HIGH-RESOLUTION MAPPING OF HIERARCHICAL GREATER SAGE-GROUSE NESTING HABITAT: A GRAIN-SPECTRUM APPROACH IN NORTHWESTERN WYOMING

Robert T. Haynam III
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HIGH-RESOLUTION MAPPING OF HIERARCHICAL GREATER SAGE-GROUSE
NESTING HABITAT: A GRAIN-SPECTRUM APPROACH IN NORTHWESTERN WYOMING

By

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Biology, B.A., University of Montana, Missoula, MT, 2009
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Thesis

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Our overall objective was to create a probabilistic nesting-habitat map for the Jackson Hole sage-grouse population that would have utility as a tool for future research, conservation, and management. The models that we developed for this purpose were specified to evaluate whether sage-grouse may be selecting nesting-habitat characteristics simultaneously at various spatial scales. Our spatially-explicit landscape-scale research was implemented primarily with readily available National Agriculture Imagery Program (NAIP) data. All nesting data was collected from 2007-2010. We tested how a broad range of grain sizes (spatial resolution) of covariate values affected the fit to logistic regression models used to estimate parameters for resource selection functions (RSFs). We analyzed habitat response signatures at three scales (extents) of analysis: (1) the nesting-patch scale, (2) the nesting-region scale, and (3) the nest-site scale. Akaike's information criterion corrected for small sample sizes ($AIC_c$) and 5-fold cross validation were used to identify the most well-supported and predictive models at each scale. The RSF models were examined separately and then combined into a weighted scale-integrated conditional RSF (SRSF) integrating habitat selection signatures across all three scales. At the nesting-patch scale we determined that sage-grouse nesting occurrence was positively associated with the size of a patch, and the average cover for the patch. At the nesting-region scale, shrub cover of a 769-m-radius grain size was positively associated with nesting-region selection. Distance to tall objects and terrain ruggedness also appeared to influence nesting-region selection at this scale. At the nest-site scale shrub cover and landscape greenness were positively associated with nest-site selection. There was also noteworthy $AIC_c$ support for terrain ruggedness at the nest-site scale. The SRSF provided a single high-resolution probabilistic GIS surface that mapped out areas that represent attractive sage-grouse nesting habitat.
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KEY WORDS

sage-grouse, RSF, grain-spectrum, multiscale, habitat selection, sagebrush cover, nesting-site
selection, remote sensing, NAIP, high resolution, AIC<sub>c</sub>, 5-fold cross validation, conditional
resource selection function, patch-size, LiDAR, nest occurrence
INTRODUCTION

The focal species of this article is the greater sage-grouse (*Centrocercus urophasianus*). This upland game bird is commonly known as a landscape species and it occupies very specific habitat, sagebrush dominated shrubland communities. As a sagebrush obligate species the sage-grouse can not survive without healthy sagebrush ecosystems. Sagebrush vegetation communities historically occupied most of the vast basins that comprise much of the North American west. Both sage-grouse populations and sagebrush habitat have experienced drastic retractions of their distributions since pre-settlement times (Schroeder et al. 2004). This is primarily due to human exploitation of the landscape which comes in the form of sod-busting, energy development, urban development, invasive plant introductions, and livestock grazing (Patterson 1952; Connelly et al. 2004). Processes such as wildfires and conifer encroachment interact with anthropogenic influences to further imperil the sagebrush-steppe and the sage-grouse, one of its most iconic inhabitants (D’Antonio 1992; Bates et al. 2011). It is clear that the future persistence of these two intimately tied ecological assets is dependent on society’s valuation of them.

A few technical questions must be answered in order to illuminate the conversation about the uncertain future of the sage-grouse. What criteria can best characterize the remaining sage-grouse habitat, and where exactly is this habitat? Any proposed criteria must address how sage-grouse respond to ecogeographical realities while attempting to maintain a high fitness. Targeting critical life history stages such as nesting is important when developing valid criteria. With this information, managers, policy makers and the broader public can take inventory of the remaining habitat. This rendering may enhance our society’s conceptual
understanding of the issues so that we can take responsibility for the fate of the sage-
grouse. Shall the remaining sagebrush habitats be maintained, in order to conserve sage-
grouse populations, or shall they be degraded and destroyed, so as to degrade or destroy the
remaining sage-grouse populations?

The what and where questions regarding sage-grouse habitat are straightforward but
the answers have proven difficult. This is largely due to the landscape-scale scope of the
questions, the varied phenologic requirements of sage-grouse, and the extremely heteroge-
eous and varied composition of sagebrush-steppe habitat. Contributing to the complexities
of defining and mapping sage-grouse habitat is ambiguity regarding the conceptual defini-
tions of habitat and scale. Henceforth in this article we will make an effort to distinguish
between structural habitat and functional habitat. We will follow the conceptual frame-
work for habitat definitions that are discussed in Gaillard et al. (2010). When referring to
sagebrush-steppe habitat, or just sagebrush habitat, we are using the term habitat in the
structural sense. Structural habitat can be considered a category of land cover such as forest
habitat or grassland habitat, in which the term encompasses broadly similar biotic (plant
communities) and abiotic (riparian, steppe, mountainous) characteristics. For this concep-
tualization, habitat is independent of the needs of any particular species. By contrast, the
term functional habitat originates from a niche-based definition of habitat as proposed by
G. Evelyn Hutchinson (Colwell and Rangel 2009). In this theoretical realm it refers to all
the resources and environmental factors that determine the presence, performance, and per-
sistence of a species. Here the concept of the niche is inextricably bound to the species; the
species’ niche is its habitat.
With respect to scale we will make a concerted effort to clarify what we mean when we use the term. It is strewn throughout the spatially-explicit habitat response literature and tends to be used very loosely. Inducing particularly high levels of confusion is the term multiscale. In this article we explicitly differentiate between the scale (spatial extent) of our analysis and the grain (spatial resolution) of our covariates, following the conventions presented in C. B. Meyer and Thuiller (2006). To analyze habitat response signatures with more than one definition for the spatial extent (scale) of the resource selection analyses is to perform a multiscale analysis. To include more than one grain of measurement in a given scale of analysis is to perform a single-scale multi-grain analysis. Hierarchical resource selection research is typically equivalent to multiscale research. If the separate scales of the analyses are conceived for separate orders of selection then the analyses are nested (hierarchical). If the separate scales of analysis are just slight alterations to the spatial extent then the research is just multiscale, not hierarchical. This type of non-hierarchical, multiscale research is recommended as a means of performing a sensitivity analysis for the specified definition of availability (e.g., analysis extent, analysis scale). The research presented herein is nested-hierarchical (therefore multiscale), and multi-grain. We generally refer to grain-size, grain, or the grain-spectrum when discussing the level to which our covariates (images) are smoothed using Geographic Information System (GIS) spatial summary statistics specified by the size (radius) of a moving window (local statistics) or circular sampling polygon (zonal statistics).

From the 1950’s through the present, fueled by increasing conservation concerns, a research pulse has been directed at answering the what and where of sagebrush-steppe ecosystems in general, and sage-grouse functional habitat in particular (Blank 2008; Homer et al.
A great deal of progress has been made but there is much room for refinement of the knowledge and tools necessary to explicitly define sage-grouse functional habitat. A comprehensive definition of sage-grouse functional habitat will necessitate the integration of habitat response and habitat performance metrics at a diverse array of scales, ranging from the immediate vicinity of a grouse, to the broader landscape and community scales with which the populations interface. A more mechanistic understanding of resource selection and spatially-explicit fitness gradients will eventually be required to move beyond the inferential limitations imposed by empirical habitat associations. This implies that all pertinent risks and rewards will have to be dynamically mapped for multiple life history stages at an appropriate grain-size; predator and prey metrics must be considered in addition to forage, cover, and abiotic factors.

While a comprehensive definition or model of functional habitat in N-dimensional space is not currently feasible, a functional-structural hybrid definition is attainable. Many underlying aspects of a structural habitat type could be integral components to a species’ functional habitat. We can identify resource gradients and factors that are measurable and have a measurable association with a species’ demographic parameters or behavior. These associations can then be compiled into a metric that represents some component of the true N-dimensional functional habitat (Gaillard et al. 2010). This is in essence what researchers are doing by fitting survival and or location data to models such as spatially-explicit resource selection functions (RSFs), spatially-explicit survival models, or spatially-explicit population models that relate environmental variables to habitat response metrics (i.e demographic parameters, occurrence, behavior). This approach is plagued by the limitations of empirical
research but can still help resolve questions that are necessary to target further research, predict population responses, or guide human conduct that may threaten a species.

In this article we push the limits of contemporary techniques by exploiting high-resolution remotely-sensed images and sophisticated GIS algorithms to map shrub cover and other landscape-scale habitat variables with suspected importance to nesting sage-grouse. We then statistically relate nesting sites and nesting regions to habitat variables thought to be important to sage-grouse, thereby developing empirical models of sage-grouse resource selection during nesting. (D. S. Johnson et al. 2008; C. J. Johnson and Seip 2008; C. J. Johnson et al. 2006; Manly et al. 1993; Boyce et al. 2002). This contributes another case study to the daunting problem of defining sage-grouse functional habitat and does so in a high-resolution spatially-explicit manner so that the habitat associations may be mapped in a GIS for both scientific and management purposes.

In general our approach aligns with sophisticated and proven contemporary methodologies. We analyzed resource selection using three separate definitions of use and availability, which represent different scales of selection (Manly et al. 2007; Erickson et al. 2001). At each scale we formulated a set of a priori models and used AIC$_c$ to identify the best approximating model (Burnham and Anderson 2002). For two out of three scales of selection we systematically investigated the influence of grain size on the support for a given model. For one scale of analysis the explanatory variables were highly discretized and spatially aggregated so a multi-grain analysis was not deemed appropriate.

Scale and sample-unit grain-size are of well known importance in wildlife habitat response relationships (Mayor et al. 2009). Many attempts have been made to address the importance
of grain sizes in resource selection research; most represent ad-hoc treatments of issues that are specific to a particular case study, and can be based upon very subjective choices. In one instance RSF models were developed for Gunnison sage-grouse using a hierarchal approach by examining multiple grain-sizes at both landscape and patch scales; specific criteria justifying grain-size choices were not provided (Aldridge et al. 2012). Other researchers used log-likelihoods to perform univariate variable selection among three grain-sizes for each landscape variable considered in their RSF analysis of habitat use by sage-grouse in winter (Doherty et al. 2008). Again, no specific justification was given for the choice of the initial set of grain-sizes. Subsequently the same researchers used grain-sizes of 100 m, 300 m, 1,500 m, and 3,000 m and provided specific conjectures as to the types of processes that influence nesting at different scales. Here they assumed that the two larger grain-sizes would be measuring something associated with landscape processes influencing nesting and the two smaller grain-sizes would be measuring some aspect of processes associated with the immediate nesting area. Following Doherty et al. (2008) they used univariate variable screening to select the grain-size and landscape variable combinations to be included in a final model set for an RSF analysis of nest-site selection (Doherty et al. 2010). Some biological assumptions pertaining to grain-size choices were made explicit but concrete ecological knowledge justifying the grain-size choices were in keeping with the pattern rendered above—absent. This is no fault of researchers; it is due to a lack of concrete mechanistically or theoretically-founded principals for identifying the biologically appropriate grains of measurement.

The grain-size reliant sage-grouse resource selection articles mentioned above closely align with our research objectives. Each one proposes a novel and progressive methodology for
modeling habitat selection for sage-grouse at the landscape scale. We highlight the issue of how to deal with ambiguities regarding grain-size choices for resource selection analysis because well-developed methodologies for addressing this potentially critical dimension of habitat response are not forthcoming; most attempts at guidance are vague (Boyce 2006).

