

GREATER SAGE-GROUSE NESTING HABITAT SELECTION AND SUCCESS IN WYOMING

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Abstract: Nesting habitat degradation and its negative effect on nesting success might contribute to the recent population and distributional declines of greater sage-grouse (*Centrocercus urophasianus*) throughout North America. We used radiotelemetry to locate greater sage-grouse nests in 7 different areas of central and southwestern Wyoming between 1994 and 2002; we studied each area for 2 to 4 years. Using binary logistic regression, we compared microsite vegetal data collected at nests ($n = 457$) and random ($n = 563$) sites and successful ($n = 211$) and unsuccessful ($n = 238$) nests to test hypotheses concerning greater sage-grouse nesting habitat selection and vegetal conditions associated with nesting success. We used Akaike's Information Criterion (AIC_c) and model averaging to make inference about the weighted support for the importance of individual habitat variables through the comparison of sets of competing models. Selected nest sites were located in areas with increased total shrub canopy cover (relative importance [RI] = 1.00), residual grass cover (RI = 0.47), and residual grass height (RI = 0.77) compared to random sites. Successful nests had increased residual grass cover (RI = 0.43) and height (RI = 0.48) relative to unsuccessful nests. Additionally, annual nest success rates (i.e., above vs. below our study's average) were related to the preceding year's spring (Apr–May; RI = 0.44) and winter–early spring (Jan–Jun) precipitation (RI = 0.32). Correct classification rates for weighted average models that we derived through the 3 comparisons were between 60 and 70%, suggesting the variables adequately differentiated between plot types. However, high model selection uncertainty (i.e., the total number of models included in the sets of AIC_c -selected models) suggested that nest site selection and nesting success may be influenced by factors not considered in the modeling process. Management strategies that protect dense sagebrush stands and enhance residual grass cover and height within those stands should be used to maintain nesting habitat and increase nesting success of greater sage-grouse.

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Breeding populations of sage-grouse (*Centrocercus* spp.) throughout North America declined an average of 33% from 1985 to 1995 (Connelly and Braun 1997), and greater sage-grouse occupied 56% of the species' presettlement range in 2000 (Schroeder et al. 2004). In central and southwestern Wyoming, sagebrush (*Artemisia* spp.)-dominated landscapes and grouse populations remain relatively contiguous and intact, and current greater sage-grouse populations cumulatively represent 1 of the species' last strongholds (Braun 1998).

However, the number of male greater sage-grouse counted per lek in Wyoming decreased 17% between 1985 and 1995 (Connelly and Braun 1997), and regional lek count declines as high as 76% were recorded between 1991 and 2002 (S. L. Cain, National Park Service, unpublished data). No single causative factor explains population declines throughout Wyoming, but the quality of sagebrush habitats has deteriorated range-wide over the last 50 years (Connelly et al. 2000). Bergerud and Gratson (1988) maintain that a female's realized loss in fitness is greater from nest failure than from any other factor. Nesting cover is important for a successful hatch (Bergerud 1988), and unsuitable nesting habitat may contribute to lower nesting success (Connelly and Braun 1997) and declining greater sage-grouse populations.

Greater sage-grouse select nesting habitat with more sagebrush canopy cover and height relative

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to available habitats (Wallestad and Pyrah 1974, Wakkinen 1990, Fischer 1994, Sveum et al. 1998), and nesting success has been positively correlated with overall shrub cover (Wallestad and Pyrah 1974, Gregg et al. 1994). In addition to sagebrush overstory, cover of taller grasses within shrub stands is important during nest-site selection (Wakkinen 1990, Connelly et al. 1991) and is associated with increased nesting success (Gregg et al. 1994). Studies using artificial greater sage-grouse nests indicated that greater sagebrush canopy cover, grass height, and forb cover were associated with increased artificial nest success (DeLong et al. 1995, Watters et al. 2002). Nest-site selection and success are likely related to a combination of suitable amounts of shrub overstory and herbaceous understorey cover (Connelly et al. 1991).

Although some studies have identified relationships between herbaceous characteristics at nest sites and nest success, the correlation remains unclear. In comparing successful to unsuccessful nest sites in southeastern Idaho and southern Canada, Wakkinen (1990) and Aldridge and Brigham (2002), respectively, reported no significant differences in vegetation immediately surrounding nests. Ritchie et al. (1994) found that vegetative characteristics at artificial nest sites in northern Utah explained only 12% of the variation in nest depredation probabilities. Sveum et al. (1998) reported greater residual grass cover and height at successful vs. unsuccessful nests in south-central Washington during 1 year, but results were not consistent the following year. Failure to identify a consistent pattern may be related to short studies (1 or 2 nesting seasons) and small sample sizes (Wakkinen 1990, Sveum et al. 1998, Aldridge and Brigham 2002).

We examined vegetation at greater sage-grouse nest sites for 2 to 4 years in 7 different areas in central and southwestern Wyoming between 1994 and 2002 to test hypotheses concerning nest site selection and nest success. We hypothesized that (1) the location of a greater sage-grouse nesting site (compared to a randomly selected site) was positively correlated with sagebrush and residual grass cover and height since greater sage-grouse select nest sites prior to the start of the growing season of most grasses and forbs (i.e., herbaceous cover), and selection is likely based on habitat conditions available at the time of nest initiation (i.e., shrub and residual herbaceous vegetation); (2) nest success probabilities were positively correlated with herbaceous cover and grass height; (3) differences in herbaceous cover and height

vs. sagebrush cover or height distinguished successful from unsuccessful nests because greater sage-grouse nesting success varies annually (Connelly et al. 2000) while sagebrush overstory remains relatively unchanged annually; and (4) average annual nesting success years coincide with above average current and preceding year early spring moisture, since early spring precipitation (particularly during Apr and May) was the primary factor affecting annual herbaceous production (Kruse 2002).

