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5 Sage-grouse habitat and energy development. Doherty et al.

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8 **Greater sage-grouse winter habitat selection and energy development**

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18 **Abstract:** Recent energy development has resulted in rapid and large-scale changes to
19 western shrub-steppe ecosystems without a complete understanding of its potential
20 impacts on wildlife populations. We modeled winter habitat use by female greater sage-
21 grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and
22 Montana to: 1) identify landscape features that influenced sage-grouse habitat selection,
23 2) assess the scale at which selection occurred, 3) spatially depict winter habitat quality in
24 a geographic information system, and 4) assess the effect of coal-bed natural gas (CBNG)
25 development on winter habitat selection. We developed a model of winter habitat
26 selection based on 435 aerial relocations of 200 radio-marked female sage-grouse

27 obtained during the winters of 2005 and 2006. Percent sagebrush cover on the landscape
28 was an important predictor of use by sage-grouse in winter. The strength of habitat
29 selection between sage-grouse and sagebrush was strongest at a 4-km² scale. Sage-
30 grouse avoided coniferous habitats at a 0.65-km² scale and riparian areas at a 4-km² scale.
31 A roughness index showed that sage-grouse selected gentle topography in winter. After
32 controlling for vegetation and topography, the addition of a variable that quantified the
33 density of CBNG wells within 4-km² improved model fit by 6.66 AIC points ($w_i =$
34 0.965). The odds ratio for each additional well in a 4-km² area (0.877; 95% CI 0.834-
35 0.923) indicated that sage-grouse avoid CBNG development in otherwise suitable winter
36 habitat. At current CBNG well density (12.3 wells per 4-km²) sage-grouse are 1.3 times
37 more likely to occupy sagebrush habitats with no CBNG development. We validated the
38 model with 74 locations from 74 radio-marked individuals obtained during the winters of
39 2004 and 2007. This winter habitat model based on vegetation, topography, and CBNG
40 avoidance was highly predictive (validation $R^2 = 0.984$). Our spatially explicit model can
41 be used to identify areas that provide the best remaining habitat for wintering sage-grouse
42 in the PRB to mitigate impacts of energy development.

43 **Key words:** CENTROCERCUS UROPHASIANUS, COAL-BED NATURAL GAS,
44 ENERGY DEVELOPMENT, HABITAT, LAND USE CHANGE, RESOURCE
45 SELECTION FUNCTION, SAGEBRUSH, SCALE, GREATER SAGE-GROUSE,
46 WINTER

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48 Understanding landscape-scale habitat selection during critical life stages is
49 essential for developing conservation plans for sensitive species. Studies of habitat

50 selection at small scales further our ecological understanding of species-habitat
51 relationships, but do not convey spatially-explicit information about habitat quality at a
52 scale useful for prioritizing landscapes for conservation. Recent advances in modeling
53 habitat selection from high-resolution satellite imagery using resource selection functions
54 (RSF) offers the ability to rank specific areas by their relative probability of use (Manly
55 et al. 2002). Resulting probability layers can then be mapped in a geographic information
56 system (GIS) to identify regions where high quality habitat is available. Further, these
57 models allow cross-validation (Boyce et al. 2002, Johnson et al. 2006) and testing against
58 independent datasets to ensure that inferences regarding habitat selection are robust. The
59 relative influence of variables thought to be important in habitat selection can also be
60 assessed in a competing-model framework (Burnham and Andersen 2002).

61 Previously widespread, greater sage-grouse (*Centrocercus urophasianus*) have
62 been extirpated from ~50% of their original range in western North America (Schroeder
63 et al. 2004), with an estimated range-wide population decline of 45-80% and local
64 declines of 17-92% (Connelly and Braun 1997, Braun 1998, Connelly et al. 2000,
65 Aldridge and Brigham 2003). Despite increased concern for their populations, little
66 effort has gone into measuring landscape-scale winter habitat selection by greater sage-
67 grouse (hereafter sage-grouse). Previous winter habitat studies have focused on the
68 importance of micro-site vegetation features such as height, canopy cover, or crude
69 protein levels of sagebrush (e.g., Eng and Schladweiler 1972, Beck 1977, Connelly et al.
70 2000, Crawford et al. 2004, Sauls 2006). In winter, sage-grouse inhabit areas with
71 moderate to dense sagebrush (Eng and Schladweiler 1972, Homer et al. 1993, Connelly et
72 al. 2000) and typically prefer areas with gentle (<10%), south or west facing slopes (Beck

73 1977, Hupp and Braun 1989). Previous demographic studies have documented high rates
74 of winter survival (reviewed in Connelly et al. 2004). However, Moynahan et al. (2006)
75 demonstrated that severe winters can have substantial population-level impacts. Birds
76 also must often move long distances to find suitable winter habitat (Patterson 1952 *in*
77 Connelly et al. 2004, Connelly et al. 1988, Robertson 1991). Impacts to wintering habitat
78 may have disproportionate effects on regional population size and persistence. For
79 example, Beck (1977) found that 80% of use sites occurred in less than 7% of the total
80 area of sagebrush available in northern Colorado, suggesting that winter habitat may be
81 limited. The relationship between sagebrush and sage-grouse is arguably the closest
82 during winter when birds switch from a diet of insects, forbs and sagebrush to one
83 composed of >96% sagebrush (Remington and Braun 1985, Welch et al. 1991, Connelly
84 et al. 2000, Crawford et al. 2004). Heavy snowfall may even further reduce the amount
85 of suitable habitat by limiting the abundance of sagebrush above the snow (Hupp and
86 Braun 1989, Connelly et al. 2000, Connelly et al. 2004).