A systematic investigation of a broad grain-spectrum may be more appropriate than subjective grain-size choices. Thus, we have attempted a methodology with the intent of avoiding the use of univariate variable screening to select from among a limited and subjective set of grain-sizes. We did this by generating all of our covariates at the highest spatial resolution that we possibly could. In this way we are able to dictate the grain-size of the covariates systematically, from fine to coarse grain, to better represent the full spectrum of grain sizes that may influence sage-grouse nesting-habitat selection.

To address the aforementioned objectives, we (1) developed a suite of alternative hypotheses involving landscape and habitat characteristics that are expected to affect sage-grouse habitat selection during nesting; (2) generated accurate and high-resolution variables that represent these hypotheses; (3) processed these variables into a full spectrum of grain-sizes representing naive hypotheses regarding the influence of the grain of measurement on habitat response signatures; (4) estimated RSF model parameters using software for logistic regression and identified the most well-supported models from a suite replicated at varying grain sizes; (5) completed objective 3 and 4 for a nest-site and nesting-region scale of analysis; (6) identified the best approximating model structure from a third patch-scale analysis; (7) validated the predictive performance of the three RSF models using cross-validation and rejected models that had low predictive potential; (8) made inferences regarding the influence
of covariates using weight of evidence approaches provided by information theory, as well
as effect sizes, effect directions, and precision of parameter estimates; (9) used scale-specific
RSF models to map out the relative probabilities of sage-grouse habitat selection at each
scale in our study area; and (10) mapped weighted conditional RSF predictions calculated
by multiplying together the resource selection surfaces at the nest-site, nesting-region, and
nesting-patch scales.

This rigorous spatial rendering of the habitat selection signature can provide stakeholders,
scientists, practitioners, citizens and stewards alike with a probabilistic map. Utilized in
conjunction with the inferences based upon the RSF models, RSF or SRSF-surface maps
can also help people conceptualize actions or events that may impact sensitive species and
ecosystems. Such projects (ecological forecasting) will facilitate well-informed policy and
behavior, thereby focusing responsibility.

STUDY AREA

Our study area covered a substantial portion of Jackson Hole which is located in Teton
County in northwest Wyoming (Fig. 1). This region has been most famous for Grand Teton
National Park (GTNP) which occupied the entire northern half of the Jackson Hole valley.
The National Elk Refuge (NER) was directly adjacent to and south of the GTNP boundary.
These federally administrated and protected lands established a unique and crucial land use
context with respect to the small sage-grouse population that persisted there.

This landscape is characterized by a poorly-dissected valley region with a gentle topo-
graphic gradient that is surrounded by well-dissected mountainous regions exhibiting extreme
topographic gradients. The mountainous regions include the Teton Range, Washakie Range, Mount Leidy Highlands, Pinyon Peak Highlands, Gros Ventre Range, Snake River Range and the Wyoming Range. These ranges surround the Jackson Hole valley, which contains the Snake River and the towns of Kelly, Moose, Wilson, and Jackson. The Snake River runs into and out of Jackson Lake in the northeast portion of the valley and then proceeds south through Jackson Hole. The two largest tributaries to the Snake River are the Buffalo Fork and Gros Ventre Rivers. The Buffalo Fork drains the northeast portion of the basin and the Gros Ventre drains the east-central part. Other streams include Pilgrim Creek, Pacific Creek, Lava Creek, Spread Creek, Flat Creek, and Fish Creek. Most of the streams, including the Snake River, originate in the mountains and are perennial. An exception is the Gros Ventre River which has been documented as intermittent along certain stretches in some years. It should be noted that classifying a stream can be somewhat arbitrary because of the temporal and spatial variation of relevant characteristics with some streams (Nolan and Miller, 1995). For instance, the Gros Ventre River has intermittent stretches only some years and only on certain reaches. This is true of a number of the water resources in the valley including ephemeral ponds and irrigation ditches. The rivers, streams, and the riparian habitats that they support serve to fragment the sagebrush-steppe in Jackson Hole.

Elevations range from 1,767 m near the Snake River, south of Jackson, to 4,197 m at the highest point in the Teton Range, the top of the Grand. The range of elevations for conceivably suitable sage-grouse habitat was 1,940 – 2,150 m. The Jackson Hole basin, from Jackson Lake to the canyon of the Snake River, is filled with unconsolidated material with various characteristics and origins. The soils that overlay this material were largely
well-drained gravelly or silty loams that provided a good growth substrate for the dominant shrub, big sagebrush (*Artemisia tridentata*).

Other shrub species that occupied the valley flats included antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos oreophilus*), rabbitbrush (*Chrysothamnus linifolius*), shrubby cinquefoil (*Dasiphora fruticosa*), spiny horsebrush (*Tetradymia canescens*), and serviceberry (*Amelanchier alnifolia*). Common forbs included wild buckwheat (*Eriogonum umbellatum*), arrowleaf balsamroot (*Balsamorhiza sagittata*), mule’s ears (*Wyethia amplexicaulis*), old man’s beard (*Geum triflorum*), slender cinquefoil (*Potentilla gracilis*), scarlet gilia (*Gilia aggregata*), yampah (*Perideridia gairdneri*), twolobe larkspur (*Delphinium nelsonii*), harebell (*Campanula rotundifolia*), hound’s tongue (*Cynoglossum officinale*), salsify (*Tragopogon dubius*), puccoon (*Lithospermum ruderale*), common yarrow (*Achillea millefolium*), sulfur buckwheat (*Eriogonum umbellatum*), and silky lupine (*Lupinus sericeus*).

Common grasses included California brome (*Bromus carinatus*), Idaho fescue (*Festuca idahoensis*), prairie Junegrass (*Koeleria macrantha*), Indian ricegrass (*Achnatherum hymenoides*), and smooth brome (*Bromus inermis*) (Kesonie 2009; Shaw 1968).

The predominant uses of private land in Jackson Hole were developed residential and commercial zones surrounding human population centers. The communities of Jackson, Wilson, Kelly, Moose, and the Village (Jackson Hole Ski Resort) were largely sustained by the tourist dollar, attracted by the grandeur and outdoor recreation opportunities provided by the Tetons and Yellowstone National Park. This majestic region has prompted many privileged elite to stake a claim in the form of extravagant and incessantly manicured leisure-time properties. The entire southern third of the valley has been allocated to development (golf
courses, high schools, parking garages, hotels, personal residences, etc.) and a legacy of
reclamation land-use thinking is still evident in the form of heritage ranching operations in
the Spring Gulch and Buffalo Fork areas. These heritage reclamation style land uses main-
tained open spaces and inhibited condominium and mansion sprawl. This was beneficial to
many species in the superficially pristine natural history and outdoor-recreation destination
of Jackson Hole. Despite some maintenance of open spaces, if not for the protected status of
GTNP and NER, the sage-grouse population undoubtedly would have been extirpated long
before our study was implemented. It was likely that the remaining habitat was approaching
the minimum requirements for a species that has evolved to perform its life history processes
at the landscape scale.

METHODS

Locating Nests

All sage-grouse trapping and monitoring that produced nesting data was conducted from
2007–2010. Following Giesen et al. (1982) and Wakkinen et al. (1992) sage-grouse were
captured using spot lighting and hoop netting techniques or by firing pre-positioned nets on
known gathering grounds, such as leks or mineral piles. Rocket-nets or net launchers were
used to propel the nets. Female sage-grouse were outfitted with either 18–22g necklace style
VHF radio transmitters or 30-g solar GPS/PTT transmitters that were attached using the
rump mount technique (Rappole and Tipton 1991). The VHF transmitters were supplied
by Holohil Systems Ltd. of Carp Ontario and Advanced Telemetry Systems, Inc., of Isanti,
Figure 1: Greater sage-grouse study area, Jackson Hole, Wyoming, USA, 2007-2010
Robert Thomas Haynam III

Minnesota. Microwave Telemetry, Inc., of Columbia, Maryland supplied the GPS/PTT transmitters.

The general location of VHF outfitted females was determined 2–3 times per week using standard telemetry triangulation techniques (Millspaugh and Marzluff 2001). If a bird began to localize in a 1 km² area then the protocol for relocating birds switched to a walk-in method. The walk-in method involved proceeding toward the signal emitted by the VHF transmitter until the observer believed they were within 100 m of the transmitter. The observer then attempted to partially circle around the signal to get a better idea of the true location by drastically altering the azimuth to the transmitter about the observer. When some confidence as to the true location of the bird was established the observer would record three pieces of information: their spatial coordinates with a GPS, an azimuth to the expected location of the bird with a compass, and the distance. The estimated bird location was calculated by converting the azimuth, based on magnetic north, to polar degrees and then using Polar to Cartesian conversion equations with the recorded distance, and the observer coordinates, to calculate the estimated spatial coordinates of the bird. If a hen was located this way on two consecutive relocation efforts then a further effort was made to get an estimate of what would likely be a nest location. This nest site estimation protocol required a single observer to do their best to carefully proceed to within 10 m of the suspected nest. The observer then circumvented the transmitter signal while recording their location with a GPS device in order to constrain the true nest site inside a rough circle with a relatively tight radius (White and Garrot 1990).

A transmitter signal thought to be nest-bound was then monitored closely, but from at
least 100 m away, on Monday, Wednesday, and Friday until the signal was acquired well outside the nesting zone. Upon this indication that the hen had either completed nesting, or had abandoned the nest, an observer would enter the nesting zone and attempt to locate the nest. A consistently more rapid transmitter pulse rate would indicate the alternative scenario; the female had been predated. Once a nest was located, a precise location was recorded with the aid of a hand held GPS device.

Producing Habitat and Landscape Variables

Anderson and Burnham (2002) explicitly note that often not enough thought is allocated to the variables that are measured or constructed for use as predictor variables in wildlife research. Our strategy to select variables for inclusion in a final model set was to develop or identify methodologies for producing high-resolution continuous-scale variables that would reasonably approximate the actual distribution of landscape or habitat variables known or thought to influence the habitat response of our sage-grouse population. Consideration was then given to our capacity to interpret an observed response to a potential variable. This precluded the use of most of the landscape ecology metrics such as fragmentation indices which are dependent upon a subjective working definition of what is considered a patch. Our list of predictor variables was derived from experience with sage-grouse ecology gained during the field research component. This knowledge was cross referenced and supplemented by reading pertinent literature. The final choice of covariates to produce for modeling was as much a function of feasibility and project resource constraints as suspected biological importance. The one exception was a shrub cover metric which was deemed indispensable.
and was allocated a disproportionate amount of our resources.

The covariates that we sought to generate were: shrub cover, habitat patch area, average cover for each patch (MeanShrub), bitterbrush cover, vegetation indices, proximity to roads, proximity to water, proximity to shadows (perching substrates), and a terrain ruggedness index. After initial methodological experimentation using 30-m resolution Landsat 5 TM data downloaded from the USGS Earth Explorer website it was decided that United States Department of Agriculture Farm Service Agency National Agriculture Imagery Program (NAIP) data would provide the best means of meeting our objectives. The 1-m spatial resolution NAIP imagery was captured by an airplane mounted optical sensor in 2006, 2009, and 2012. The 2006 imagery has only three bands representing the red, green, and blue visible light spectrum. For the 2009 and 2012 NAIP imagery a 4-band version was sourced from USGS Earth Explorer Tiles in the NAIP JPEG2000 collection. These products had an additional near-infrared band (NIR). Each individual image tile was based on a 3.75-minute longitude by 3.75-minute latitude quarter quadrangle plus a 300-m buffer on all four sides. This imagery was downloaded and mosaicked together in QGIS to create a contiguous image for the entire study area (QGIS version 2.2, www.qgis.org, accessed 1 Apr 2014). All three of these multi-band images were split into individual bands and the bands of corresponding spectral ranges were recombined into four new multi-band images where each image band represents the year of acquisition for the same spectral range. The red, green, and blue images were 3-band images and the NIR image was a 2-band image. A principal component transformation (PCT) was then performed separately on each one of the four multi-temporal images and the first principal component was inverse transformed back to
the original scale. These PCT processed images yielded a single PCT color band containing
the bulk of unique information in each multi-temporal image. The four inverse transformed
first principal component (PCT-1i) images were then concatenated back into a single PCT-1i
4-band color near infra-red image. These methods represent a form of image averaging where
the average is being taken for the same color band across multiple years. See Mather (2004)
and Gao (2009) for a description and illustration of the application of principal component
analysis in GIS and remote sensing. This processed imagery, along with the original NAIP
images, was used to derive most of the habitat variables for our RSF models.