STUDY AREAS

We studied greater sage-grouse during 1994–2002 at 7 areas in central and southwestern Wyoming, USA (Fig. 1, Table 1). Slope on the 7 areas ranged from zero to 25% with generally north or south aspects. Vegetation was dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*). Black sagebrush (*A. nova*) and low sagebrush (*A. arbuscula*) occurred on relatively flat terrain in shallow soils; basin big sagebrush (*A. t. tridentata*) and silver sagebrush (*A. cana*) occurred in deeper soils; and mountain big sagebrush (*A. t. vaseyana*) occurred in mixed stands with Wyoming big sagebrush at higher elevations. Rabbitbrush (*Chrysothamnus* spp.), black greasewood (*Sarcobatus vermiculatus*), antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos* spp.), and serviceberry (*Amelanchier alnifolia*) were interspersed throughout the study areas. Shrub height varied with topography, with taller growth occurring in deep, more mesic soils associated with the bottoms of draws. Dominant grasses included bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Agropyron smithii*), junegrass (*Koeleria pyramidata*), needlegrass (*Stipa* spp.), bluegrass (*Poa* spp.), Indian ricegrass (*Oryzopsis hymenoides*), Idaho fescue (*Festuca idahoensis*), and cheatgrass (*Bromus tectorum*). Common understorey forbs included lupine (*Lupinus* spp.), phlox (*Phlox* spp.), buckwheat (*Eriogonum* spp.), common dandelion (*Taraxacum officinale*), milkvetch (*Astragalus bisulcatus*), sandwort (*Arenaria capillaris*), and several species of Asteraceae.

METHODS

Field Methods

We captured female greater sage-grouse on and near leks from mid-March through April, 1994–2002 by spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We classified each captured female as a juvenile (first

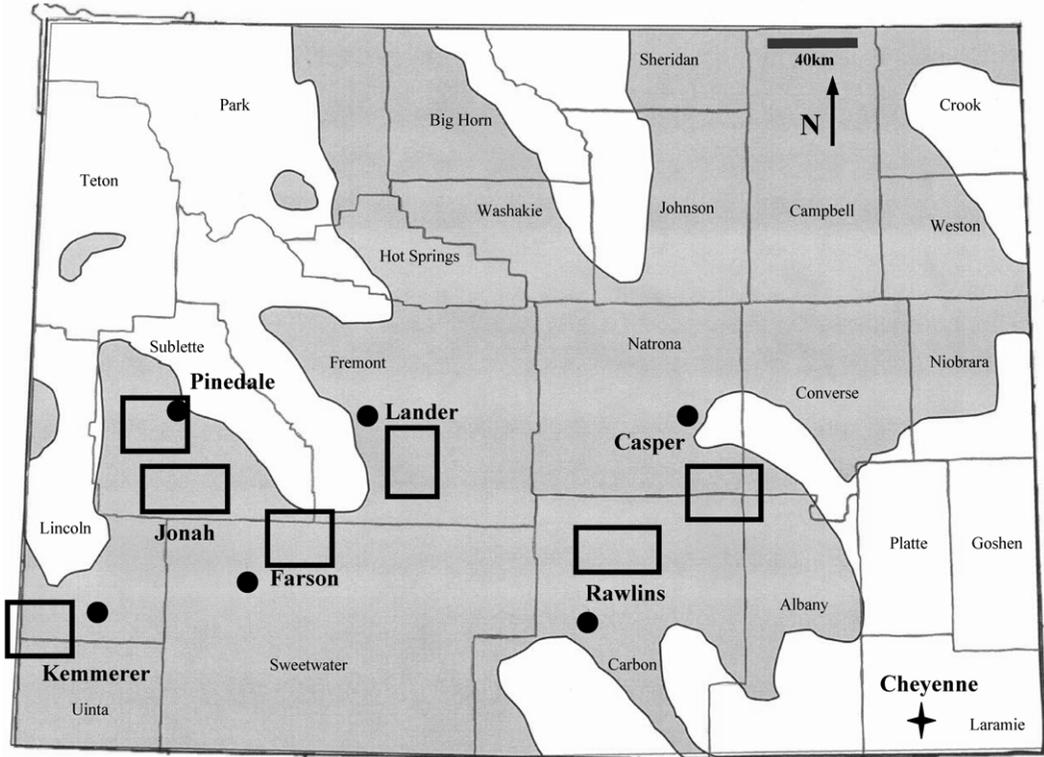


Fig. 1. Greater sage-grouse study locations and 1998 greater sage-grouse distribution (delineated by shading) in Wyoming, USA, 1994–2002. County names and boundaries and relevant city names are included for orientation (Farson 1994–1996; Rawlins 1996–1997; Casper 1997–1999; Pinedale 1998–1999 and 2001–2002; Jonah 2000–2002; Lander 2000–2002; and Kemmerer 2001–2002).

breeding season) or adult (\geq second breeding season) based on the shape of the outermost wing primaries (Eng 1955). We secured radio transmitters to females with a PVC-covered wire necklace (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA). The transmitters we used in Farson, Rawlins, and Casper weighed 12 g and

had a battery life expectancy of 305 days. In 1998, ATS developed transmitters weighing 25 g with a battery life expectancy of 610 days, and we used them in Pinedale, Jonah, Lander, and Kemmerer.

We used hand-held receivers and Yagi antennas to monitor radiomarked females at least twice weekly through pre-laying (Apr) and nesting

Table 1. Study areas, latitude and longitude, years studied, approximate study area size (ha), elevational range (m), average annual precipitation during years studied, and average annual precipitation for greater sage-grouse study sites in Wyoming, USA, 1994–2002.