87 Coal bed natural gas (CBNG) development in the PRB has caused rapid, large-
88 scale changes to sagebrush habitats in Montana and Wyoming. The sage-grouse sub-
89 population in the Powder River Basin (PRB) is a critical component of the larger
90 Wyoming Basin population, which represents 25% of sage-grouse in the species' range
91 (Connelly et al. 2004). The population in the PRB has a high density of active leks and
92 serves as a link to populations in eastern Wyoming and western South Dakota, and
93 between the Wyoming Basin and central Montana (Connelly et al. 2004). The CBNG
94 field in the PRB is one of the largest developed energy fields in North America. In this
95 region, ~29,000 CBNG wells have been drilled on public and private lands, and another

96 ~37,000 are expected within a ~2.4 million ha area, roughly the size of the state of New
97 Hampshire (BLM 2003a, b). Drilling is typically authorized at a maximum density of 1
98 well/32ha on lands where federally owned gas reserves are extracted, however there is no
99 well density restrictions placed on private or state owned gas reserves. Wells, power
100 lines, roads, vehicle traffic, pipelines, compressor stations, and water storage ponds
101 within a gas field this size contribute to fragmentation of sagebrush habitats and may
102 impact sagebrush obligates (Knick et al. 2003).

103 We investigated sage-grouse winter habitat use in the PRB as part of a larger
104 study of the potential impacts of CBNG development on sage-grouse populations.
105 Objectives of our study were to: 1) create a robust habitat selection model for sage-grouse
106 in winter, 2) evaluate the appropriate scale at which females select winter habitat, 3)
107 spatially depict habitat suitability in a GIS to identify areas with a high probability of use,
108 and 4) assess the influence of CBNG development on winter habitat selection.

109 **Study area**

110 Our study area in the PRB covered portions of Johnson, Sheridan, and Campbell
111 counties in Wyoming, and Bighorn, Rosebud, and Powder River counties in Montana.
112 Shrub-steppe habitat in the PRB was dominated by Wyoming big sagebrush (*Artemisia*
113 *tridentata wyomingensis*) with an understory of native and non-native grasses such as
114 bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Agropyron*
115 *smithii*), prairie junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*),
116 Japanese brome (*Bromus japonicus*), cheatgrass (*Bromus tectorum*), and crested
117 wheatgrass (*Agropyron cristatum*). Plains silver sagebrush (*Artemisia cana cana*) was
118 also present in drainages but at much lower abundance. Rocky mountain juniper

119 (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) were located in wooded
120 draws and formed forests across the extreme northern extent of the study area. Conifers
121 were largely absent from the southern half of the study area. Land use was dominated by
122 cattle ranching; only 4% of the landscape consisted of dry land or irrigated agriculture.
123 The PRB typically is cold and dry in January with average temperatures of -6.0 °C and
124 16.3 cm of snowfall. Winter weather conditions were almost identical to historical
125 averages in the winters of 2004 and 2005. The winter of 2006 was mild; in January,
126 temperatures were 6.5 °C above normal and snowfall was 15 cm below average. The
127 January 2007 average temperature of -5.5 °C was near historical norms; however
128 snowfall was 60% above normal.

129 **Methods**

130 **Marking and monitoring protocols**

131 We captured sage-grouse by rocket-netting (Giesen et al. 1982) and spotlighting
132 (Wakkinen et al. 1992) on and around leks in 3 study areas: 1) Bighorn County, Montana,
133 2) Campbell County, Wyoming and 3) Johnson County, Wyoming during March-April
134 and August of 2003-2006. We aged and sexed grouse and fitted females with a 21.6 g
135 necklace style radio collar with a 4-hour mortality switch (model A4060 ATS, Isanti,
136 Minnesota). Sage-grouse in the Bighorn and Campbell county study areas were non-
137 migratory. In contrast, many birds in the Johnson Country study area were migratory,
138 with distinct breeding, summer, and winter ranges. In all study sites, we obtained winter
139 locations after birds in our migratory population had moved to wintering areas but before
140 they had moved back to the breeding grounds. We monitored sage-grouse via aerial
141 radiotracking during the winters of 2005-2007. We used a fixed-wing Cessna with aerial

142 telemetry antennas mounted on both wings struts and connected to a switch box. We
143 used a Global Positioning System (GPS) receiver to record locations of used sites as we
144 circled sage-grouse at approximately 100-200m elevation above the ground. Sage-grouse
145 were radio-tracked on foot during the winter of 2004 and their positions were recorded
146 with a GPS receiver when we obtained visual sightings of radiomarked birds. We
147 estimated the 95% error ellipse of aerial locations by relocating a transmitter placed in
148 rolling sagebrush cover 40 times from the air in a blind trial. We then calculated a
149 bivariate normal home range estimator (Jennrich and Turner 1969) using these
150 relocations to quantify our maximum resolution to estimate the location of an unknown
151 collar (78.2 m radius). The ability of our plane to tightly circle sage-grouse was not
152 constrained by rugged areas nor conifer dominated landscapes in the PRB because birds
153 were not located in these habitat features, thus our test was representative of the
154 maximum precision of our aerial telemetry locations in rolling sagebrush habitats. We
155 did not quantify error for ground based locations, but assumed error estimates were
156 smaller than aerial based methods. Since we treated our aerial telemetry error test as a
157 maximum precision estimate, we conducted all analyses at scales ≥ 100 -m to ensure that
158 our inference was not confounded by location error.