The methodology used to develop our index of shrub cover is analogous to a multiple
criteria evaluation (MCE). A MCE integrates multiple sources of data and combines them
with logical (e.g., boolean constraints) or mathematical rules and weights regarding how
their values influence the output of the evaluation; the output is typically some form of
subjective expert-knowledge based suitability or risk index (Pechanec and Machar 2013;
Chakhar and Martel 2003). We did not rely on a formalized MCE but instead combined
supervised classifications, texture metrics, and change detection algorithms with a fine-scale
spatial residual analysis. In essence we created a binary classification of the study area
representing either arid shrubland or grassland-and-other. Within this restricted region we
calculated an index to shrub cover using an analysis that picked up the image texture created
by local variation in the digital numbers of the image. The methods and results of our shrub
cover covariate synthesis are provided in the appendix A.

Partially relying on our shrub texture index we produced a GIS raster layer that delin-
eated separate sagebrush habitat patches and gave their respective areas. This was done by
smoothing our shrub texture metric and then using threshold values for reclassifying the GIS study area into a patch and non-patch category. An algorithm to calculate the patch area from discrete patches was then employed. The methods and results of our patch delineation and area estimation are provided in the appendix B.

A GIS raster layer providing an index for bitterbrush cover was created by identifying the regions where bitterbrush was present in the study area. This was combined with a classification of bitterbrush pixels and the shrub texture metric used for estimating sagebrush. The methods and results of our bitterbrush covariate synthesis are provided in appendix C.

To produce a metric for perceived and actual risk posed by perching substrates and tall objects we binary classified a support-vector-machine (SVM) classified 2012 NAIP image into two classes where the target class was one that did very well at identifying shadows. We then processed this image with a Euclidean raster distance algorithm, also known as a proximity algorithm, in QGIS. Two additional distance layers were produced by doing the same thing with a layer of water sources in the study area, and then again on a roads layer.

The water layer was created through a combination of classification using NAIP imagery, hand digitizing by viewing RGB composite NAIP imagery, and viewing USGS topographic quads overlayed with water resources vector files downloaded from the Wyoming Geographic Information Center (WyGISC). Lakes, ponds, wetlands, rivers, streams, and irrigation ditches were all included in this water source map. Further effort would improve completeness particularly for seeps, springs and small seasonal water impoundments or flooded zones. Though the relevance to wildlife may be substantial, information regarding intermittent or ephemeral water sources, such as rain puddles or dew, is difficult or impossible.
to record.

The road layer was created from a combination of Topologically Integrated Geographic Encoding and Referencing (TIGER) line files and hand digitization on top of the NAIP imagery. One of three categories of roads was specified for each line segment. The categories were based upon personal knowledge of most of the roads in the study area. They correspond to state highways, heavy use residential or rural roads, and moderate use dirt roads, or four-wheel drive recommended roads. The criterion used to categorize the roads was whether one expected to witness constant traffic, certain but not constant traffic, or potential light traffic for any daylight hour during the nesting period. A buffer of 9, 49, or 99 meters was applied to each road segment dependent upon the category. These buffer sizes were selected by lying down at various distances to the different categories of roads and subjectively deciding at what distance the road noise became uncomfortable. Next a proximity algorithm was run on a raster version of the buffered road layer. The proximity algorithm was also run on a raster version of the original unbuffered road vector file. These two distance layers were added together using raster algebra to produce a road exposure index where distance increases linearly with a slope of 1 from the GIS road center to the edge of the buffer. Beyond the buffer the distance values increase at a rate twice that of standard Euclidean distance from the roads.

A terrain ruggedness index (TRI) was generated from a 1/3 arc-second (≈10-m) DEM, downloaded from the USGS The National Map website, using the raster analysis DEM (terrain analysis) module in QGIS (Wilson et al. 2007). This terrain ruggedness index was then resampled to a 1-m resolution and rescaled so that it matched the resolution of all the
other variables. Lastly it was linearly rescaled to the range 0–255 by viewing the image
histogram to aid in choosing rescaling parameters that would sufficiently rescale the index
values while not causing excess clipping of values.

The final two variables generated were an excess green index (ExG) and a custom veget-
etation index that performed well in highlighting sagebrush in addition to other vegetation
types. We call this index a green shifted grayness index (GSGI). GSGI was calculated as fol-
lows: $\sqrt{(R - \frac{R+(G+55)+B}{3})^2 + \sqrt{(G + 55) - \frac{R+(G+55)+B}{3})^2} + \sqrt{(B - \frac{R+(G+55)+B}{3})^2}$, where
$R =$ red, $G =$ green, and $B =$ blue (spectral bands). ExG and GSGI are both examples of
visual spectrum vegetation indices. The utility of these low cost vegetation indices has been
established for agricultural purposes and in our case they provided desired spatial and tem-
poral resolution due to the availability of NAIP imagery (Ponti 2013; G. E. Meyer and Neto
2008; Kazmi et al. 2015). Both of these vegetation indices were created three times using
the red, green, and blue bands from each year of NAIP data. The three index-year images
were then added together and linearly rescaled to a range of 0–255 by viewing the image
histogram to aid in choosing rescaling parameters that would sufficiently rescale the index
values while not causing excess clipping of values. Adding the images together is a form
of image averaging and was employed so that the vegetation indices would better represent
the typical distribution of vegetation on the landscape. This highlights persistent vegetation
zones, such as mesic areas, that are more likely to be present at any given time, and not just
the moment a single image was captured.

All habitat variables except the ruggedness index were generated wholly or partly by
extracting information from the 1-m NAIP images from 2006, 2009, and 2012. Any rescaling
was done to ensure that covariates had a similar range of values which can alleviate estimation
issues when fitting the data to regression models (Kleinbaum et al. 1998).

**Grain-Spectrum Multiscale Resource Selection Analyses**

By only considering the limited number of variables that we were able to produce with
outstanding quality, we were able to avoid using univariate variable screening. This seems to
be more in keeping with the conventions imposed by using AIC for model selection. Harrell
(2001) provides substantive discussion of the issues of model selection and variable selection
advocating for the use of the step-down method and equating univariate variable screening to
a form of forward stepwise variable selection that never reexamines insignificant variables in
later steps. A thorough reading of the multivariate modeling strategies and model selection
sections of Harrell (2001), Burnham and Anderson (2002), and Hosmer et al. (2013) offers
conflicting recommendations for variable selection, or model selection. Even so, none of these
authors advocate the mixing of univariate variable screening and AIC based model selection.

Despite our quality over quantity approach to covariate synthesis, all of our variables
imperfectly represent the distribution of resources or landscape variables that our nesting
sage-grouse experienced or had access to. All of the variables described above should be
considered indices of the actual landscape characteristics that they approximate. To simplify
discussion of the covariates in the models we will now refer to them as shrub, patch area,
MeanShrub, bitterbrush, water, roads, shadows, ruggedness, veg-ExG, and veg-GSGI. The
two vegetation indices were included because they both performed well as an index for
highlighting the relative amount of green leaf area. The veg-ExG index seemed to excel
at identifying areas that were especially and consistently green, such as mesic habitat or irrigated fields. While still highlighting lush vegetation, the veg-GSGI index picked up a more full spectrum of greenness across the landscape, most notably the olive drab greens of sagebush-steppe areas. This assessment is solely based on the visual inspection of the vegetation indices combined with personal knowledge and experience with the study area.

Throughout the modeling process we evaluated the correlation between predictor variables and the variance inflation factors (VIF) of variables in models. We estimated the parameters for all RSF’s using software for logistic regression that employed the logit link function. The RSF was assumed to take a log-linear form (Boyce et al. 2002).

The multiscale aspect of our analysis strategy involved defining use and availability at three scales. The coarsest—first scale—of analysis is discussed separately in the following section because a different methodology was employed. The ordering of analysis scales is loosely in keeping with the commonly adopted concept of hierarchical selection orders originally defined by D. H. Johnson (1980). Our third scale can be considered the nest-site scale and would correspond most closely with Johnson’s third-order selection. Here we defined use as being centered on the spatial coordinates of the nest. We defined availability as centered upon points distributed randomly within a 500-m buffer around all nests. To determine the necessary number of random points needed to eliminate sampling error we iteratively fit all of the candidate models while varying sampling density (Manly et al. 2007). We then checked for stability in the estimates, as indicated by the direction and magnitude of the parameter estimates. We also checked the AICc ranking of models. Parameter estimates and AICc model rankings exhibited notable instability until we reached an availability sample
of 61 sample points per km$^2$.

For the nesting-region (second-scale) analysis we defined use the same way that availability was defined for the nest-site (third-scale) analysis. This nested approach was adopted to allow for creating a conditional selection surface by combing the nest-site and nesting-region RSF (DeCesare et al. 2012). We randomly distributed 61 points per km$^2$ within the 500-m buffer zone around each nest. We then randomly sampled availability at this same density within the entire study area. To enforce a biologically reasonable definition of availability we created a mask that excluded forests, wetlands, willow flats, and water bodies. We deleted all availability sample points that fell within our availability mask. Using a mask in this way helped eliminate the confounding of resource selection signatures by structural habitat types that really represent biophysically and behaviorally unavailable resources that are not a component of a species functional habitat. Sage-grouse categorically avoid forests and expansive willow flats; wildlife biologists and managers are generally not interested in such well established resource selection signatures. Considering non-habitat as available can alter the observed association between predictor and response variables. This changes the biological interpretation of the associations and can obfuscate those of interest. See appendix D for a description of the methodology used to synthesize the availability mask.

The sources of inference that we produced for our nesting-region (second scale) and nesting-site (third scale) RSF models include the AIC$_c$ support for each grain size, the confidence set of models within the most well-supported grain size, the most well-supported variables across all models in the model set (balanced across predictors), and the size/direction of the estimated parameters or odds ratios for the most well-supported models. We calcu-
lated confidence intervals based on nonparametric bootstrap percentile intervals that used a
bootstrap covariance matrix derived from 10,000 bootstrap estimates. We made every effort
to structure our model set to maintain a balance among variables for the 2,664 models across
24 grain sizes for the nesting-region analysis. We did the same for the 1,794 models across
all 13 grain sizes for the nesting-site analysis.

The grain sizes used for the nest-site scale of resource selection analysis were calculated
to provide approximately 50% more areal coverage at each increment, from a 20-m radius up
to a 228-m radius. This produced 13 sampling polygon sets, each set with a different radius.
A circular sampling polygon of a given radius defines the grain size. The specification that
areal coverage increase by 50% every increment was subjectively decided upon because it was
hoped that it would produce meaningful changes in the summary statistics for each covariate,
without skipping over grain sizes with unique habitat response signatures. To calculate the
grain radius for each increment, we used this equation: \( radius_{i+1} = \sqrt{(radius_i^2) \times 1.5} \). The
same calculation was used to produce the target grain sizes for the nesting-region analysis.
These grain-sizes were incremented from 20 m up to 2,119 m, producing 24 sampling polygon
sets. For each of our 7 chosen covariates (patch-size and MeanShrub excluded) we calculated
the mean value within each sampling polygon at each grain-size. Other summary statistics
could be calculated but we felt that the central tendency of a continuous spatial variable
aggregated for varying grain-sizes would have the most approachable interpretation. The
landscape context of a processed covariate changes as it is aggregated to varying degrees
based on the designated grain-size radii. For example, a covariate such as distance to roads
is a proxy for exposure to traffic noise and other disturbances. At smaller grain-sizes this
proxy represents linear exposure features across the landscape. At larger grain sizes it
represent more of an index of the density of these linear exposure features. The standard
deviation, maximum, or number of unique values of a covariate could be calculated at varying
grains of aggregation, but interpreting a habitat-selection response to such metrics would be
challenging.