Study area	Latitude, Longitude	Years	Size ^a	Elevation	Precipitation ^b			
					Study		Average	
					cm	SE	cm	SE
Farson	42°20'N, 109°08'W	1994–1996	54.0	2,050–2,440	32	2.8	27	0.4
Rawlins	44°07'N, 107°16'W	1996–1997	65.3	1,980–2,260	26	0.3	25	0.4
Casper	42°25'N, 106°10'W	1997–1999	31.0	2,170–2,350	35	3.6	28	0.7
Pinedale	42°45'N, 109°55'W	1998–1999						
		2001–2002	30.4	2,140–2,300	25	4.0	30	0.8
Jonah	42°33'N, 109°40'W	2000–2002	53.4	2,140–2,250	12	1.9	21	1.9
Lander	42°33'N, 108°29'W	2000–2002	45.9	1,950–2,520	23	2.9	34	0.4
Kemmerer	45°53'N, 110°54'W	2001–2002	55.0	1,900–2,510	13	0.9	27	0.6

^a Times 1,000.

^b Western Regional Climate Center, Reno, Nevada, USA.

(May–Jun). We located nests of radiomarked birds by circling the signal source until females could be directly observed. We wore rubber boots while confirming nest locations to reduce human scent, and we monitored incubating females after nest identification from a distance of ≥ 60 m to minimize chance of human-induced nest predation or nest abandonment.

We recorded nest fate (successful or unsuccessful) when radio monitoring indicated the female had left the area. We considered nests successful if ≥ 1 egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). We searched the area around destroyed nests for hair, scat, tracks, or other sign, and we sent hair and scat to the Wyoming Game and Fish Laboratory (Laramie, Wyoming, USA) for identification. We monitored unsuccessful females twice weekly to assess renesting attempts. Because we typically identified nest sites following clutch completion (i.e., following the initiation of incubation) and we might have missed nests destroyed during the egg-laying or early incubation stages (i.e., individuals classified as not initiating nest), observed nesting propensity was a minimum, and nest success could be over estimated. To further address this issue, we computed adjusted annual nest success (ANS) for each site and year following Johnson and Klett (1985):

$$ANS = [(N_s/N_t)^{1/(h-f)}]^h,$$

where N_s = number of successful nests, N_t = total number of confirmed nests, h = mean age of a clutch at hatch (34 days; estimated as 25 days for incubation and 9 days for laying; Patterson 1952:120), and f = mean age of a clutch when found (estimated as the annual average for successful nests by back-dating from hatch).

We evaluated vegetation between late May and early June at nest sites and independent random locations. We identified locations of independent random sites by randomly generated Universal Transverse Mercator (UTM) coordinates. To minimize differences resulting from herbaceous growth, we evaluated vegetation at successful nests, unsuccessful nests, and random plots concurrently beginning from the first successful hatch (mean first hatch date Jun 4 [± 12 days]). The duration of vegetation sampling averaged approximately 20 days annually, and we did not quantify vegetation at nests until females had vacated the area. To increase the likelihood that potential nesting habitat was measured, we cen-

tered random plots on the nearest (to the randomly generated point) sagebrush plant ≥ 35 cm tall (average nest bush height in Wyoming 35 cm; Patterson 1952).

We evaluated vegetation along 2 perpendicular 30-m transects that intersected the nest or random plot center. Orientation of the first transect was randomly assigned. We used the line-intercept method (Canfield 1941) to estimate percent live sagebrush, dead sagebrush (i.e., $< 15\%$ of the plant composed of living stems based on presence of leaves), and total shrub canopy cover. We expressed dead sagebrush canopy cover as a proportion of total shrub canopy cover to estimate sagebrush stand decadence. Live sagebrush height was the maximum height, excluding flowering stalks, of each intercepted sagebrush plant. We estimated sagebrush density (plants/m²) as the number of sagebrush plants in a 1-m wide belt along each transect; at least 50% of a plant had to be within the belt to be counted.

We measured herbaceous vegetation characteristics within a 20 × 50-cm quadrat using the Daubenmire (1959) canopy-cover method at 0.0 m (transect intersection), 1.0 m, and 2.5 m from the intersection along each 15-m portion of the 30-m transect radiating from the nest or random center (12 points measured). Herbaceous vegetation variables included total herbaceous cover, standing grass cover, and forb cover (including winterfat [*Eurotia lanata*] and fringed sagewort [*A. frigida*]). We also estimated litter and bare ground cover. We grouped and classified grass species as either new or residual (i.e., standing-dead). We estimated maximum droop height (i.e., the highest naturally growing portion of the plant excluding flowering stalks) of new and residual grasses by measuring the average tallest grasses (estimated visually) occurring within each quadrat. We converted categorical estimates of herbaceous cover to percentages (1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 85%, 6 = 97.5%; Daubenmire 1959) for each of 12 quadrates per plot, and we averaged height and converted cover estimates from the 12 points to derive a single estimate for each variable per plot.

We estimated precipitation by averaging monthly totals from weather stations within and near each study area (Western Regional Climate Center, Reno, Nevada, USA). To standardize precipitation levels across study sites and years, we calculated percent normal precipitation by dividing current levels by long-term averages (mean 32-year average; Western Regional Climate Cen-

ter, Reno, Nevada, USA). Because nesting success and precipitation differed between study sites annually, we used observed nesting success categorized as above or below our study's average for each site-year combination (e.g., Farson and Rawlins in 1996 included individually; 20 site-year combinations). We compared years of above- vs. below-average nesting success using annual (May–Apr), winter–early spring (Jan–Jun), spring (Apr–May), and summer (Jun–Aug) precipitation estimates.