159 **Designation of used and available sites**

160 We employed a used/available design to evaluate sage-grouse habitat
161 relationships in winter (Manly 2002, Boyce 2002, Johnson et al. 2006). We defined used
162 points as the sites where radio-marked sage-grouse were located during radiotracking.
163 Sage-grouse used locations were split into those used to build a statistical model to
164 quantify large scale habitat relationships and those used to test the predictive ability of

165 our spatially explicit winter habitat model. Birds used to build the model were located
166 during 3 flights from 2-25 January 2005 ($n = 292$ locations on 106 individuals) and on 3
167 flights from 24 December 2005 - 1 February 2006 ($n = 241$ locations on 94 individuals).

To test the model, we used 87 locations

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188 panchromatic and multi-spectral images were combined into a single panchromatic,
189 multi-spectral file. We then used the panchromatic 25-m² pixel image to perform pan-
190 sharpening to reduce the multi-spectral image pixel size from 100-m² to 25-m², greatly
191 increasing the resolution of our analysis. eCognition™ 4.0 software was used to cluster
192 the pixels into regions representing spectrally similar ground features. Clusters were
193 exported into ArcInfo 9.2 software to create a polygon database. We collected field
194 training points ($n = 7,092$) that were stratified by space and landowner access to classify
195 5 habitat cover classes as sagebrush, conifer, grassland, riparian and barren.
196 Classification accuracy assessed by withholding subsamples of data (i.e., k-fold cross
197 validation with 10 folds; Boyce et al. 2002) was 83% for sagebrush, 77% for conifer,
198 76% for grassland, 70% riparian, and 80% for barren with an overall accuracy of 78%.
199 Urban areas and strip mines were removed from analyses.

200 **Vegetation, topography, and energy development variables**

201 To evaluate landscape predictors of sage-grouse winter habitat selection, we
202 quantified characteristics of vegetation, topography (e.g., Beck 1977, Remington and
203 Braun 1985, Hupp and Braun 1989, Sauls 2006) and energy development around used
204 and available points using a GIS. Used and available points were used to select
205 individual 5 x 5-m raster pixels which were then buffered by 100-m, 400-m, and 1,000-m
206 respectively. Variables were quantified within a square centered on each used and
207 available pixel at 3 spatial scales: 205 x 205-m or (0.04-km²), 805 x 805-m (0.65-km²),
208 and 2005 x 2005-m (4-km²). We calculated the percent of total area covered by each of
209 the 5 vegetation cover classes to quantify vegetation. To quantify topography, we
210 processed a 900-m² resolution digital elevation model (DEM) using Spatial Analyst from

211 Environmental Systems Research Institute and used it to estimate slope and solar
212 radiation for each pixel in the landscape. Solar radiation calculates how much sun a
213 particular pixel receives dependent on slope and aspect. This was estimated using the
214 hillshade command in Spatial Analyst and was parameterized using the angle and aspect
215 of the sun during 15 January 2007 at 1:00pm (U.S. Navy 2007). We used the standard
216 deviation of the DEM elevations within each buffer size to calculate an index to describe
217 the roughness of the landscape. Elevation was not included as a predictor variable for
218 GIS habitat modeling because elevational migration of sage-grouse does not occur in the
219 PRB, and minor differences in elevation at used and available locations were biologically
220 irrelevant. In the northern PRB, mean elevation was 1210 m (3.8 SE) for available
221 locations and 1248 m (3.9 SE) for used locations. In the southern PRB, mean elevation
222 was 1363 m (4.1 SE) for available locations and 1378 m (3.4 SE) for used locations. We
223 used the density of CBNG wells as a measure of the extent of energy development.
224 Wells are the only segment of the energy footprint accurately mapped and publicly
225 available for the entire PRB from the Wyoming Oil and Gas Conservation Commission
226 and Montana Board of Oil and Gas Conservation, and well density within a buffer is
227 strongly correlated with other features of CBNG development such as roads, ponds, and
228 power lines (D. E. Naugle, University of Montana, unpublished data).

229 **Statistical analyses**

230 We employed logistic regression with used and available points for model
231 selection and RSF model parameter estimates (Manly 2002, Boyce 2002, Johnson et al.
232 2006). Used locations of individual animals were pooled and inferences were made at
233 the population level (Design I; Erickson et al. 2001, Manly et al. 2002).

234 We first assigned variables into one of 3 model categories: vegetation,
235 topography, or energy development. Because no published landscape scale studies
236 existed upon which to base *a priori* models (Burnham and Anderson 2002), we tested all
237 variables individually and removed variables with odds ratios overlapping 1. We tested
238 all buffer distances for each variable and identified the scale that best represented sage-
239 grouse habitat selection for each variable using log-likelihood values. The best scale for
240 each variable was then allowed to compete with all possible combinations of other
241 variables within the same category to identify the most parsimonious model. We used
242 information-theoretic methods (Burnham and Andersen 2002) to choose between
243 competing models by converting log-likelihood values computed in logistic regression to
244 Akaike's Information Criterion (AIC) values. We brought models within 2 AIC points to
245 the next hierarchy of model selection. After identifying the top model(s) within
246 vegetation, topography, and energy development, we allowed models to compete across
247 categories to see if the additional information increased model fit.

248 Correlated predictors ($r \geq |0.7|$) were not allowed in the same model at any level
249 of model selection. If variables were correlated ($r \geq |0.7|$), we chose the variable we felt
250 had the greatest biological meaning according to known characteristics of winter sage-
251 grouse habitat from published studies. When variables were moderately correlated (i.e.,
252 $|0.3| \leq r < |0.7|$), we checked for stability and consistency of regression coefficient
253 estimates as predictor variables were added to models. If a regression coefficient
254 switched signs or standard errors increased substantially when correlated variables were
255 in the same model, one variable was removed from analysis if the other was an important
256 predictor.