For the nest-site and nesting-region scales of analysis, we formulated models to represent
possible habitat response relationships, irrespective of the position along the grain spectrum.
The shrub covariate was included in every model because there is a well-established rela-
tionship between sagebrush cover and the nesting ecology of sage-grouse. Interpreting other
covariate effects that were not corrected for sagebrush cover would be problematic. With the
rest of the covariates except veg-ExG we specified a candidate model set that included all
permutations of two, three, and four additive combinations of our covariates. Every model
that contained veg-GSGI was then duplicated substituting veg-ExG, thereby allowing the
two vegetation indices to compete in the model set; we did not possess any a priori knowledge
that would help us make a selection between the two vegetation indices.

To address linearity assumptions we added restricted cubic spline terms to as many of
the previously specified models, and model terms, as was possible while keeping the degrees
of freedom below 7. Here we employed the guideline that models should not be specified
that have more degrees of freedom than the number of responses divided by 10 (Harrell 2015;
Hosmer et al. 2013). We then duplicated the model sets for each grain-size along the grain
spectrum. This was done for the nesting-region and nest-site scale of analysis. There were
138 formulations of the nest-site models and 111 formulations of the nesting-region models.
This discrepancy is an artifact of the increased sample size for the nesting-region analysis. We could allocate more degrees of freedom to restricted cubic spline knots at the larger scale of analysis. Assumptions of linearity for each covariate were tested with fewer models because cubic spline terms could be specified for more than one variable without exceeding the degrees of freedom to sample size ratio.

The use-availability likelihood for our RSF models was maximized using the `lrm` function of the `rms` package in R (R Core Team 2013; T. L. McDonald 2013). We relied on information-theoretic methods to quantify the relative support for our suite of alternative models. We calculated Akaike’s Information Criterion (AIC) corrected for small sample sizes (AIC<sub>c</sub>) (Burnham and Anderson 2002) for each model in each of the model sets at the three different analysis scales. We also calculated statistics that derive from AIC<sub>c</sub> and aid in interpreting the evidence for a given model: \( \Delta \text{AIC}_c \), Akaike weights \( w_i \), evidence ratios (ER), and model likelihoods (LM).

There was substantial model selection uncertainty for our nest-site scale of analysis so we model-averaged all models with a \( \Delta \text{AIC}_c \) value less than 5. This criterion for selecting a confidence set was chosen from the options outlined in chapter 4 of Burnham and Anderson (2002). Here the likelihood of the lowest ranked model \( g_{\text{max}} \) in the confidence set is small relative to the highest ranked model \( g_{\text{min}} \). This basis for a confidence set is the stated preference in Burnham and Anderson (2002) where the statistics of interest are referred to as likelihood evidence ratios where \( \mathcal{L}(g_i|x)/\mathcal{L}(g_{\text{min}}|x) \equiv \exp\left(-\frac{1}{2}\Delta_i\right) \) and for \( \Delta_i = 5 \) this ratio would be 0.082 (small). Many authors choose a confidence set of models based upon the Akaike weights in their model set where the top set weights sum to some percentage,
often 90%. Based on this criterion our confidence set corresponds to \(\approx 29\%\) of the model weight from all models in the nest-site model set. Given the multi-grain nature of our model set, and therefore the numerous partially redundant models with low Akaike weight values, our confidence set is more than adequate for integrating model selection uncertainty. This is particularly true given the consistency of parameter estimate direction and effect size between models and the fact that shrub was forced into all models as a biologically critical predictor. The model set used for model averaging, prediction and validation was composed of 52 models. For these 52 models the Akaike weights were rescaled to the range 0 – 1 for use as model averaging weights. Using the Orfeo Toolbox Band Math module in QGIS we generated a predictive RSF surface which mapped values proportional to the probability of use by a nesting sage-grouse in our study area at the nest-site scale. This was done by summing all of the 52 weighted RSF scores for every pixel using the pertinent GIS covariates that had been smoothed with a circular 41-m averaging moving window. This smoothing corresponds to the 20-m radius sampling polygons within which covariate averages were used as our RSF predictor variables.

The highest \(\text{AIC}_c\) ranked nesting-region model was of the 1730-m grain size and had overwhelming support so no model averaging was necessary. However, this highest ranked RSF was rejected on account of having poor predictive performance, and other models at this analysis scale were assessed instead.
Patch-Scale Resource Selection Analysis

For the first and final scale of our multiscale analysis we investigated selection of individual patches. This scale was defined as a hybrid between the nest-site and nesting-region scales of analysis. Use was defined by the patch in which a nest was placed and availability was defined as the entire study area. This scale of analysis does not correspond with first-order selection—the selection of the geographical range of a species. It is closer to a variation of second-order selection that targets the selection signature of coarse habitat patch characteristics. Our patch-scale analysis should not be confused with third-order selection either; the term patch is often associated with third-order selection in the primary literature. Use was sampled using the nest locations and availability was sampled using the random availability points from the region-scale analysis. This structure was conceived because a grain-spectrum analysis would not be appropriate for the highly discretized patch-size variable. Here we make the assumption that a sage-grouse selects for the size and general shrub cover of a habitat patch and not for the central tendency of patch areas within a buffer centered a particular location. In this case the value of the predictor variables is contingent upon the membership of the nest to a patch, and not the landscape context surrounding the nest. The broader assumption that we are making is that a sage-grouse first selects a patch, then a region within a patch, and finally a specific nest-site.

The patch-scale analysis included only two predictor variables. The model set that we specified only included 13 models. The two covariates were the area of patches in square kilometers and the average shrub cover in each patch. The average shrub cover in each patch was calculated using the GRASS GIS r.statistics algorithm—Martin Schroeder, and
GRASS Development Team, 2016 r.statistics. Geographic Resources Analysis Support System (GRASS) Software, Version 7.0. Open Source Geospatial Foundation. https://grass.osgeo.org/grass70/manuals/r.statistics.html—which calculates summary statistics of one data layer based upon the categorical membership of pixels in another data layer. Each of the computer pixels that make up an individual patch is allocated a value representing the arithmetic mean of all the pixel values of our shrub index within a patch.

We assessed linear and restricted cubic spline models of the natural-log transformed and non-transformed patch area variable, controlling for the mean shrub cover in each patch. The transformation of the patch area variable was attempted to compress the range of values for this variable because it is highly discretized with substantial continuous-numeric-scale gaps in the range of values; all used or available samples that fall in the same patch have the same value. One of our 13 models which had 5 knots for a restricted cubic spline term was unable to be fitted using the rms library in R.

Model Evaluations

The assessment of nest-site model predictive ability was implemented following C. J. Johnson et al. (2006) which is an extension of methods proposed by Boyce et al. (2002). First we split the response data into five nearly equal datasets and then fit the data in 4 out of five sets to our model averaged RSF model, leaving 1 of 5 datasets as a validation dataset. We did this for five possible permutations of training versus validation datasets. To make the comparison between the nest-site predictions and the nest-site validation datasets we created five predictive surfaces in QGIS and reclassified the raw RSF scores into 9 equally
spaced bin intervals, plus a larger bin interval to capture the more rare maximum range of predictions. This resulted in 10 bins altogether. We restricted the validation analysis to the nest-site definition of availability which had constrained our sampling to a half kilometer radius around each nest. For inference regarding predictive performance and validity of the nest-site RSF we used statistics from an ordinary linear regression of the area-weighted expected utilization proportion versus the proportion of observed use in each of the ten bins. To further examine the correspondence between predicted and observed values of use we performed a Spearman rank-based correlation on these proportions as well as a goodness-of-fit $\chi^2$ test. For the $\chi^2$ test we used the observed counts in each bin and compared them to the expected proportions based upon the bin utilization value $U(x_i) = w(x_i)A(x_i)/\sum_j w(x_j)A(x_j)$ where $w(x)$ is the midpoint value for a bin interval and $A(x)$ is the area of a particular bin (C. J. Johnson et al. 2006; Boyce and L. L. McDonald 1999).

Similar cross-validation methods as described above were used to determine that the highest ranked and overwhelmingly supported nesting-region model had horrendous predictive ability. This was partially attributed to an anomalously good fit of the roads variable. It was deemed biologically unrealistic that nesting sage-grouse behavior was responsible for the observed affinity for nesting in close proximity to roads. There appears to be a confounding relationship between roads and high quality sagebrush stands in our study area. All models containing the roads variable were eliminated from the model set due to this biologically unrealistic association with the response variable, which compromised model predictive ability. Here we relied upon the strategy of consulting both cross validation and AIC$_c$ model support to identify a well-supported model that also had sound predictive ability. The highest AIC$_c$
ranked model after elimination of all models containing the roads variable was a similarly structured model, with the same grain size. It became evident that the prior issue—a biologically unrealistic association between a covariate and a response variable—had not been eliminated. In this new context the water variable played a similar role. The lack of biological realism regarding the association between 1730-m proximity to water and nest occurrence is not as certain as is the case with proximity to roads. However, our interpretation is that both water and roads follow paths along the mild topographic gradients of the valley bottoms. For this reason they are both confounded with productive sagebrush flats, given the nesting-region definition of use and availability. Furthermore, many of the nests from our sample were in a habitat patch adjacent to a large residential region where roads, irrigation, and landscaping ponds are abundant. This region has one of the highest areal densities of these two covariates within our study area.

Models containing the water variable were also eliminated from the model set. Though permanent water supplies can be an important resource for sage-grouse during dry conditions, nesting sage-grouse can generally obtain water from rain events, vegetation, and dew. There exists evidence from prior research that persistent open water can be negatively associated with nest survival. Inclusion of this variable was prompted by the hypothesis that sage-grouse would avoid nesting near high animal traffic areas adjacent to water sources, such as ponds or irrigation ditches. Other species such as foxes, coyotes and bison may converge to drink at such water sources. We also hypothesized that sage-grouse would avoid nesting near edge habitat created by riparian systems (correlated with water) due to increased risk from more diverse predator assemblages and activities at habitat edges. We expected either
a neutral or avoidance signature with respect to the water variable. Our analysis indicates an affinity for nesting near open water and we interpret this as biological indifference masked by a confounding relationship with suitable sagebrush stands, at the nesting-region scale of analysis, particularly for the 1730-m grain size.

We re-ran the analysis with roads and water excluded from the candidate model set. The highest AIC$_c$ ranked model was still of the 1730-m grain size and also had overwhelming support. This indicated that while the roads and water variables were culprits in producing the anomalously strong model fits there was something about the 1730-m grain size that resulted in strong model fits. This third attempt at identifying a model with sound predictive performance also produced a non-linear RSF with poor predictive performance. This was established with cross-validation. This third nesting-region scale model was rejected and a model with good predictive performance was identified by performing a final 5-fold cross validation on the next highest AIC$_c$ ranked model.

A 5-fold cross validation was also performed for the top nesting-patch scale model which led to the rejection of this highest AIC$_c$ ranked model in the nesting-patch model set. A model with acceptable cross-validation results was identified by cross-validating lower AIC$_c$ ranked models.

**Single-Scale and Conditional Nesting-Habitat Selection**

To map out the predictions from our three RSF models we entered the fitted RSF equation into the QGIS raster calculator module. This GIS operation used the values of our covariates for every pixel in the study area to calculate an RSF prediction for each pixel. This produced
three RSF surface maps.