Statistical Analysis

We used logistic regression to analyze vegetative differences between greater sage-grouse nests and random sites, successful and unsuccessful nests, and precipitation differences between years of above- and below-average nesting success (SAS Institute 1990). To avoid multicollinearity, we selected 1 of a pair of correlated independent variables ($r \geq 0.70$; Pearson correlation coefficient) based on variable importance established through previous research (Wallestad and Pyrah 1974, Wakkinen 1990, Connelly et al. 1991, Fischer 1994, Gregg et al. 1994, Sveum et al. 1998). We developed 38 models to predict nest sites, 31 models to predict successful nests, and 23 models to predict above average nest success years (precipitation candidate models). The candidate models predicting nest sites (vs. randomly selected sites) included the vegetative variables (total number of candidate models containing variable): sagebrush density (11), total shrub canopy cover (26), proportional dead sagebrush canopy cover (7), sagebrush height (21), and residual grass height (18) and cover (19). We included the following variables in the candidate models predicting successful nests (vs. unsuccessful nests): total shrub canopy cover (8), proportional dead sagebrush canopy cover (4), sagebrush height (6), new grass cover (2) and height (6), residual grass cover (9) and height (12), forb cover (4), and total herbaceous cover (10). Precipitation variables included: preceding year (5 candidate models contained this variable) annual (May–Apr), preceding (5) and current year (7) spring (Apr–May), preceding (6) and current year (6) winter–early spring (Jan–Jun), and preceding (6) and current year (6) summer (Jun–Aug) moisture.

To account for variability explained by study site and year, we included all site-year combinations (e.g., Farson 1994, 1995) as indicator variables in each vegetative candidate model (i.e., 19 total indicator variables included in each model; Manly et al. 2002:89). By including all site-year combina-

tions in each of the candidate models, the variability explained by site and year for each of the comparisons was essentially standardized across all models in the candidate sets. Thus, any differences between the models in the candidate sets were due to differences in the predictive ability of the vegetative variables. We did not include indicator variables in the tables for ease of interpretation. We only considered models with ≤ 3 main effect variables in the nest vs. random set, and models with ≤ 2 main effect variables in the successful vs. unsuccessful nest set because large numbers of predictor variables with respect to n response variables may result in data too thin to accurately estimate parameters (Hosmer and Lemeshow 1989). Sample size for the precipitation comparison was site-year combinations ($n = 20$); thus, the candidate set only considered models with ≤ 2 main effect variables.

We used multiplicative interactions to investigate the possibility that the ability of individual vegetative variables to distinguish between plot types could be related to the level of another vegetative variable (e.g., taller sagebrush might be important in areas with lower sagebrush canopy cover). We included models in the nest vs. random set that involved multiplicative interactions (total number of candidate models containing interaction) between: total shrub canopy cover and sagebrush height (5), total shrub canopy cover and residual grass cover (4) and height (3), sagebrush height and residual grass height (3), and residual grass cover and residual grass height (3). The successful vs. unsuccessful nest models included interactions between: total shrub canopy cover and residual grass cover and height and total herbaceous cover, sagebrush height and residual grass height, and total herbaceous cover and grass and residual grass height. Because the successful vs. unsuccessful candidate set of models included only 2 main effect variables, we included each interaction in only 1 model.

We examined the assumption of linearity in the logit for each independent variable following Hosmer and Lemeshow (1989:90). Each independent variable was grouped and treated categorically. Following the fit of a univariate logistic model, we plotted estimated coefficients vs. group mid-points and assessed plots visually (Hosmer and Lemeshow 1989). We transformed nonlinear variables based on the shape of the resulting plot.

We adjusted AIC for small sample size (AIC_c ; Burnham and Anderson 2002) to compare models within the candidate sets. We included 19 indicator variables in the calculation of AIC_c . We cal-

culated the difference between the AIC_c value for the best model (i.e., model with the lowest AIC_c) and every other model (ΔAIC_c), and we presented results from all models with $\Delta AIC_c \leq 2$ (considered the subset of best models; Burnham and Anderson 2002). When observations are independent, sample sizes are large, and models are nested, Burnham and Anderson (2002:170) suggest there is substantial empirical support that the Kullback-Leibler best model is in the subset of all models having $\Delta AIC_c \leq 2$. We calculated Akaike weights (w_i), that represent the relative likelihood of a model given the data (Burnham and Anderson 2002), and we used the Hosmer-Lemeshow (1989:141) goodness-of-fit test to assess model fit for each model within the subset of best models.

We used a model averaging procedure, based on the w_i -likelihood for each model in the subset of best models, to calculate mean coefficients for each variable present in at least 1 of the best models following Burnham and Anderson (2002:152). To assess averaged model fit, we used correct classification contingency tables (predicted probability = 0.5; Menard 1995) adjusted for chance agreement due to differences in sample sizes (Titus et al. 1984). We calculated odds ratios and 95% confidence intervals (CI) following Hosmer and Lemeshow (1989:43–44) to facilitate interpretation of the averaged model. If a variable was transformed, we examined odds ratios in terms of scale change (e.g., log transformed odds examined in terms of proportional vs. absolute change).

To establish evidence for the importance of each independent habitat variable, we calculated a relative importance estimate by adding w_i -values for all models containing the variable (Burnham and Anderson 2002). The relative importance of an individual variable provided a better weight of evidence for the importance of that variable in the context of the entire set of models considered (Burnham and Anderson 2002). As a further indication of individual variable importance, we considered the num-

ber of times a variable was included in the candidate set of models where $\Delta AIC_c \leq 4$, which was a conservative approximation of empirical support for the given group of models (Burnham and Anderson 2002:170). Variables whose odds ratios included 1 within the 95% CI were generally considered ineffective as predictors; however, a skewed interval suggested association between a variable and response (Hosmer and Lemeshow 1989:100). We therefore relied primarily on the relative importance analysis results, and we used odds ratios (95% confidence intervals) to assess direction, magnitude, and reliability of relationships. We used probability plots to assess the relationship between variables in important interactions.