257 We evaluated whether sage-grouse avoided energy development in winter by
258 using AIC values to determine if the addition of CBNG wells/km² to the top habitat
259 model explained more information than habitat alone. We then examined the resulting
260 corresponding model coefficient for CBNG wells to determine if sage-grouse avoided or
261 were attracted to energy development and to what degree. We performed a bootstrap
262 analysis to quantify the change in odds of use with the introduction of CBNG wells in the
263 form of 95% CI's around the odds ratios for differences in the number of wells. Because
264 the best approximating model had a high AIC weight ($w_i = 0.965$), we used beta
265 coefficients from the best approximating model for all computations (see Results)
266 (Burnham and Anderson 2002). For each bootstrap data set ($n = 5,000$) we calculated
267 and stored model coefficients and the mean value for all used locations for each variable.
268 We then repeated this bootstrap analysis, varying the number of CBNG wells in a 4-km²
269 area from 0-22 wells, the full range of well density observed in our original data set. For
270 each of the 5,000 simulations we computed the odds of use with the logistic equation.
271 We then ordered these ratios and used a rankit adjustment (Chambers et al. 1983) to
272 compute 2.5% and 97.5% percentiles for the upper and lower 95% CI bounds.

273 We then used the same bootstrap technique to quantify how the amount of
274 sagebrush within a 4-km² area affected the odds of use in winter with and without CBNG
275 development (12.3 wells/4-km² and 0.0 wells/4-km² respectively). We used the logistic
276 equation to generate odds of use for each bootstrap dataset ($n = 5,000$) by applying stored
277 model coefficients to mean values of parameters at used locations while systematically
278 varying percent sagebrush within 4-km² from 0-100% at both 0.0 and 12.3 wells/4-km².
279 To test if the odds of use were significantly different with the addition of CBNG we

280 computed the difference in odds generated from each bootstrap data set with and without
281 CBNG. Again, we ordered odds ratios with and without CBNG and their differences and
282 used a rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles
283 for the upper and lower 95% CI bounds.

284 To turn our statistical model into a spatially explicit GIS habitat model, we
285 employed a RSF model that had the form:

$$286 \quad w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k), \quad 1$$

287 where $w(x)$ is the raw RSF value for each pixel in the landscape, and x_1, x_2, \dots, x_k
288 represent values for vegetation, topography and energy development generated from a
289 moving-window analysis for each pixel, and β_1, \dots, β_k are the model parameters estimated
290 with logistic regression (Manly 2002, Boyce 2002, Johnson et al. 2006). We applied β -
291 coefficients from (Equation 1) to GIS layers in ArcView Spatial Analyst. The output was
292 a new GIS layer that represents the RSF values generated from (Equation 1) for each
293 individual 25-m² pixel for the entire landscape. Each component GIS layer was created
294 by moving-window analyses for key vegetation, topographic, and energy development
295 variables identified in model selection. These analyses result in summary statistics for
296 each pixel in the GIS layer at the desired scale. We re-sampled sagebrush to a 900-m²
297 pixel size because the time required to process a 4-km² buffer area for 625 million pixels
298 exceeded our computational capacity. Sagebrush resampled well and little information
299 was lost when evaluating the 900-m² resampled sagebrush layer versus the original 25-m²
300 resolution sagebrush layer ($r = 0.934$). Conifer resampled poorly ($r = 0.793$) so this
301 variable was kept at the original pixel size.

302 We categorized RSF values into 5 ordinal 20% quantile bins representing
303 progressively selected habitats. We validated our spatial model with the test data set of
304 sage-grouse locations collected during the winters of 2004 and 2007. We regressed the
305 observed proportion of the test data set in each RSF bin against the expected proportion
306 of use from the original RSF model to evaluate model fit (Johnson et al. 2006). A good
307 model fit should have a high validation R^2 value, a slope not different from 1.0, and an
308 intercept not different from 0 (Johnson et al. 2006).

309 Results

310 Vegetation, topographic, and energy variables were each important to winter
311 habitat selection in univariate space (Table 1). The scale at which variables were
312 measured strongly influenced log-likelihood values and odds of use (Table 1). Sagebrush
313 at the 4-km² scale was the dominant variable in univariate space. Sagebrush and
314 grassland accounted for >95% of the total vegetation cover at used locations which
315 explains their strong negative correlation ($r = -0.78$). Within a 4-km² area, used sites
316 contained >75% sagebrush cover intermixed with grassland. There was 14.5% more
317 sagebrush at used (76.0%, SE 0.55) than at available sites (61.5%, SE 0.61). Sage-grouse
318 used sites that averaged 19.1% (SE 0.53) grassland cover within a 4-km² area.

319 The best model for sage-grouse vegetation use consisted of sagebrush and riparian
320 (4-km² scale), as well as conifer and barren (0.65-km² scale) (Table 2). The second best
321 vegetation model was the same as above with the exception that barren was removed
322 (Table 2). The roughness index at a 0.65-km² scale and slope were both important
323 topographic predictors of sage-grouse use (Table 2). The number of CBNG wells within
324 a 4-km² area was the best model to represent energy development (Table 1).

325 Model fit increased when the best approximating models from vegetation,
326 topography, and energy development combined (Table 3). We removed barren ground
327 from the final vegetation model because it lacked stability and consistency due to its
328 correlation with roughness ($r = 0.32$). When roughness and barren ground were in the
329 same model, the coefficient for barren ground switched from a negative to a positive
330 effect and its SE increased causing the odds ratio interval to overlap one (odds 0.96-
331 1.06). Roughness was a more stable predictor and was unaffected by the inclusion of
332 barren ground. The final combined model was 1.96 AIC points better when barren
333 ground was removed.