Our nest-site and nesting-region RSF models employed hierarchical sampling so that these two surfaces could be combined into a single scale-integrated conditional RSF (SRSF) surface (DeCesare et al. 2012). This SRSF was then weighted by the relative probability of selecting a patch in order to calibrate the SRSF by incorporating additional information about nesting-patch selection. Conceptually this was accomplished as follows: $P(\text{nesting-patch}) \times P(\text{nesting-region}) \times P(\text{nesting-site} \mid \text{nesting-region})$. The distinction between weighting an RSF by multiplying it by another RSF and multiplying two RSF’s together to create a conditional RSF (SRSF) is dependent upon how use and availability, or unused samples are taken. In this case the nesting-patch model was sampled in such a way as to represent a variation of the same scale of sampling as for the nesting-region model. The nesting-patch model employed an unconstrained sampling design for available samples but used samples were taken as the actual nest locations. For this reason the nesting-patch model cannot be considered a distinct third hierarchy of nesting-habitat selection.

RESULTS

Nesting Data

We acquired accurate locations of 69 nests from 2007-2010. In 2007 we located 11 nests; in 2008, 30 nests; in 2009, 19 nests; and 9 nests in 2010. Of these 69 nesting attempts, many were not initiated by a unique individual. We monitored 13 individuals that provided 1 nest, 14 provided 2 nests, 8 provided 3 nests, and 1 provided 4 nests. In total we acquired at least
1 accurate nest location from 36 individuals.

Nesting-Site Scale Resource Selection

The top model in the nesting-site model set was of the 20-m grain size. The veg-GSGI variable had the most support among variables considering that no comparison with our shrub index can be made because it was in all 1,794 models (Table 1). The second most well-supported variable was the ruggedness index, with all other variables contributing similarly to the support for any given model. It should be noted that the bitterbrush index was at a disadvantage in this comparison due to the need for an extra degree of freedom for a binary indicator variable, in addition to the continuous bitterbrush term. The shadow variable (perching substrate proxy) had one less degree of freedom than desired for the balanced design due to numerical estimation issues with a model which necessitated the removal of a restricted cubic spline knot. The support for any given model systematically decreased with the radius (grain size) of the sampling polygons within which the average of 1-m pixels was

Table 1: Nesting-site relative variable importance: number of models out of the total 1,794 models (n) containing each covariate with the corresponding number of degrees of freedom (df) and small sample corrected Akaike’s information criterion model weights ($w_i$), summed up by covariate, for Jackson Hole, Wyoming, USA, 2007-2010.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>models (n)</th>
<th>sum(df)</th>
<th>sum($w_i$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>shrub</td>
<td>1794</td>
<td>10685</td>
<td>1.000</td>
</tr>
<tr>
<td>veg-ExG</td>
<td>494</td>
<td>2964</td>
<td>0.210</td>
</tr>
<tr>
<td>veg-GSGI</td>
<td>494</td>
<td>2964</td>
<td>0.544</td>
</tr>
<tr>
<td>ruggedness</td>
<td>663</td>
<td>3978</td>
<td>0.437</td>
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<td>water</td>
<td>663</td>
<td>3978</td>
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</tr>
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<td>roads</td>
<td>663</td>
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<td>0.287</td>
</tr>
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<td>663</td>
<td>4251</td>
<td>0.283</td>
</tr>
</tbody>
</table>
calculated for each covariate (Fig. 2).

Our highest ranked model:

\[ X^*: X \text{ odds ratio} = \frac{\exp(X^*\hat{\beta})}{\exp(X\hat{\beta})}, \text{ where} \]

\[ X\hat{\beta} = -6.663492 + 0.07131386 \text{ Atmean} + 0.01873871 \text{ GSGImean} \]

did not possess a substantial weight of evidence as compared to many of the competing models. For this reason we model averaged over the top 52 models chosen with the model

Figure 2: Boxplots of ΔAICc values for 138 nest-site models for each of 13 grain sizes, for Jackson Hole, Wyoming, USA, 2007-2010. ΔAICc is the difference between the model with the lowest small sample corrected Akaike’s information criterion (AICc) and any other model.
likelihood ratio confidence set as discussed above. This confidence set of models and associated AIC_\text{c} statistics are tabulated in appendix F. The model averaging was implemented for making predictions only. For making inference we relied solely on the top ranked model.

The odds ratio is the factor by which the odds of nesting-site use changes from one specified set of values for the X variables relative to the odds of use given alternative values of the X variables (X^*). A value of 1 indicates no change. The bootstrap-based 95th percentile confidence interval for the shrub variable odds ratio nearly overlapped 1, but did not. The odds ratio confidence intervals for the veg-GSGI variable did overlap 1. The odds ratio confidence intervals give the range of values that the actual odds ratio could be with 95% confidence. The highest ranked model had an odds ratio for shrub of 1.57 given an increase in shrub cover from 22.75 to 29.00 and adjusting for veg-GSGI. Adjusting for shrub cover and increasing veg-GSGI from 65.65 to 89.9 yielded an odds ratio of 1.54. Both odds ratios indicate an increasing probability of nest occurrence with increasing values of the covariates (Table 2). The range that we used for computing the odds ratios were the upper and lower quartiles of the distribution of a given predictor.

Table 2: Highest small sample Akaike’s information criterion (AIC_\text{c}) ranked nesting-site model estimates with bootstrap standard errors and percentile confidence intervals, for the effects and the odds ratios, for Jackson Hole, Wyoming, USA, 2007-2010. The rows labeled with the variable names provide the change in the log odds for a specified change in the predictor.

<table>
<thead>
<tr>
<th></th>
<th>Low</th>
<th>High</th>
<th>Δ</th>
<th>Effect</th>
<th>S.E.</th>
<th>Lower 0.95</th>
<th>Upper 0.95</th>
</tr>
</thead>
<tbody>
<tr>
<td>shrub</td>
<td>22.752</td>
<td>29.078</td>
<td>6.3258</td>
<td>0.45111</td>
<td>0.26985</td>
<td>0.065485</td>
<td>1.1270</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>22.752</td>
<td>29.078</td>
<td>6.3258</td>
<td>1.57010</td>
<td>1.067700</td>
<td>2.6068</td>
<td></td>
</tr>
<tr>
<td>veg-GSGI</td>
<td>65.650</td>
<td>88.918</td>
<td>23.2670</td>
<td>0.43600</td>
<td>0.29014</td>
<td>-0.187110</td>
<td>0.9581</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>65.650</td>
<td>88.918</td>
<td>23.2670</td>
<td>1.54650</td>
<td>0.829350</td>
<td>2.6068</td>
<td></td>
</tr>
</tbody>
</table>

The RSF plots from the highest AIC_\text{c} ranked model indicate that sage-grouse nest oc-
occurrence is positively associated with both shrub cover and greener regions of the study area (Fig. 3).

Figure 3: Relative probability of nest occurrence from highest Akaike’s information criterion ranked—corrected for small sample size (AICc)—nest-site model, Jackson Hole, Wyoming, USA, 2007-2010. Shrub index values of the 20-m grain size are varied while holding veg-GSGI constant at its median, and visa-versa. The confidence intervals are basic bootstrap intervals calculated from the 10,000 bootstrap estimates.

The 5-fold cross validation indicated that the model averaged predictions from the 90% confidence set nest-site model had good predictive performance. The linear model that was fit by regressing the observed proportions on the area adjusted expected proportions from 10 RSF bins (Fig. 4) had the following properties: (1) the intercept was not significantly different from 0; (2) the slope was significantly different from 0 but not significantly different from 1; (3) the coefficient of determination indicated a fair regression fit; (4) the Spearman rank-based correlation confirmed strong correspondence between observed and expected proportions.
Figure 4: Plot of observed and expected proportions of nests falling in each of 10 nest-site RSF raw-value bins, for top nest-site model, Jackson Hole, Wyoming, USA, 2007-2010. The dark line represents the fitted regression line and the dotted line represents a theoretical perfect fit. The light solid line indicates the worst possible fit where use is proportional to availability and the RSF has zero predictive ability. A Spearman rank correlation is provided for further examination of the association between observed and expected values. The expected proportions are based on bin utilization values, as defined here: \( U(x_i) = w(x_i)A(x_i)/\sum_j w(x_j)A(x_j) \) where \( w(x) \) is the midpoint value for a bin interval and \( A(x) \) is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0–1.
Nesting-Region Scale Resource Selection

The highest correlation among covariates was between our shrub index and the veg-ExG index. These two variables were inversely related. For our nesting-region model the correlation between the two consistently rose from \( r = -0.47 \) at the 20-m grain to \( r = -0.70 \) at the 2119-m grain. All other variables were less correlated than this; the variance inflation factors (VIF) for all parameters in all linear models were far below 5, typically in the range 1–2.

The model that will be used for making inferences and predictions was chosen using the criteria that it firstly be predictive and secondly have the highest AIC \(_c\) ranking, excluding models with poor predictive performance. The first stipulation necessitated the removal of models that included the roads or water variables. Given this reduced model set, the AIC \(_c\) support for a given grain size steadily increased from 20 – 769 m. After this minimum in \( \Delta \text{AIC}_c \) values the trend changed to that of declining support (increasing \( \Delta \text{AIC}_c \) values) with increasing grain size. Despite this trend there was a model in the 1730-m grain size with greater support than any models in the 769-m model set (Fig. 5). This model also had poor predictive performance and was rejected.

The general shape of the curve created by the boxplots remained the same after models with the roads variable were removed. The same is true after removal of all models with the water variable. This indicates that these variables did not dictate the trend of support with increasing grain size, though they dramatically enhanced the fit of the largest grain size models, particularly at the 1730-m grain size. Multiple-boxplot plots of grain size against \( \Delta \text{AIC}_c \) for the model sets with both roads and water variables included, and just the roads
variable removed, are presented in appendix E. Included in the same section of appendix E are the results of the 5-fold cross validation of the top models when roads and water, or just water, were retained in the model set. These plots illustrate that the poor predictive performance of the initial highest AIC\textsubscript{c} ranked models was due largely to the roads and water variables.

The highest AIC\textsubscript{c} ranked nesting-region model that had good predictive ability included restricted cubic spline terms for shrub, ruggedness, and shadows. It is structured as follows:

\[
X^* \cdot \text{X odds ratio} = \frac{\exp(X^*\hat{\beta})}{\exp(X\hat{\beta})}, \quad \text{where}
\]

\[
X \hat{\beta} =
\]

\[
-12.13853 \\
+0.6041303 \text{shrub} - 0.002439096 (\text{shrub} - 3.07011) \text{\_}\text{\_} \\
+0.008247342 (\text{shrub} - 11.02345) \text{\_}\text{\_} - 0.01010609 (\text{shrub} - 17.10809) \text{\_}\text{\_} \\
+0.005394744 (\text{shrub} - 22.00504) \text{\_}\text{\_} - 0.001096895 (\text{shrub} - 26.65833) \text{\_}\text{\_} \\
-0.1766529 \text{ruggedness} + 0.000921223 (\text{ruggedness} - 3.036928) \text{\_}\text{\_} \\
-0.001331587 (\text{ruggedness} - 7.716957) \text{\_}\text{\_} + 0.0004463298 (\text{ruggedness} - 23.12779) \text{\_}\text{\_} \\
-3.596576 \times 10^{-5} (\text{ruggedness} - 79.08941) \text{\_}\text{\_} \\
+0.0442253 \text{shadows} - 1.117763 \times 10^{-6} (\text{shadows} - 34.6268) \text{\_}\text{\_} \\
+1.727124 \times 10^{-6} (\text{shadows} - 104.9531) \text{\_}\text{\_} - 6.100472 \times 10^{-7} (\text{shadows} - 234.5004) \text{\_}\text{\_} \\
+6.86495 \times 10^{-10} (\text{shadows} - 719.2811) \text{\_}\text{\_}
\]
where \((x)_+ = x\) if \(x > 0\), 0 otherwise. The odds ratio is the factor by which the odds of nesting-region use changes from one specified set of values for the \(X\) variables relative to the odds of use given alternative values of the \(X\) variables \(\left(X^*\right)\).