RESULTS

Between 1994 and 2002, we radiomarked 543 female greater sage-grouse (95 Farson, 56 Rawlins, 95 Casper, 99 Pinedale, 70 Jonah, 61 Lander, 67 Kemmerer) and located 484 nests. Minimum estimates of annual nesting propensity averaged 81% (adult 86% [SE = 2.6], juvenile 72% [SE = 4.6]), and observed nest success averaged 49% (adult 49% [SE = 4.1], juvenile 47% [SE = 14.8]). Age-related nesting propensity ($\chi^2_1 = 2.09$; $p = 0.15$) and nest success ($\chi^2_1 = 0.14$; $p = 0.71$) were statistically similar. Adjusted nest success averaged 37% (Table 2). An average of 9% of females renested (range 0–31%). We did not consider renests (27) independent and removed them from nest

Table 2. Greater sage-grouse average annual nest propensity, observed nest success, and adjusted nest success by study area and overall in Wyoming, USA, 1994–2002.

Study area	Years	n^a	Nest propensity ^b		Observed success ^c		Adjusted success ^d	
			%	SE	%	SE	%	SE
Farson	1994–1996	90	86	1.9	38	7.9	30	7.3
Rawlins	1996–1997	53	76	6.3	72	6.9	62	7.7
Casper	1997–1999	120	93	3.9	66	10.0	56	10.8
Pinedale	1998–1999							
	2001–2002	120	74	3.3	41	4.1	30	3.4
Jonah	2000–2002	72	81	9.0	54	8.4	38	7.6
Lander	2000–2002	75	79	8.6	43	4.4	26	2.4
Kemmerer	2001–2002	67	76	8.6	33	2.2	22	0.4
Overall average	1994–2002	597	81	2.4	49	3.7	37	3.7

^a Number of potentially nesting radiomarked females; we omitted birds that died prior to nest initiation, and we included birds whose radio-transmitters were functioning for multiple nesting seasons ($n = 58$) multiple times.

^b Average annual number of radiomarked females documented incubating a nest relative to number of potentially nesting radiomarked females.

^c Average annual number of nests that hatched ≥ 1 egg(s) relative to the annual total number of nests. Observed nest success estimates include renests but do not include researcher induced abandoned nests.

^d Average annual adjusted nest success (Johnson and Klett 1985 [see text for equation used]). Adjusted nest success estimates include renests but do not include researcher-induced abandoned nests.

Table 3. Weighted means (SE) of vegetal variables measured at successful and unsuccessful greater sage-grouse nests and random plots in Wyoming, USA, 1994–2002.

Variable	Successful nest		Unsuccessful nest		Random	
	Mean	SE	Mean	SE	Mean	SE
Sagebrush density (plants/m ²)	2.29	0.15	2.40	0.14	2.30	0.18
Total shrub canopy cover (%)	30.43	1.36	30.31	1.23	26.06	1.82
Proportional dead sagebrush canopy cover (%)	10.74	1.80	9.59	1.88	9.31	1.48
Sagebrush height (cm)	32.17	1.72	31.60	2.98	28.27	1.08
Residual grass height (cm)	10.39	0.62	9.25	0.66	8.60	0.61
Residual grass cover (%)	2.51	0.27	2.23	0.24	2.07	0.31
Live grass height (cm)	16.56	0.98	15.60	1.08	15.00	0.82
Live grass cover (%)	6.01	0.58	5.97	0.99	5.73	0.54
Forb cover (%)	5.29	1.12	4.69	1.10	4.67	0.86
Total herbaceous cover (%)	23.12	3.65	20.41	3.04	21.16	3.86
Litter cover (%)	17.90	3.46	17.61	3.58	14.50	2.20
Bare ground (%)	18.68	4.16	22.29	3.93	25.06	4.70

selection and success analyses. Eight nest failures were caused by researcher-induced abandonment and excluded from nest success analysis; the remaining failed nests were most likely the result of predation. The most common nest predators we identified were badger (*Taxidea taxus*), common raven (*Corvus corax*), bobcat (*Lynx rufus*), and red fox (*Vulpes vulpes*). However, we were unable to accurately identify nest predators for approximately 40% of destroyed nests (see Major 1991 and Lariviere 1999 for discussions on predator identification from nest remains). We used 457 nests for nest selection comparisons, 449 nests for nest fate comparisons, and 563 random plots. We supplied weighted mean and standard error values for plots used in logistic regression analyses for reference (Table 3).

Table 4. Logistic regression models predicting greater sage-grouse nests ($n = 457$) versus random sites ($n = 563$) using vegetal data collected in Wyoming, USA, 1994–2002. Log likelihood ($-2 \ln [L]$), number of parameters including site-year indicator variables (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weights (w_i), Hosmer-Lemeshow goodness-of-fit statistic (p -value), and the model averaged coefficients ($\hat{g}(x)$) are provided. Only models with $\Delta AIC_c \leq 2$ are presented.

Model ^{ab}	$-2 \ln [L]$	K	AIC_c	ΔAIC_c	w_i	Hosmer-Lemeshow	
						\hat{C}	p -value
TSCC, Log(RGHT), RGRS	1354.704	23	1401.796	0	0.236	9.14	0.331
TSCC, SGHT, Log(RGHT), TSCC \times SGHT	1352.656	24	1401.844	0.048	0.230	9.58	0.296
TSCC, SGHT, Log(RGHT)	1355.091	23	1402.183	0.387	0.194	12.01	0.151

$$\hat{g}(x) = -2.835 + 0.027 (\text{TSCC}) + 1.515 [\text{Log}(\text{RGHT})] + 0.032 (\text{RGRS}) + 0.0005 (\text{SGHT}) + 0.0003 (\text{TSCC} \times \text{SGHT})$$

^a We included the following habitat variables in our models: sagebrush density (DEN), total shrub canopy cover (TSCC), proportional dead sagebrush canopy cover (DSC), sagebrush height (SGHT), residual grass height (RGHT), and residual grass cover (RGRS).