334 Sage-grouse selected large expanses of sagebrush with gentle topography and
335 avoided conifer, riparian, and energy development (Table 4). The addition of the average
336 number of wells per 4-km² improved model fit by 6.66 AIC points (Table 3). An Akaike
337 weight ($w_i = 0.965$) indicated that the model with both habitat and energy variables had
338 overwhelming support (Table 3). The resulting model coefficients from the habitat and
339 energy model indicate that after adjusting for sage-grouse habitat preference, birds avoid
340 CBNG development in otherwise suitable habitat (Table 4).

341 Our bootstrap analysis demonstrated that current legal maximum well density on
342 federal lands (~12.3 wells/4-km², or 32 ha spacing) decreased the odds of sage-grouse
343 use by 0.30 compared to the average landscape selected by our radio-marked sage-grouse
344 (odds 0.57 vs. 0.87) (Figure 1). Sage-grouse were 1.3 times more likely to use winter
345 habitat if CBNG development was not present. The odds of sage-grouse winter habitat
346 use increased with greater percentage sagebrush cover within 4-km² (Figure 2a). The
347 difference in odds of use with and without CBNG development was statistically

348 significant at all levels of sagebrush ($P < 0.05$); however these differences were more
349 pronounced in high quality winter habitats dominated by sagebrush cover (Figure 2b).
350 Avoidance of CBNG was not relevant to winter habitat selection at low levels of
351 sagebrush cover because sage-grouse showed strong avoidance of those areas prior to
352 development (Figure 2a).

353 The best approximating model including vegetation, topography, and energy
354 variables accurately predicted an independent data set of 74 winter locations (validation
355 $R^2 = 0.98$, Figure 3). Using 6, 7, or 8 bin ordinal RSF models with quantile breaks did
356 not change the strength or pattern of model validation. The slope of observed versus
357 expected values did not differ from 1.0 (slope = 1.14, 95% CI 0.87 - 1.41) and the
358 intercept did not differ from zero (-2.85, 95% CI = -1.06 - 4.9). The top 2 RSF classes
359 accounted for 86.6% of the 435 locations used to build the RSF model and 90.5% of the
360 74 locations used to test the winter habitat model (Figure 3).

361 **Discussion**

362 This study is the first to show that abundance of sagebrush at a landscape scale
363 influences sage-grouse habitat selection in winter. Recent advances in RSF modeling and
364 habitat mapping using satellite imagery enabled us to document what all major reviews
365 on sage-grouse habitat requirements have suggested (Schroeder et al. 1999, Connelly et
366 al. 2000, Connelly et al. 2004, Crawford et al. 2004). At the largest scale evaluated (4-
367 km^2), sage-grouse selected for sagebrush and grassland landscapes (>95% area) that were
368 dominated by sagebrush (>75%) with little tolerance for other cover types. Conversion
369 of sagebrush negatively influences sage-grouse populations (Leonard et al. 2000, Smith
370 et al. 2005). Sage-grouse avoided riparian areas at the 4- km^2 scale, and conifer habitats

371 and rugged landscapes at a 0.65- km² scale, relationships that would have been less
372 discernible at broader spatial scales. Our roughness index was a much stronger predictor
373 than the rest of our suite of topographic variables, but slope further increased model fit.
374 Roughness is readily calculated from available DEMs and may be applicable to other life
375 stages for sage-grouse. In the only other sage-grouse landscape study that has evaluated
376 habitat selection at multiple scales, birds selected large expanses (>1 km²) of sagebrush
377 and avoided anthropogenic edge during the breeding season (Aldridge and Boyce 2007).
378 Our findings from winter in conjunction with those of Aldridge and Boyce (2007)
379 highlight the need for landscape scale research to gain further insight into sage-grouse
380 ecology.

381 Our habitat model was highly predictive. We built our model using sage-grouse
382 locations collected during mild to average winter conditions and validated it in years with
383 average temperatures and/or above-average snowfall. We do not know whether we
384 defined winter habitat broadly enough to include refugia necessary for birds to survive a
385 50- or 100-year winter storm event (Moynahan et al. 2006), but believe the model is
386 useful to identify habitat available in most winters. Extreme events may move birds into
387 rugged landscapes as they search for exposed sagebrush, thermal cover, and protection
388 from high winds (Beck 1977, Hupp and Braun 1989, Robertson 1991, Connelly et al.
389 2004).

390 A multi-scale approach is needed to understand the relative importance of local
391 and landscape factors influencing sage-grouse habitat selection. Local vegetation
392 measures have been the primary focus of sage-grouse habitat research to date (Eng and
393 Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006).

394 Ideally, local variables should compete against landscape factors in an AIC framework to
395 predict sage-grouse habitat use. Examination of ecological processes at the landscape
396 scale does not eliminate the need to understand habitat relationships at local scales;
397 rather, it will likely require a combination of scales to completely understand how sage-
398 grouse respond to their environment.

399 Our spatially explicit habitat model provides resource managers with a practical
400 tool to guide conservation planning. Effective planning requires that we know what
401 habitats are selected at landscape scales, where those habitats are located, and how
402 species respond to disturbances. Recent advances in wildlife ecology enable biologists to
403 develop RSF models that link resource use with changes in habitat quality and potential
404 stressors (Boyce and McDonald 1999, Manly et al. 2002, Johnson et al. 2004).
405 Moreover, RSFs estimate the strength of selection and enable predictive equations to be
406 linked in a GIS to depict spatial relationships across a planning region (Manly et al. 2002,
407 Johnson et al. 2004). Spatially-explicit planning tools should be used to prioritize
408 landscapes with the highest probability of supporting populations. Once identified, local
409 biologists provide on-site recommendations for how to best deliver on-the-ground
410 conservation.