The nesting-region model had an odds ratio for shrub of 2.09 given an increase in 769-m shrub cover from 10 to 20. Increasing ruggedness from 3 to 30 yielded an odds ratio of 0.27. The odds-ratio for a change in distance-to-shadow from 50 m to 300 m was 2.82. None of these odds ratios overlap 1. The confidence intervals were based on nonparametric bootstrap percentile intervals that used a bootstrap covariance matrix derived from 10,000 bootstrap estimates (Harrell 2015; R Core Team 2013) (Table 3).

The 5-fold cross-validation regression for this model indicates that the intercept is significantly different from 0. The slope is also significantly different from 0 and is different

\[ \text{delta AICc} \]

Figure 5: Boxplots of \(\Delta\text{AIC}_c\) values from 39 nesting-region models for each of 24 grain sizes, for Jackson Hole, Wyoming, USA, 2007-2010. \(\Delta\text{AIC}_c\) is the difference between the model with the lowest small sample corrected Akaike’s information criterion (\(\text{AIC}_c\)) and any other model.
from 1 (Fig. 6). The difference of the slope from 1 and intercept from 0 indicates a degree of non-proportionality to the probability of use. The coefficient of determination indicates that the model’s predictions are reasonable $R^2 = 0.9$. The Spearman rank-based correlation also indicates a strong trend of correspondence between observed and expected proportions of use in each bin ($r_s = 0.99, p \approx 0$). The chi-squared goodness-of-fit test indicates a poor overall agreement of observed and expected values ($\chi^2 = 149, df = 19, p \approx 0$).

There was a lack of precise correspondence between observed and expected counts, though the general trend of correspondence was strong. The highest levels of expected use are greater than what was observed. If prudence is exercised when interpreting high-use predictions, this RSF has utility for mapping predictions of sage-grouse nesting-region selection in Jackson Hole.

The nuanced curves afforded by the spline terms for the shrub index, as demonstrated by the local maximum near 12, were likely to have no biological relevance (Fig. 7). The focus of interpretation should be restricted to the general pattern. Nesting-region selection begins to increased starting at a shrub cover index of $\approx 5$. It remained low until a value of $\approx 17$ at which point it increased rapidly as the shrub index increased to $\approx 32$.

The relationship between the relative probability of nesting-region use and the shadow variable also exhibits some nuances. There is a precipitous increase of the relative probability as distance increases from 0 m to around 200 m. At this point the relative probability steadily drops all the way back down near zero, as the distance from shadows increases out to around 1400 m. As the RSF curve nears a maximum at around 200 m the uncertainty spikes and remains high, but with a slight taper, as distance from shadows increases (Fig. 8).
Figure 6: Cross-validation plot from selected nesting-region model. Provided are observed and expected proportions of nesting region use samples falling in each of 20 RSF raw-value bins. The dark line represents the fitted regression line and the dotted line represents a theoretical perfect fit. The light solid line with a slope of zero indicates the worst possible fit where use is proportional to availability and the RSF has zero predictive ability. A Spearman rank correlation and overall goodness-of-fit are provided for further examination of the association between observed and expected values. The expected proportions are based on bin utilization values, as defined here: \( U(x_i) = w(x_i)A(x_i) / \sum_j w(x_j)A(x_j) \) where \( w(x) \) is the midpoint value for a bin interval and \( A(x) \) is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0 to 1.
Figure 7: Relative probability of nesting-region selection from highest small sample corrected Akaike’s information criterion (AICc) nesting-region model, Jackson Hole, Wyoming, USA, 2007-2010. The RSF values are calculated varying our shrub index and holding shadows and ruggedness at their median values. The confidence intervals are basic bootstrap intervals calculated from the 10,000 bootstrap estimates.
Figure 8: Relative probability of nesting-region selection from highest Akaike’s information criterion ranked—corrected for small sample size (AICc)—nest-site model, Jackson Hole, Wyoming, USA, 2007-2010. The RSF values are calculated varying distance to shadows and holding shrub and ruggedness at their median values. The confidence intervals are basic bootstrap intervals calculated from the 10,000 bootstrap estimates.
Figure 9: Relative probability of nesting-region selection from highest small sample corrected Akaike’s information criterion ($AIC_c$) ranked model, after eliminating models with poor predictive performance, Jackson Hole, Wyoming, USA, 2007-2010. The RSF values are calculated varying terrain ruggedness and holding shrub and shadow at their median values. The confidence intervals are basic bootstrap intervals calculated from the 10,000 bootstrap estimates.

The relative probability of nesting occurrence declined steeply as the rescaled terrain ruggedness index increased from 0 to around 12. From 12 to 25 the RSF values began to increase slightly. After an RSF value of 25 the curve steeply declined again (Fig. 9).
Table 3: Estimates for highest small sample Akaike’s information criterion ($AIC_c$) ranked nesting-region selection model, after eliminating models with poor predictive performance. The rows labeled with the variable names provide the change in the log odds for a specified change in the predictor. Estimates are provided with bootstrap standard errors and percentile confidence intervals, for the change in the log odds and the odds ratios, for Jackson Hole, Wyoming, USA, 2007-2010.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Low</th>
<th>High</th>
<th>Δ</th>
<th>Effect</th>
<th>S.E.</th>
<th>Lower 0.95</th>
<th>Upper 0.95</th>
</tr>
</thead>
<tbody>
<tr>
<td>shrub</td>
<td>10</td>
<td>20</td>
<td>10</td>
<td>0.74</td>
<td>0.13</td>
<td>0.50</td>
<td>1.00</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>10</td>
<td>20</td>
<td>10</td>
<td>2.09</td>
<td></td>
<td>1.65</td>
<td>2.72</td>
</tr>
<tr>
<td>ruggedness</td>
<td>3</td>
<td>30</td>
<td>27</td>
<td>-1.30</td>
<td>0.10</td>
<td>-1.51</td>
<td>-1.11</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>3</td>
<td>30</td>
<td>27</td>
<td>0.27</td>
<td></td>
<td>0.22</td>
<td>0.33</td>
</tr>
<tr>
<td>shadow</td>
<td>50</td>
<td>300</td>
<td>250</td>
<td>2.82</td>
<td>0.17</td>
<td>2.51</td>
<td>3.16</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>50</td>
<td>300</td>
<td>250</td>
<td>16.70</td>
<td></td>
<td>12.32</td>
<td>23.48</td>
</tr>
</tbody>
</table>
Nesting-Patch Scale Resource Selection

Of the 13 nesting-patch models that were fit, the untransformed linear model and the natural-log transformed linear model had the least support. The addition of the variable giving the average shrub cover in each patch (MeanShrub) improved model fits. The model with a restricted cubic spline term with 3 knots on PatchArea and 4 knots on MeanShrub had the highest Akaike weight \( w_{AIC_c} = 0.41 \), see Table 5. This model did not cross-validate well so ultimately a different model was chosen by cross-validation of models with slightly lower AIC support. The model chosen for making inference had a restricted cubic spline term with 3 knots on PatchArea and included the MeanShrub term.

This fitted model is specified as follows:

\[
X^*: X \text{ odds ratio} = \frac{\exp(X^*\hat{\beta})}{\exp(X\hat{\beta})}, \quad \text{where}
\]

\[
X\hat{\beta} =
\]

\[
-13.28788
\]

\[
+3.490508 \text{PatchArea} - 28.14443 (\text{PatchArea})^3
\]

\[
+28.23939 (\text{PatchArea} - 0.01398574)^3 - 0.09496626 (\text{PatchArea} - 4.158833)^3
\]

\[
+0.2313495 \text{MeanShrub}
\]

and \((x)_+ = x \text{ if } x > 0, \text{ 0 otherwise.} \) PatchArea is pre-transformed as \log(\text{PatchArea} + 1)\).
Table 4: Highest small sample corrected Akaike’s information criterion ranked nesting-patch selection model estimates with bootstrap standard errors and percentile confidence intervals, for the log odds and the odds ratios, for Jackson Hole, Wyoming, USA, 2007-2010. The rows labeled with the variable names provide the change in the log odds for a specified change in the predictor. Patch area (Area) was transformed as ln(Area+1) where Area had units of km².

<table>
<thead>
<tr>
<th></th>
<th>Low</th>
<th>High</th>
<th>Δ</th>
<th>Effect</th>
<th>S.E.</th>
<th>Lower 0.95</th>
<th>Upper 0.95</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (transformed)</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>1.08</td>
<td>0.27</td>
<td>0.71</td>
<td>1.77</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>2.94</td>
<td>2.03</td>
<td>5.87</td>
<td></td>
</tr>
<tr>
<td>MeanShrub</td>
<td>10</td>
<td>20</td>
<td>10</td>
<td>2.31</td>
<td>0.58</td>
<td>1.20</td>
<td>3.46</td>
</tr>
<tr>
<td>Odds Ratio</td>
<td>10</td>
<td>20</td>
<td>10</td>
<td>10.11</td>
<td>3.32</td>
<td>31.96</td>
<td></td>
</tr>
</tbody>
</table>

The odds ratio is the factor by which the odds of nesting-patch use changes from one specified set of values for the X variables relative to the odds of use given alternative values of the X variables ($X^*$).

The patch area and the MeanShrub covariates have odds ratios that do not overlap 1. This indicates that differential use relative to what was available was not due to random chance alone. The odds ratio for the patch area variable indicates that the odds of patch-use increases approximately three-fold between a patch $e^{1−1} \approx 1.7$ km² and $e^{4−1} \approx 54$ km² in area. The MeanShrub odds ratio indicates that a patch with 20% average cover is 10 times more likely to be utilized for nesting than a patch with 10% average cover (Table 4).

The nesting-patch model exhibits steeply increasing RSF values from non-patches (area zero) up to the maximum patch area (Fig. 10). The maximum patch area in our study area was 62 km². When 1 is added and the natural log is taken this corresponds to a transformed value of 4.16. For this model, the magnitude of the RSF values increase asymptotically with patch area and appear to interact with MeanShrub, see the 3-D wireframe plot in appendix G.
Table 5: AIC<sub>c</sub> support, and related metrics, for the nesting-patch scale models for Jackson Hole, Wyoming, USA, 2007-2010. Area is the patch area in km<sup>2</sup> where non-patch pixels had a area of zero. MeanShrub is our shrub index averaged over entire patches. As an example, rcs(MeanShrub, 3) represents a restricted cubic spine term, with 3 knots, fit to the patch-average shrub index values.