^b To facilitate interpretation, we excluded site-year indicator variables from model column.

Logit plots suggested that residual grass height be examined on the log scale for nest selection and fate analyses, which effectively changed measurements from absolute (cm) to relative (i.e., proportional; %). We examined residual grass height on the Log_{10} (i.e., 10%) scale. All other variables were linear with respect to the logit.

Nest Selection

The subset of best models ($\Delta AIC_c \leq 2$) predicting nesting habitat included 3 models (of 38 candidate models; Table 4). The Hosmer-Lemeshow (1989) tests indicated that all models statistically fit the data. The resulting averaged model correctly classified 60% of the plots (43% of nests, 74% of random), which was 42% ($K = 0.423$, $Z = 20.28$) better than chance. The relative importance estimates identified total shrub canopy cover (TSCC), sagebrush height (SGHT), residual grass cover (RGRS), and residual grass height (RGHT) as important determinants of nesting habitat (Table 5). The subset of models identified by $\Delta AIC_c \leq 4$ included 7 models, of which 7 contained TSCC, 5 SGHT, 4 RGRS, and 4 RGHT. Sagebrush density and proportional dead sagebrush canopy cover were not included in any of the 7 models. The odds ratios indicated increasing TSCC, RGRS, or RGHT by 10% or increasing SGHT by 10 cm increased the probability of a nest by 31.3, 38.1, 20.7, or 0.5%, respectively (Table 5). The 95% CI around the odds ratio for RGHT included 1 with relatively low precision (i.e., large interval), but the interval was noticeably skewed to the right. The 95% CI for SGHT was centered about 1. The interaction between TSCC and SGHT was the only interaction

included in the top models (Table 4). The probability plot suggested that increases in total shrub canopy cover vs. sagebrush height had a more substantially positive influence on the probability of a nest.

Nest Fate

The subset of best models predicting successful vs. unsuccessful nests included 9 models (of 31 candidate models; Table 6). The Hosmer-Lemeshow (1989) tests indicated that all models statistically fit the data. The resulting averaged model correctly classified 65% of the plots (54% of successful nests, 75% of unsuccessful nests), which was 48% ($K = 0.483$, $Z = 14.67$) better than chance. The relative importance estimates identified residual grass cover and height as important determinants of successful nests (Table 5). The subset of models identified by $\Delta AIC_c \leq 4$ included 22 models, of which 9 contained RGRS and 8 RGHT. Of the 22 models, total shrub canopy cover was included in 4, proportional dead sagebrush canopy cover in 3, sagebrush height in 4, live grass height in 5 and cover in 2, forb cover in 2, and total herbaceous cover in 5. The odds ratios indicated increasing RGRS or RGHT by 10% increased the probability of a successful nest by 57.0 or 11.1%, respectively (Table 5). The 95% CIs around the odds ratios for both variables included 1. The interval for RGRS was distinctly skewed to the right. However, although skewed to the right, the

Table 5. Relative importance and odds ratio (95% confidence interval) of habitat variables included in logistic regression models predicting greater sage-grouse nests ($n = 457$) versus random plots ($n = 563$) and successful ($n = 211$) vs. unsuccessful nests ($n = 238$) using vegetative data collected in Wyoming, USA, 1994–2002. Odds ratios were calculated for only those variables included in 1 of the models with $\Delta AIC_c \leq 2$.

Variable	Nest vs. random			Successful vs. unsuccessful nest		
	Relative importance ^a	Odds ratio ^b	Confidence interval	Relative importance ^a	Odds ratio ^b	Confidence interval
Sagebrush density	0.034					
Total shrub canopy cover	1.000	1.313	1.066–1.617	0.156	0.999	0.998–1.001
Dead sagebrush canopy cover	0.042			0.105	1.001	0.998–1.003
Sagebrush height	0.617	1.005	0.866–1.166	0.183	1.001	0.997–1.005
Log _{1,1} (residual grass height)	0.773	1.207	0.480–3.039	0.478	1.111	0.420–2.939
Residual grass cover	0.471	1.381	1.041–1.830	0.428	1.567	0.925–2.654
Live grass height				0.146	1.003	0.997–1.009
Live grass cover				0.064		
Forb cover				0.063		
Total herbaceous cover				0.189	1.001	0.999–1.002

^a We estimated relative importance by adding Akaike weights for all models in the candidate set in which variable was present; large values suggest high relative importance; blank values indicate variable was not considered in candidate models.

^b Odds ratios >1 indicate positive relationship; <1 indicate negative relationship.

relatively small odds ratio and large CI for RGHT suggested low precision.

The subset of best models predicting above vs. below average nesting success years included 2 models (of 22 candidate models; Table 7). The Hosmer-Lemeshow (1989) tests indicated that both models statistically fit the data. The result-

Table 6. Logistic regression models predicting successful ($n = 211$) versus unsuccessful greater sage-grouse nests ($n = 238$) using vegetative data collected in Wyoming, USA, 1994–2002. Log likelihood ($-2 \ln [L]$), number of parameters including site-year indicator variables (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weights (w_i), Hosmer-Lemeshow goodness-of-fit statistic (p -value), and the model averaged coefficients ($g(x)$) are provided. Only models with $\Delta AIC_c \leq 2$ are presented.