411 After adjusting for sage-grouse habitat preference, we show that sage-grouse
412 avoid energy development in otherwise suitable habitats in winter. Previous research
413 shows that breeding sage-grouse in oil and gas fields avoid development, experience
414 higher rates of mortality, or both (Aldridge and Boyce 2007, Holloran 2005, Kaiser
415 2006). Accumulating evidence of the impacts of energy development in sagebrush-
416 steppe ecosystems extends beyond that of sage-grouse. Mule deer (*Odocoileus*

417 *hemionus*) avoided otherwise suitable habitats within 2.7-3.7 km of gas wells (Sawyer et
418 al. 2005) and densities of Brewer's sparrow (*Spizella breweri*) and sage sparrow
419 (*Amphispiza belli*) declined 36-57% within 100-m of dirt roads in gas fields (Ingelfinger
420 and Anderson 2004). Some suitable winter habitat remains undeveloped for sage-grouse
421 in the PRB (RSF bins 4 and 5; Figure 3). But the anticipated addition of another 37,000
422 CBNG wells at 32-ha spacing has the potential to affect >1.18 million ha of land. As
423 remaining winter habitats are developed, and sage-grouse can no longer avoid CBNG, it
424 is unclear whether birds will be able to adapt to a disturbance of this magnitude.

425 **Management Implications**

426 Sage-grouse avoidance of energy development in winter shows that a
427 comprehensive strategy is needed to maintain suitable habitats in all seasons. Identifying
428 and setting aside areas of undeveloped, high-quality habitat within the project area should
429 be top priority. Currently, only 0.5-km² of land surrounding a lek (1/4 mile buffer) is
430 excluded from development, an area that is 8 times smaller than the scale at which
431 individual sage-grouse selected winter habitats (i.e., 4-km²). Timing stipulations that
432 restrict CBNG development within 3.2 km of a lek during the breeding season (15 March
433 – 15 June) are insufficient because they do not prevent infrastructure from displacing
434 sage-grouse in winter. An additional stipulation in Montana that restricts new drilling
435 activities within "crucial winter range" (1 December - 31 March) only protects sage-
436 grouse habitat during the winter in which the drilling is scheduled. Current stipulations
437 leave only a small fraction of the land undeveloped, place no restrictions on the location
438 of wells in winter habitat, and allow human access to all areas throughout the life of the

439 producing gas field. Our spatially explicit winter habitat model can be used to identify
440 areas that provide the best remaining habitat for sage-grouse in winter.

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568 Figure Legends:

569 Figure 1. Reduction in the odds (solid line) and 95% CIs (dashed line) of sage-grouse
570 winter habitat use versus available habitat with increasing CBNG well density, Powder
571 River Basin, Montana and Wyoming, 2005-2006. Odds and 95% CIs are based on 5,000
572 bootstrap samples with well densities varying between 0-22, the range of CBNG
573 development observed in our sample of used and available points.

574
575 Figure 2. Odds of sage-grouse winter habitat use in relation to percent sagebrush
576 cover/4-km², Powder River Basin, Montana and Wyoming, 2005-2006. Odds and 95%
577 CIs are based on 5,000 bootstrap samples with sagebrush varying from 0-100%, with and
578 without CBNG development. In (a) grey line represents CBNG development (12.3
579 wells/4-km², 95% CI small dashed line) and the black line represents no CBNG
580 development (0.0 wells/4-km², 95% CI large dashed line). In (b) the difference of means
581 for odds of use with and without CBNG (black line minus grey line from part [a] above)
582 is plotted against varying amounts of sagebrush cover/4-km² (95% CI dashed line).

583
584 Figure 3. Percent of sage-grouse use locations in each of 5 ordinal resource selection
585 function bins (RSF category) used to build (black bars $n = 436$) and test (grey bars $n =$
586 74) the winter habitat model.

587 Table 1. Vegetation, topographic, and energy development variables that were evaluated as potential landscape predictors of sage-
 588 grouse winter habitat selection, Powder River basin, Montana and Wyoming, 2005 and 2006. Log-likelihoods were used to identify
 589 best scale at which selection occurred for individual variables and to select variables (in bold) that competed in model selection.

Model Category	Variable	Buffer area	Log Likelihood	Odds ratio	95% upper	95% lower
Vegetation ^a	Sagebrush	4-km²	-799.550	1.052	1.060	1.044
	Sagebrush	0.65-km ²	-814.010	1.048	1.043	1.034
	Sagebrush	0.04-km ²	-825.694	1.030	1.035	1.024
	Grass	4-km²	-877.583	0.972	0.980	0.964
	Grass	0.04-km ²	-878.044	0.982	0.987	0.976
	Grass	0.65-km ²	-884.551	0.980	0.987	0.973
	Conifer	0.65-km²	-813.051	0.765	0.822	0.712
	Conifer	0.04-km ²	-833.587	0.793	0.859	0.732
	Conifer	4-km ²	-818.951	0.810	0.850	0.772
	Riparian	4-km²	-851.246	0.843	0.882	0.805

	Riparian	0.65-km ²	-860.729	0.870	0.909	0.833
	Riparian	0.04-km ²	-889.368	0.958	0.979	0.938
	Barren	0.65-km²	-890.643	0.897	0.940	0.856
	Barren	4-km ²	-890.197	0.866	0.919	0.816
	Barren	0.04-km ²	-898.349	0.960	0.987	0.934
Topography	Roughness	0.65-km^{2b}	-838.257	0.888	0.909	0.868
	Roughness	0.04-km ²	-844.885	0.815	0.850	0.782
	Roughness	4-km ²	-848.668	0.921	0.936	0.905
	Solar radiation	0.0009-km ²	-902.677	0.997	1.002	0.992
	Slope	0.0009-km²	-863.384	0.879	0.907	0.852
Energy Development	Distance to nearest well	-	-865.638	1.000	1.002	0.997
	Number wells	4-km²	-857.717	0.961	0.985	0.939
	Number wells	0.65-km ²	-859.699	0.833	0.943	0.736
	Number wells	0.04-km ²	-863.083	0.434	1.102	0.171

590 ^a Grass was excluded from further habitat models because of its correlation with sagebrush (r = -0.78)

591 ^b Roughness = Index calculated using the standard deviation of a digital elevation model.