<table>
<thead>
<tr>
<th>model</th>
<th>IL</th>
<th>k</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>∆AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;AIC&lt;sub&gt;c&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>-481.52</td>
<td>2</td>
<td>967.03</td>
<td>197.91</td>
<td>0.00</td>
</tr>
<tr>
<td>log(I(Area + 1))</td>
<td>-470.80</td>
<td>2</td>
<td>945.59</td>
<td>176.47</td>
<td>0.00</td>
</tr>
<tr>
<td>rcs(log(I(Area + 1)), 3)</td>
<td>-391.15</td>
<td>3</td>
<td>788.31</td>
<td>19.18</td>
<td>0.00</td>
</tr>
<tr>
<td>rcs(log(I(Area + 1)), 4)</td>
<td>-391.57</td>
<td>3</td>
<td>789.14</td>
<td>20.02</td>
<td>0.00</td>
</tr>
<tr>
<td>Area + MeanShrub</td>
<td>-392.63</td>
<td>3</td>
<td>791.26</td>
<td>22.14</td>
<td>0.00</td>
</tr>
<tr>
<td>log(I(Area + 1)) + MeanShrub</td>
<td>-393.11</td>
<td>3</td>
<td>792.22</td>
<td>23.09</td>
<td>0.00</td>
</tr>
<tr>
<td>rcs(log(I(Area + 1)), 3) + rcs(MeanShrub, 4)</td>
<td>-379.56</td>
<td>5</td>
<td>769.12</td>
<td>0.00</td>
<td>0.41</td>
</tr>
<tr>
<td>rcs(log(I(Area + 1)), 4) + rcs(MeanShrub, 3)</td>
<td>-379.93</td>
<td>5</td>
<td>769.87</td>
<td>0.74</td>
<td>0.28</td>
</tr>
<tr>
<td>rcs(log(I(Area + 1)), 3) + MeanShrub</td>
<td>-381.51</td>
<td>4</td>
<td>771.02</td>
<td>1.90</td>
<td>0.16</td>
</tr>
<tr>
<td>rcs(log(I(Area + 1)), 4) + MeanShrub</td>
<td>-381.54</td>
<td>4</td>
<td>771.09</td>
<td>1.97</td>
<td>0.15</td>
</tr>
<tr>
<td>log(I(Area + 1)) + rcs(MeanShrub, 4)</td>
<td>-390.69</td>
<td>4</td>
<td>789.39</td>
<td>20.26</td>
<td>0.00</td>
</tr>
<tr>
<td>log(I(Area + 1)) + rcs(MeanShrub, 3)</td>
<td>-390.55</td>
<td>4</td>
<td>789.10</td>
<td>19.98</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Figure 10: Plot of raw RSF values from patch-scale model, as a function of the natural log of patch area, for Jackson Hole, Wyoming, USA, 2007-2010. A value of 1 km<sup>2</sup> was added to the patch areas before the log was taken to prevent negative values and undefined values at ln(0). The RSF values are plotted for varying values of patch area at three constant values of average shrub cover (MeanShrub). The confidence intervals are basic bootstrap intervals calculated from 10,000 resamples.
Figure 11: Plot of observed and expected proportions of nests falling in each of 5 RSF raw-value bins. The dark line represents the fitted regression line and the dotted line represents a theoretical perfect fit. The light solid line with a slope of zero indicates the worst possible fit where use is proportional to availability and the RSF has zero predictive ability. A Spearman rank correlation is provided for further examination of the association between observed and expected values. The expected proportions are based on bin utilization values, as defined here: \( U(x_i) = w(x_i) A(x_i) / \sum_j w(x_j) A(x_j) \) where \( w(x) \) is the midpoint value for a bin interval and \( A(x) \) is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0–1.

The 5-fold cross-validation regression for this model indicates that the intercept is not significantly different from 0. The slope is significantly different from 0 and only slightly different from 1 (Fig. 11). The coefficient of determination indicates that the model’s predictions are strong, \( R^2 = 0.98 \). The Spearman’s rank-based correlation also indicates a strong trend of correspondence between observed and expected proportions of use in each bin, \( r_s = 0.95, p \approx 0 \). The general trend of correspondence was strong and clearly positive with little evidence that the model estimates were not proportional to the probability of use.
Single-Scale and Scale-Integrated Habitat Mapping

The nesting-patch RSF predictions for the study area are displayed in figure 12. For this RSF the areas inside the rounded availability sampling extents represent predictions that are not spatially extrapolated. All areas outside these polygons display predictions that are spatial extrapolations.

The nesting-region RSF predictions are displayed in figure 13 and the nesting-site RSF predictions are displayed in figure 14. Figure 15 maps out the scale-integrated relative probability of nesting-habitat selection in Jackson Hole.
Figure 12: The highest AIC$_c$ ranked nesting-patch model calculated from the patch area and shrub-index patch average for every pixel within the study area extent, Jackson Hole, WY, USA. Nesting occurrence data collected 2007-2010. Progressively higher bin intervals represent progressively higher relative probabilities of nesting-patch use by sage-grouse for nesting.
Figure 13: The highest $\text{AIC}_c$ ranked nesting-region RSF, that cross validated well, calculated from 769-m grain shrub, ruggedness, and shadows within the study area extent of Jackson Hole, WY, USA. Nesting occurrence data collected 2007-2010. The progressively higher bin intervals represent progressively higher relative probabilities of region use by sage-grouse for nesting. The circular polygons represent the sampling extent for used points for this scale of analysis; the polygons are 500-m buffers around all nests.
Figure 14: The AIC$_c$ model averaged nesting-site RSF calculated from 20-m grain shrub, ruggedness, veg-GSGI, veg-ExG, roads, water, shadows, and bitterbrush values for every pixel within the study area extent of Jackson Hole, WY, USA. Nesting occurrence data collected 2007-2010. Progressively higher bin intervals represent progressively higher relative probabilities of nesting-site use by sage-grouse. The circular polygons represent the extent of availability sampling which was defined as a 500-m buffer around all nests. Note that some high RSF values are spatial extrapolations which are typically owing to high vegetation index values in wetlands and irrigated fields, where no nesting was observed.
Figure 15: Weighted conditional relative probability RSF (i.e., scale-integrated RSF, SRSF) for Jackson Hole, WY, USA. Nesting occurrence data collected 2007-2010. The nesting-patch, nesting-region, and nesting-site RSF were multiplied together to produce this SRSF. Progressively higher bin intervals represent progressively higher relative probabilities of nesting occurrence for sage-grouse. The circular polygons represent the 500-m buffers, around all nests, that were used to define the extent of use and availability for the nesting-region and nesting-site analysis scales, respectively.
DISCUSSION

Grain-Spectrum Approach, Pros and Cons

A potential deficiency of our modeling strategy is that we did not allow multi-grain models to compete in our model sets. This was because the permutations of multi-grain models for a relatively comprehensive grain-spectrum would be unmanageably large. It is often the case that multi-grain RSF’s outperform single-grain RSF’s, particularly for unconstrained sampling designs of use-availability, where the entire study area is all that constrains availability. The fact that we employed a constrained hierarchical design may alleviate the need for inclusion of multi-grain RSF’s because the selection signature is more restricted to the specific scale of analysis, which should diminish the variety of grains that affect nesting-occurrence for a given scale (C. B. Meyer and Thuiller 2006). However, despite employing a hierarchical use-availability design, Aldridge et al. (2012) had many multi-grain landscape-scale models in their AIC<sub>c</sub>-based 90% confidence set, developed for Gunnison Sage-Grouse nesting.

Presently there are many trade-offs that must be considered when structuring statistical modeling designs. A universal methodology is not available and multi-grain models may enhance model fit and predictive performance but do not address the subjective nature of grain-size choices. Our grain-spectrum approach identified selected models where all the variables fit relatively well at a single highest ranked grain size. The overall fit of the top-grain models could be due to a highly influential covariate at the top grain, a decent fit of a number of variables at the top grain, or both. Whatever the case, well-fitting grain-size variable combinations are identified. This is not guaranteed when only a handful of grain sizes are chosen as initial variables.
Another benefit of this approach is that only a single grain-size needs to be mentioned when making an inference from a chosen model; inferences from all variables (parameter estimates) apply to one scale-grain combination. For our case this was true even when employing model averaging, but conceivably a 90% confidence set could include models of different grain-sizes.

This highlights an equally crucial advantage of the grain spectrum approach. Models that fit a researcher’s data well are of marginal interest in resource selection or habitat suitability research. In this context statistically significant results are as readily attainable as colorful eggs during an Easter egg hunt. This is because the distribution of organisms is rarely random with respect to ecogeographical gradients (Boyce et al. 2002). Of interest is what the disproportionate use of resources or sensitivity to perceived risk gradients can tell us about the possible underlying mechanisms that cause these signatures to manifest. For resource selection signatures to lead us to an understanding of these mechanisms we must eliminate as many sources of subjectivity as possible in order to home in on multiple comparable findings that allow consistent patterns to be rendered. The comparisons that can be made with similar research are limited by the fact that from study to study the same grain sizes have not been included in model selection procedures. If evidence for the importance of a particular grain-size was documented in Study A but it was not included in the analysis for Study B nothing can be said about whether or not it was important in both studies, therefore little can be said about whether it is important in general.
Multiple Benefits of Developing High-Resolution Covariates

It is typical for GIS data to be selected because they are easy to process, or they have already been pre-processed for a purpose that aligns poorly with the spatial or temporal context of a researcher’s objectives. While this is partly unavoidable due to trade offs with project resources, we believe that spatially-explicit research designs could greatly benefit from a greater allocation of resources to the synthesis of biologically realistic covariates.

Strategies for covariate synthesis and/or acquisition can influence grain-size options, limiting choices, and potentially compromising the appropriateness of covariates used in spatially-explicit research. With advancements in computer processing capabilities, analysis methods, and developments in remote sensing acquisition technologies, the sophistication of covariate synthesis should continue to progress. The rate at which it progresses does not seem to keep pace with wildlife statistical modeling and analysis methodologies. Book titles representing the adoption and development of statistical analysis methods with wildlife ecology applications can fill bookshelves (e.g., Amstrup et al. (2005), Burnham and Anderson (2002), Hosmer et al. (2013), Manly et al. (2007), and Williams et al. (2002)), yet the fundamental assumption of unbiased and accurate explanatory data is almost never convincingly addressed.

The less detailed and reliable the information in ecological explanatory variables the less confidence we can have in observed associations between explanatory and response variables which may describe some component of a species’ functional habitat. Categorical spatial variables do not reconcile well with reality in many wildlife research contexts. This is particularly true for purely empirical research where the categories do not represent carefully
manipulated treatments, or well-delineated zones of disturbance. While statistical associations with these types of variables are commonly documented, it is difficult to reason exactly what these associations mean in an on-the-ground biological sense. All of our covariates were generated from detailed and relatively accurate data on a continuous numeric scale to maintain realism when characterizing associations between used and available resources. All of our grain sizes were related to the original high-resolution data by systematic adjustments to the image frequency (smoothing with different window sizes) (Mather 2004; McGarigal and Cushman 2005).

In addition to preserving more information about the actual risk/reward gradients that sage-grouse may be responding to, our high-resolution covariates allowed us to explore how model support was affected by grain sizes along an extensive grain-spectrum, and we gained a number of insights. The highest AIC$_c$ ranked grain sizes roughly corresponded to the scale of analysis. The 20-m grain had the most support at the nest-site scale. The 769-m grain size was highly competitive for the nesting-region scale, after the water and roads variables were excluded from the analysis. This is because the 769-m grain size was no longer out-competed by the extraordinary fit of the water and roads variables models at the 1412-m and 1730-m grain sizes. Prior to excluding these variables, the 1730-m grain had far and away the most AIC$_c$ support at the nesting-region scale, but produced non-predictive models where roads and water dominated the selection signature.

This correspondence between grain and scale roughly matches general grain-choice recommendations and findings in the literature (Boyce 2006; C. B. Meyer and Thuiller 2006). Unfortunately this will not always be the case and will depend upon the species as well as
the way extent and grain are analyzed. For instance, the appropriate grain of measurement for a given variable will depend upon the way availability is constrained in an analysis. Additionally, there was a constant change in $\text{AIC}_c$ support with varying grain sizes. Without examining a comprehensive continuum of grain sizes (grain-spectrum) there would be no way to choose the grain that would best fit a statistical model. This is true even if previous research identified grain sizes that fit similar models well. A researcher could be off by a 50% increment in areal coverage from a chosen grain and end up making interpretations from a different model, regardless of the model or variable selection method used.

Grain-size choices affect model fits, model fits affect model rankings, and model rankings affect biological interpretations. If a model fits the data well, and the model is predictive, the model may be useful, but a substantially different model with a better fit may have been chosen if different grain-size choices were made. Formulating balanced model sets across the grain spectrum allowed us to assess individual covariate support independent of grain size. This helps identify associations that occur at the scale of analysis (sampling extent) but could be subdued or eliminated if a particular grain was not chosen as an initial variable. It seems best to examine the grain spectrum so there is a more complete picture of how grain-size influences model or covariate support.