Model ^{ab}	$-2 \ln [L]$	K	AIC_c	ΔAIC_c	w_i	Hosmer-Lemeshow	
						\hat{C}	p -value
Log(RGHT)	583.708	21	627.837	0	0.101	5.28	0.727
RGRS	584.005	21	628.134	0.297	0.087	2.88	0.942
Log(RGHT), RGRS	581.980	22	628.317	0.480	0.079	6.50	0.592
SGHT, RGRS	582.390	22	628.727	0.890	0.065	3.27	0.916
SGHT, Log(RGHT)	582.630	22	628.967	1.130	0.057	7.72	0.462
TSCC, Log(RGHT)	582.896	22	629.233	1.396	0.050	5.93	0.655
GHT, RGRS	582.901	22	629.238	1.401	0.050	2.92	0.939
Log(RGHT), TOCO	582.939	22	629.276	1.439	0.049	5.88	0.660
DSC, Log(RGHT)	583.360	22	629.697	1.860	0.040	7.42	0.492

$$g(x) = -1.140 + 0.934 [\text{Log}(\text{RGHT})] + 0.045 (\text{RGRS}) + 0.0012 (\text{SGHT}) - 0.0008 (\text{TSCC}) + 0.0032 (\text{GHT}) + 0.0007 (\text{TOCO}) + 0.0007 (\text{DSC})$$

^a We included the following habitat variables in our models: total shrub canopy cover (TSCC), proportional dead sagebrush canopy cover (DSC), sagebrush height (SGHT), residual grass height (RGHT), residual grass cover (RGRS), live grass height (GHT), live grass cover (GRS), forb cover (FORB), and total herbaceous cover (TOCO).

^b To facilitate interpretation, we excluded site-year indicator variables from model column.

Table 7. Logistic regression models predicting above average ($n = 8$) versus below average greater sage-grouse nesting success years ($n = 12$) using percent normal precipitation data (Western Regional Climate Center, Reno, Nevada, USA) collected in Wyoming, USA, 1993–2002. Log likelihood ($-2 \ln [L]$), number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weights (w_i), Hosmer-Lemeshow goodness-of-fit statistic (p -value), and the model averaged coefficients ($g(x)$) are provided. Only models with $\Delta AIC_c \leq 2$ are presented.

Model ^a	$-2 \ln [L]$	K	AIC_c	ΔAIC_c	w_i	Hosmer-Lemeshow	
						\hat{C}	p -value
Spring previous	22.829	2	27.535	0	0.210	8.92	0.349
Winter previous	24.260	2	28.966	1.431	0.103	9.86	0.275

$$g(x) = -2.352 + 0.114 (\text{Spring previous}) + 0.066 (\text{Winter previous})$$

^a We included the following precipitation variables in our models: winter–early spring precipitation (Jan–Jun), winter–early spring precipitation the preceding year (Jan–Jun; Winter previous), summer precipitation (Jun–Aug), summer precipitation the preceding year (Jun–Aug), spring precipitation (Apr–May), spring precipitation the preceding year (Apr–May; Spring previous), and annual precipitation the preceding year (May–Apr).

ing averaged model correctly classified 70% of the plots (50% of above average years, 83% of below average years), which was 52% ($K = 0.516$, $Z = 2.95$) better than chance. The relative importance estimates identified spring (Apr–May) precipitation the preceding year ($RI = 0.444$) and winter–early spring (Jan–Jun) precipitation the preceding year ($RI = 0.323$) as important determinants of above average nesting success years. The relative importance estimates for the other variables considered were < 0.186 . The subset of models identified by $\Delta AIC_c \leq 4$ included 10 models, of which 5 contained spring and 4 contained winter–early spring precipitation the preceding year. The other precipitation variables considered were included in 1 to 2 of the 10 models. The odds ratios (95% CI) indicated increasing percent normal spring (1.121 [0.989–1.269]) or winter–early spring (1.068 [0.981–1.163]) precipitation the preceding year by 10% increased the probability of an above average nesting success year by 12.1 or 6.8%, respectively. The 95% CIs around the odds ratios for both variables included 1, but both were noticeably skewed to the right.

DISCUSSION

The statistical procedures we selected were used to allow several lines of quantitative evidence concerning the importance of vegetal characteristics to nesting greater sage-grouse in Wyoming. Relatively high correct classification rates of the averaged models for the 3 comparisons suggested the variables adequately differentiate between plot types. However, the subsets of

models identified by $\Delta AIC_c \leq 4$ included several models, suggesting model selection uncertainty (Burnham and Anderson 2002); this is especially true of the subset predicting successful nests that incorporated a majority of the original models considered (i.e., 22 of 31 models). Additionally, although the confidence interval around the odds ratio for residual grass height in the nest success analysis was positively skewed, the wide interval suggested low precision. In areas of relatively good, uniform habitat, the vegetal differences among nests appeared to be relatively minor, and success could be further influenced by other abiotic or biotic factors operating at spatial scales larger than those we examined. We theorize, however, that our analysis identified vegetal attributes that could be important for nesting greater sage-grouse at the microsite spatial scale.

Nest Selection

Greater sage-grouse in Wyoming selected nesting sites with more shrub and residual grass cover than was present at randomly selected sites, supporting our hypothesis that nest sites were characterized by appropriate sagebrush and herbaceous cover (Connelly et al. 1991). Several studies have established the importance of sagebrush canopy cover (Patterson 1952, Wallestad and Pyrah 1974, Wakkinen 1990, Fischer 1994, Sveum et al. 1998) and grass screening cover (Wakkinen 1990, Connelly et al. 1991, Sveum et al. 1998) to greater sage-grouse selecting nesting habitat. Our results support these findings, while establishing that the sagebrush overstory and herbaceous understory are cumulatively important.