592 Table 2. Log-likelihood (LL), number of parameters (K), Akaike value (AIC), change in
 593 AIC value from the top model (Δ AIC) and Akaike weight (w_i) results of sage-grouse
 594 winter habitat selection for vegetation and topography models, Powder River Basin,
 595 Montana and Wyoming, winters of 2005 and 2006.

Model	LL	K	AIC	Δ AIC	w_i
Vegetation Models					
Sagebrush ^a + Conifer + Riparian + Barren	-716.337	5	1442.674	0.000	0.998
Sagebrush + Conifer + Riparian	-723.772	4	1455.544	12.870	0.002
Sagebrush + Conifer + Barren	-744.539	4	1497.078	54.404	0.000
Sagebrush + Conifer	-749.355	3	1504.710	62.036	0.000
Sagebrush + Riparian + Barren	-780.350	4	1568.700	126.026	0.000
Sagebrush + Riparian	-787.762	3	1581.524	138.850	0.000
Sagebrush + Barren	-799.877	3	1605.754	163.080	0.000
Topography Models					
Roughness ^b + Slope ^c	-835.881	3	1677.762	0.000	0.798
Roughness	-838.257	2	1680.514	2.752	0.202
Slope	-863.384	2	1730.768	53.006	0.000

596 ^a Vegetation variables = percent cover of each GIS vegetation category within a selected
 597 buffer distance chosen by LL values in Table 1.

598 ^b Roughness = Index calculated using the standard deviation of a digital elevation model.

599 ^c Slope = slope of pixel calculated using a DEM

600 Table 3. Log-likelihood (LL), number of parameters (K), Akaike value (AIC), change in
 601 AIC value from the top model (Δ AIC) and Akaike weight (w_i) results of sage-grouse
 602 winter habitat model selection, Powder River Basin, Montana and Wyoming, winters of
 603 2005 and 2006.

Model ^a	LL	K	AIC	Δ AIC	w_i
Vegetation ^b + Topography ^c + CBNG ^d	-683.644	7	1381.288	0.000	0.965
Vegetation + Topography	-687.974	6	1387.948	6.660	0.035
Vegetation + CBNG	-718.083	5	1446.166	64.878	0.000
Vegetation	-723.772	4	1455.544	74.256	0.000
Topography + CBNG	-826.657	3	1659.314	278.026	0.000
Topography	-835.881	3	1677.762	296.474	0.000
CBNG	-857.717	2	1719.434	338.146	0.000

604 ^a Models represent the AIC best combination of variables within each model category

605 ^b Vegetation = % sagebrush and riparian within 4-km² + % conifer within 0.65- km²

606 ^c Topography = roughness of land within 0.65-km² + slope

607 ^d CBNG = number of wells/4-km²

608 Table 4. Logistic regression β -coefficients (SE) and odds ratios from the best model (w_i
 609 = 0.965) describing winter habitat selection and energy avoidance for sage-grouse,
 610 Powder River Basin, Montana and Wyoming, 2005 and 2006.

Parameters	Estimate	SE	Odds Ratio	95% upper	95% lower
Constant	-1.106	0.369			
Roughness ^a	-0.039	0.017	0.962	0.994	0.931
Slope ^b	-0.102	0.022	0.903	0.943	0.865
Conifer ^c	-0.203	0.033	0.966	0.992	0.940
Sagebrush ^d	0.028	0.004	0.816	0.871	0.765
Riparian ^e	-0.131	0.026	1.028	1.037	1.020
CBNG wells ^f	-0.035	0.014	0.877	0.923	0.834

611 ^aRoughness = topographic index calculated as the SD of a DEM within 0.65-km².

612 ^bSlope = slope of pixel calculated from DEM.

