ and divided by 100.

We drew 600 samples from the resulting beta or truncated normal distributions to simulate a cover sample from a typical nesting study. We chose this sample size because the typical sample size of nests or available plots among reviewed studies was about 50 and a typical protocol involved sampling 12 quadrats at each plot ($50 \times 12 = 600$). We then converted these 600 known cover values into cover classes as if we were using 1) Daubenmire's method, or 2) the nearest 1% or 5% method. We converted simulated Daubenmire data to midpoints of the 6 proportional cover classes (i.e., 0.025, 0.15, 0.375, 0.625, 0.85, or 0.975) and rounded simulated nearest 5% data to the nearest 5% (e.g., 0, 0.05, 0.1, 0.15). Finally, we averaged the resulting data from each simulated dataset. We repeated this procedure 1,000 times to obtain the expected (mean) cover estimate associated with each method for each simulated known cover value.

Assuming observers accurately assign cover to the appropriate classes, Daubenmire's method was negligibly biased (expected cover—known cover) at the upper range of tested values (Fig. B2). Estimates of cover values below about 20%, however, were significantly positively biased using Daubenmire's method. In particular, cover values from 1–11% had expected bias in excess of 20% of the mean. The nearest 5% method, on the other hand, produced a negligible expectation of bias across the range of cover values commonly

reported for sage-grouse nesting habitat, though estimates of cover values $\leq 10\%$ were slightly negatively biased (Fig. B2). This did not pose a problem for our particular analyses because cover values reported in studies using the nearest 5% method were all $> 2.5\%$, where absolute bias was expected to be $< 0.5\%$.

Cover of grasses and forbs in sage-grouse nesting and brood-rearing habitat is typically $< 15\%$ (Hagen et al. 2007), a range where Daubenmire's method is particularly biased. However, Daubenmire's method has been established as the standard for monitoring sage-grouse habitat (Connelly et al. 2003), reflected in the fact that 85% of reviewed studies used it (Table S1). Therefore, we standardized all studies to be consistent with estimates using Daubenmire's method rather than attempt to correct the bias inherent in the majority of reported cover values.

We assumed studies using either the nearest 5% or nearest 1% visual estimation method were unbiased and we adjusted estimates to reflect the expected bias associated with Daubenmire's cover class method. For the study employing line-point intercept, we first adjusted estimates using percent differences reported in Symstad et al. (2008), then standardized as above. Specifically, Symstad et al. (2008:427) report that line-point intercept estimates were 36% higher for cover of grasses and 4% lower for cover of forbs than estimates from the nearest 1% visual estimation method.

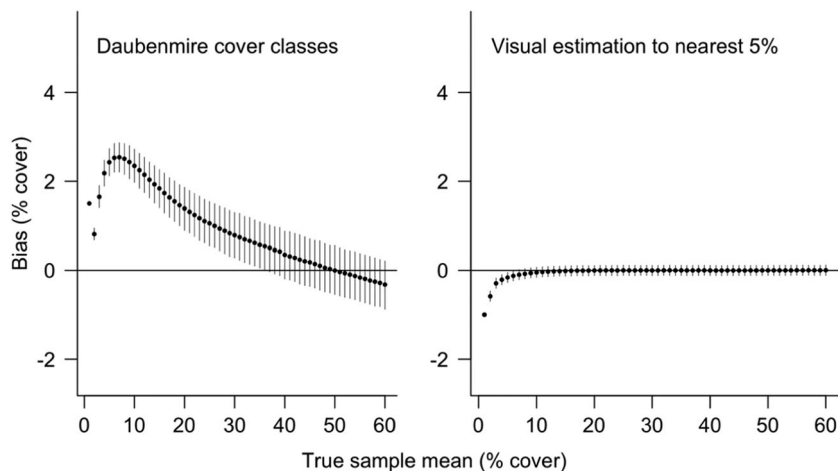


Figure B2. Using cover classes described by Daubenmire (1959), average cover among 600 simulated quadrats was biased up to $> 2.5\%$ at values typical of sage-grouse nesting habitat. Estimating cover to the nearest 5% was minimally biased over the range reported in most studies, though a slight negative bias was apparent at cover $\leq 10\%$.