The interaction between total shrub canopy cover and sagebrush height in the nest selection analysis suggested a relative relationship (i.e., the relative importance of total shrub canopy cover or height was related to the level of the other). However, the probability plot indicated increasing sagebrush height did not substantially influence the probability of a nest, suggesting that greater sage-

grouse selected for increased total shrub canopy cover given adequate sagebrush height. This contention was also supported by the relative variable importance analysis. Additionally, the confidence interval around the odds ratio for sagebrush height was centered about 1, suggesting that sagebrush height was not a good predictor of nesting habitat. Greater sage-grouse generally select sagebrush patches in mid-range canopy cover conditions (i.e., 15 to 25%; Connelly et al. 2000) for nesting, and avoid sparse and excessively dense patches. However, the relationship between shrub canopy cover and the probability of a nest was linear (not quadratic), and suggested that selection was for sagebrush patches with the highest canopy cover in the range of canopies measured (i.e., range 15–40% for grouped means).

Nest Fate

The relative importance analysis suggested that taller and thicker residual grass cover characterized successful greater sage-grouse nesting habitat. Studies reporting the importance of grass cover and height to nesting greater sage-grouse did not distinguish between height and cover attributes individually, but they indicated that cover of taller grasses was important for nest success (Gregg et al. 1994, Sveum et al. 1998). Our results support findings that cover of taller grasses was important to nesting grouse, while further suggesting both increased residual grass cover and height could be important individually. The relative importance analysis additionally indicated that herbaceous cover and height were more important than shrub cover or height in distinguishing successful from unsuccessful nests. However, the nest selection analysis established that nests were in areas with increased shrub canopy cover relative to available areas. Thus, taller, thicker residual grass cover in dense sagebrush stands appeared to increase the probability of a successful nest.

Our results suggest the timing and amount of moisture received were important to nest success. Cool season grasses, which, in Wyoming, are generally species capable of taller growth, grow primarily during the spring and early summer and rely on moisture stored in the soil profile during winter and early spring (Skinner et al. 2002). Therefore, cool season grass growth during the preceding year (i.e., available as residual grass to nesting females) appeared to be important for overall greater sage-grouse nesting success.

Residual grass cover was linearly related to the probability of a selected and a successful nest.

These relationships indicate that selection was for areas with the densest residual grass available and, within those selected areas, nests with the densest residual grass were most successful. The log relationship between selected and successful nesting habitat and residual grass height implied proportional correlations (i.e., when residual grass was short vs. tall, increased probability of a selected or successful nest required relatively small vs. large increases in height, respectively). This relationship suggested that increased residual grass height was important when grasses were short and that the data used for developing the models approached a threshold. Although we cannot conclusively pinpoint a threshold, weighted mean values (Table 3) indicated that residual grass heights should be a minimum of 10 cm within Wyoming big sagebrush dominated habitats. The sage-grouse habitat management guidelines (Connelly et al. 2000) recommend average perennial herbaceous cover ≥ 18 -cm tall within breeding habitats. However, the 18-cm level was established using primarily height measurements that included flowering portions of grasses, while our measurements did not include these portions and might not be directly comparable (i.e., shorter grass height estimates could result from our measurement technique). Additionally, the guidelines (Connelly et al. 2000) did not differentiate residual from live grasses, and average live grass heights ≥ 18 cm might be required to ensure that the highest naturally growing portion of residual grasses excluding flowering stalks average at least 10-cm tall the following spring.

The selected subsets of models identified by ΔAIC_c in our analyses included several models, indicating model selection uncertainty (Burnham and Anderson 2002) and suggesting that additional variables should be considered. The inclusion of 1 and the relatively wide confidence interval around the odds ratio further suggested low precision in the ability of residual grass heights to predict successful nests. Greater sage-grouse nesting success may be influenced by vegetal characteristics not measured, or other abiotic (e.g., habitat fragmentation [Braun 1998], single weather events [Wallestad 1975]) and biotic (e.g., nonnative predator density [Connelly et al. 2000], nest density [Niemuth and Boyce 1995]) factors not considered. Conclusions based on our results should be viewed from the standpoint of the spatial scale and variables considered. Additional research is needed to fully understand the importance of vegetal cover to

nesting grouse in the context of other potentially influential factors.

Our results suggest that sagebrush patches with a combination of dense shrub (overhead) and residual grass (lateral) cover are preferred greater sage-grouse nesting areas and that tall, dense residual grasses within these dense shrub stands may be important for nesting success. The results additionally suggest that factors other than the vegetative characteristics immediately surrounding the nest influence nesting success. However, because of the large spatial and temporal extent and location (greater sage-grouse population stronghold) of our study, we contend the results accurately reflect microsite scale vegetative parameters that are selected by nesting greater sage-grouse and those that may influence nesting success within Wyoming big sagebrush dominated habitats.

MANAGEMENT IMPLICATIONS

Dense sagebrush stands with adequate herbaceous vegetation represent desirable greater sage-grouse nesting habitat. To maintain greater sage-grouse populations, we recommend that managers limit strategies that negatively affect this type of habitat (i.e., prescribed fire and herbicide application) and protect adequate amounts of suitable nesting habitat during treatment. Our results further suggest that reducing the amount of residual grass in sagebrush habitats can negatively impact the quantity and quality of greater sage-grouse nesting habitat. Thus, we recommend management activities that allow for maintenance or restoration of dense, taller residual grass within suitable sagebrush stands to enhance greater sage-grouse populations. Although little direct evidence associating livestock grazing practices with greater sage-grouse population levels exists (Connelly et al. 2000), our results suggest annual grazing in nesting habitat, regardless of the timing, could negatively impact the following year's nesting success. Beck and Mitchell (2000) recommended removing livestock from greater sage-grouse nesting areas prior to peak standing-crop development (to maintain residual grasses) and delaying livestock use of the area until after nesting the following spring. Further research is needed regarding livestock management to identify appropriate levels, methods, and timing of use in greater sage-grouse nesting habitat. Additionally, research is needed that identifies live grass heights required in the fall that ensure adequate residual grass heights the following spring.

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