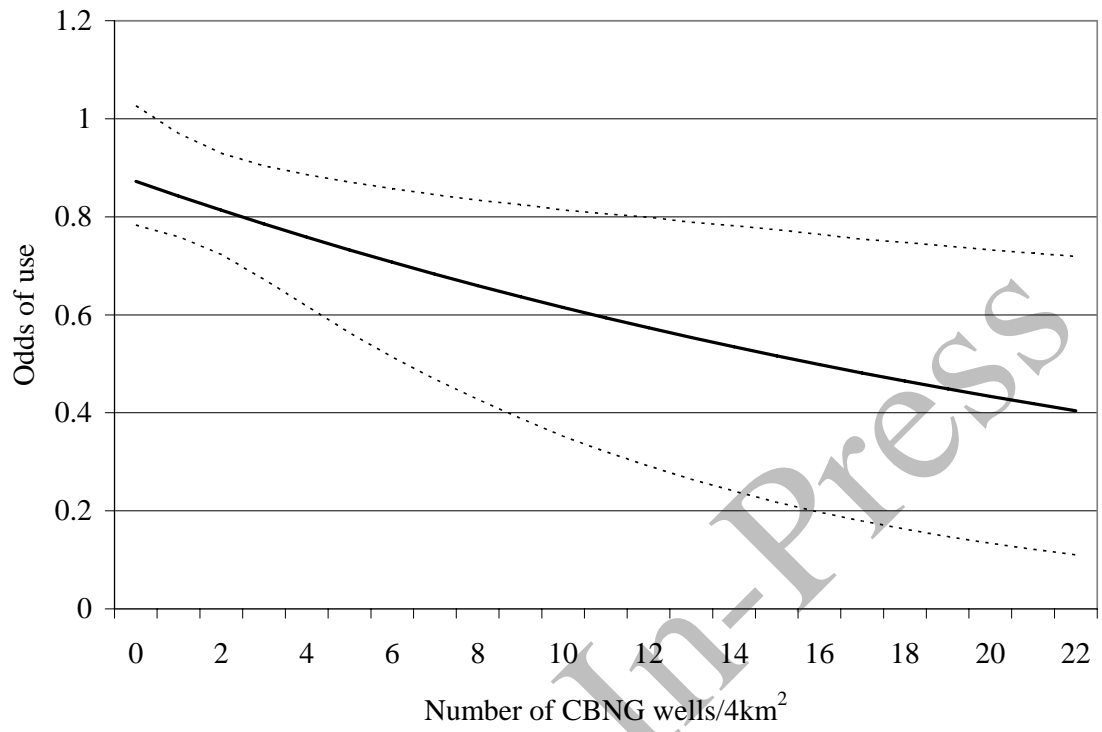
613 ^cConifer = % conifer cover within 0.65-km².

614 ^dSagebrush = % sagebrush cover within 4-km².

615 ^eRiparian = % Riparian cover within 4-km².

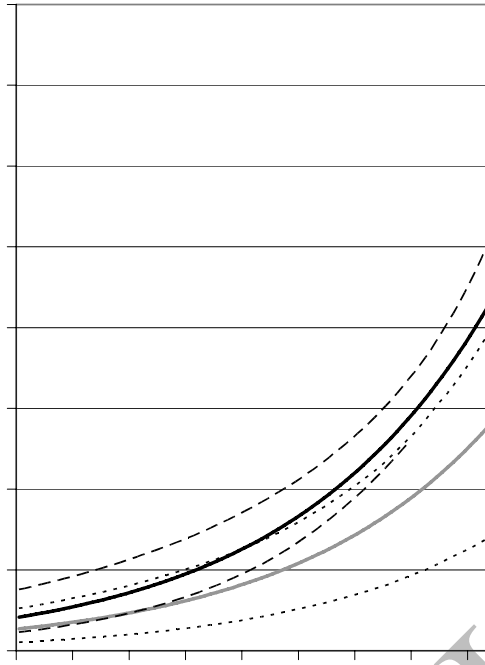
616 ^fCBNG = number of CBNG wells within 4-km².

1 Figure 1



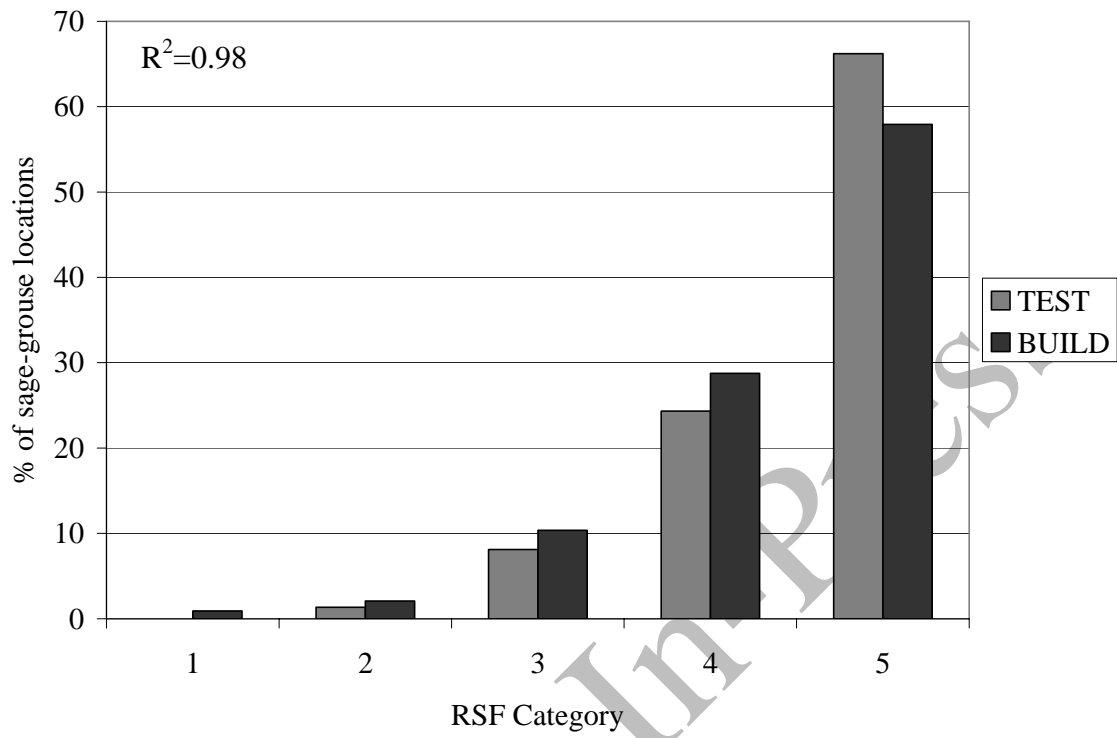
2

3 Figure 2
40 a



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8 Figure 3



9