Systematic data-driven approaches characterizing and identifying optimal grain sizes from the grain spectrum are an area that requires further research. Implicit here is the need for accurate and high-resolution spatially-explicit predictors (GIS data) for which the image spatial-scale (i.e., grain, image frequency) can be manipulated to produce a grain spectrum that derives from an ecogeographical reality. Exploratory landscape scale resource selection
research based on modeled GIS realities that only loosely correlate with theorized components of an animal’s functional habitat (niche) offer a treacherous and convoluted path to understanding and defining a functional habitat. We advocate for grain spectrum analyses that are derived from data with a strong correspondence to on-the-ground biological realities from the study area and that have some established ecological importance with respect to the research questions (e.g., survival, selection, movements). This necessitates the use of imagery with a sufficient spatial-resolution to provide the minimum grain-size of interest. If this approach were refined and consistently employed, the ability to make comparisons between research results would be greatly enhanced.

**Response to Shadow Variable (Perching Substrate Proxy)**

Despite some of the difficulties of comparing results from separate studies we will make an attempt to place our results in context. We tested for a response to nesting in proximity to trees and other tall objects at two scales (extents) of analysis. A well-supported shadow response signature was only identified at one scale of analysis. At the 769-m grain nesting-region scale Jackson Hole sage-grouse generally avoid nesting in direct proximity to tall objects, which are typically trees. This avoidance signature is lost at around a 200-m average distance to shadows. It is important to note that as the grain size increases the shadow variable represents more of a shadow density metric than a strict proximity metric. At average distances beyond 200-m we suspect that sage-grouse may no longer respond to trees. This signature of avoiding regions where there is a relatively high density of trees in the surrounding region is consistent with recent research linking trees in the sagebrush-steppe to both occurrence and survival of sage-grouse (Coates et al. 2017). A possible reason for this
behavior is an evolutionary pressure to be wary of tall objects due to increased predation
near perching substrates that could facilitate hunting by avian predators.

There was also an apparent avoidance of regions very far from trees. There were a
lack of nests observed in habitats furthest removed from trees. This is partly attributed to
the fact that the densest sagebrush stands, representing the most attractive habitat, were
located in areas with irrigation ditches. These irrigation ditches had facilitated the growth
of cottonwood trees. If we plot our nesting-region sample points on a map showing the
largest treeless expanses of sagebrush habitat, there is an indication that sage-grouse are
using regions closer to the edge of these patches than toward the middle. We observed
far fewer nests in these largest sagebrush patches—therefore there is less nesting-region use
there. This compromises our confidence in this apparent affinity for nesting nearer to patch
edges where mean distances to shadows are smaller. The data are relatively sparse for this
subset of nesting-region samples. This is indicated by the confidence intervals in Figure
8. Nevertheless, our results do indicate avoidance of the central portions of larger habitat
patches. There is a decline in the relative probability of nesting as the average distance from
shadows exceeds \(\approx 200 \text{ m}\) (Figure 8).

This patch-edge affinity or patch-core avoidance relationship is contrary to our expecta-
tion and we have no conjecture as to why this would occur. The results of previous research
indicate that there is greater raven abundance in regions adjacent to developed areas (Bui
et al. 2010) in our study area. Nest occurrence near patch edges where sagebrush meets res-
idential or industrial zones could confer lower fitness due to increased predator abundance.
However, such a dynamic may be ameliorated by the high sagebrush cover in the regions
that attracted the most nesting in our study area (Coates and Delehanty 2010).

Response to Topographic Ruggedness

The inferences garnered from our nesting-region and nesting-site models support the possibility that topographic characteristics may be an important component of the sage-grouse functional niche. The step-like shape to the plot of nesting-region RSF values against 769-m ruggedness (figure 9) was due to a few use regions being located in a portion of the study area containing glacial potholes; this area is characterized by undulating hills and large depressions. The selection signature for ruggedness indicates that Jackson Hole sage-grouse generally avoid rugged terrain at the 769-m grain for the nesting-region scale. They have a tolerance for rescaled ruggedness values (no meaningful unit of measure) between 12 and 25 but seem to avoid any more rugged terrain than that. In addition to being included in our nesting-region model, terrain ruggedness had a high relative importance based on the sums of Akaike weights for the nesting-site model set. Many of the models used in our 90% confidence set for the 20-m grain nesting-site scale contained the ruggedness variable.

Other sage-grouse nesting-occurrence researchers have also found support for inclusion of terrain metrics in RSF models at larger scales of analysis. For their landscape-scale model set, Aldridge et al. (2012) had a mean compound topographic index across a 1-km² radius moving window included in many of their AICc selected 90% confidence set models, including the highest ranked model. Another study employing GPS relocations of nesting females (Dzialak et al. 2011) had terrain roughness at a 90-m² grain included in their egg-laying and incubation RSF. Research in the Powder River Basin of Wyoming and Montana, by Doherty et al. (2010), produced a landscape-grain and landscape-scale RSF that retained
a 100-m radii (grain) roughness index. A roughness avoidance signature also of a 100-m grain size was reported for an isolated population in Colorado where the researches had assessed models with 7 other grain sizes, including one at 800 m (similar to our 769-m grain) (Walker et al. 2015). The definition of use and availability (scale) for these analyses does not perfectly correspond with our nesting-region or nesting-site RSF, but there is overlap. Using a somewhat different approach (Maximum Entropy modeling) with presence-only nesting data researchers identified a selection response signature associated with topographic slope derived from 10-m Digital Elevation Model (DEM) data.

In all cases the terrain-metric parameter estimates indicated avoidance of steep or dissected terrain at moderate to coarse grain sizes.

**Sagebrush is Established as a Component of the Functional Niche**

Given the distribution of shrubs in our study area, and the ways that we defined availability, the values of the shrub index strongly corresponded to sagebrush cover. The two can be thought of analogously. That is not to say that our shrub cover index fully matches the level of detail and accuracy attainable from field sampling (see appendix A) but that it performs nearly as well as a sagebrush index as it does a shrub index. Sagebrush was by far the most prolific shrub in the xeric shrubland zones to which our analysis was constrained by our availability mask.

Our results indicate that sagebrush cover is the fundamental driver of nesting habitat selection in our study area. This relationship that we assumed between sage-grouse nesting and sagebrush was confirmed by the sound fit of the shrub variable to the most well-supported and performing models at our three disparate scales of analysis. Only one research article
has recognized that for sage-grouse nesting ecology it would be inappropriate to examine
landscape factors or variables without forced inclusion of a sagebrush cover metric (Aldridge
et al. 2012). Authors of one other research article that examined nest occurrence included
a sagebrush cover metric despite the fact that the coefficients became non-significant after
both the linear and quadratic term were retained in the model (Dzialak et al. 2011). Most
other researchers structure sage-grouse nesting ecology model selection procedures such that
a sagebrush cover metric could be absent from the chosen model, or if using AIC, potentially
absent from a confidence set of models. This is somewhat justified given the theoretical foun-
dations supporting the use of an a priori model set with AIC model selection procedures to
identify a best approximating model. To our knowledge every published best-approximating
landscape-scale model from sage-grouse nesting-habitat research has included a sagebrush
metric. Still, given the wealth of published research on sage-grouse nesting ecology, it may no
longer be appropriate to consider models or a model selection procedure that would allow the
chosen model to exclude any or all sagebrush metrics. This is further stressed by our results
which indicate that sagebrush cover is a fundamental predictor, positively correlated with
sage-grouse nesting-ecology selection patterns for the three spatial scales that we examined.

Our high-resolution shrub index allowed us to delineate habitat patches using a flexi-
ble quantitative methodology that had at its foundation a study-area validated estimate of
shrub habitat. This in turn was the foundation of our nesting-patch scale analysis. We
defined the patches somewhat subjectively (see appendix B) but this was done with relative
transparency; the spatial continuity of the smoothed (local summary statistics) shrub-cover
index values is primarily what defines the size and shape of the patches. Unlike typical
hand-digitized patches the area of any given patch is discounted by low shrub cover pockets or involutions. Our automated method also delineates small fragments that may require too much time or be too tedious to hand digitize. This allows for more precise estimates of the relationship between patch use and size for smaller habitat patches. The high resolution of the initial data makes the delineation more exact than when patches are derived by image classification from coarser resolution imagery (e.g., 30-m Landsat). Furthermore, if image classification is used to delineate patches then the association between patch usage and size cannot include estimates of the average shrub cover in each patch. To our knowledge this approach of delineating and characterizing shrub patches (habitat fragments) from a continuous metric has not been employed before. The approach has promise both for modeling a patch size constraint on sage-grouse resource selection as well as prioritizing patches for conservation and management.

Our highest ranked patch-scale model indicates that Jackson Hole sage-grouse select for relatively large habitat polygons (i.e., patches, habitat fragments) with higher average shrub cover. The variation in patch area for our study area was limited for the larger range of patch areas, and less nests were observed in the largest patches. For this reason the relationship between the relative probability of patch usage and size was not estimated with good precision for the larger range of patches within our study area. Another consideration is that patches with moderate average shrub cover could have either uniform-moderate shrub cover or patchy but dense shrub cover. This limits the scope of inference to the range of habitat patch areas present in this study area, and we have the most confidence in the estimates for small or medium-sized patches and the highest and lowest sagebrush cover
values.

Nesting sage-grouse in Jackson Hole demonstrate selection for medium sized patches with high average shrub cover and large patches with moderate average shrub cover. Small patches and patches with low average shrub cover are generally avoided. We observed one nest with no patch membership that was constructed in smooth brome directly adjacent to a $\approx 9 \text{ km}^2$ patch. The smallest patch used for nesting was a $\approx 0.33 \text{ km}^2$ patch. The smallest patch with substantial nesting use was $\approx 3.15 \text{ km}^2$ and the largest patch with substantial nesting use was $\approx 63 \text{ km}^2$. The two patches with the greatest nesting abundance had high average shrub cover. The two largest patches had moderate average shrub cover and exhibited notable but lesser nesting abundance. These relationships establish that larger patches with higher average shrub cover attract sage-grouse for nesting in Jackson Hole. Large patches with lower cover were less utilized, and those with very low cover or very small size represent unattractive nesting habitat. The asymptotic increase in the relative probability of nesting occurrence with increasing patch area indicates that after some threshold the size of a patch may no longer be a primary driver of nest site selection. The precision of estimates for larger patches is poor; no extrapolation is warranted and the scope of inference should remain limited to the patch area values observed in our study area.

At the next scale of analysis the nesting-region model indicates that the sage-grouse of Jackson Hole have little tolerance for regions of sagebrush habitat with very low cover, measured at a 769-m grain. It is not until cover in the immediate region increases to a moderately high level that the relative probability of a region being utilized becomes substantial. This is consistent with the inferences attained from the nesting-patch analysis.
At highest order of selection (third-order) the sage-grouse of Jackson Hole are attracted to nest sites with shrub cover that is higher than what is available within 500-m of a nest. This is inferred from our top AIC$_c$ ranked nesting-site RSF which was the finest spatial-scale resource selection analysis that we performed. This affinity for high shrub cover at the nest site is consistent with an abundance of microhabitat research.

After covariate correcting for shrub cover there is also an indication that nesting sage-grouse select sites with greater greenness (veg-GSGI). Given that there was substantial model selection uncertainty for this scale of analysis, it is difficult to interpret the biological underpinnings of the association between veg-GSGI and nesting occurrence. The parameter for this covariate was non-significant in all 90% confidence set models but it has the most support among any variables across the entire grain-spectrum nest-site model set. We cannot confidently propose a biological reason for the importance of this variable because it represents both herbaceous and non-sage shrub cover, particularly antelope bitterbrush, at the nest-site scale. The bitterbrush variable was also in many of the 90% confidence set models but the overall support based on summed Akaike weights across the entire model set cannot be accurately assessed because the bitterbrush covariate had to be modeled using two model terms (two degrees of freedom). The shrub index also contains a signature from bitterbrush cover and other non-sage shrubs so the variation explained by the separate bitterbrush variable may be compromised. We were not able to cleanly tease apart the influence of these ecological variables, though we suspect, and previous research indicates, that bitterbrush and herbaceous cover are important for nesting-habitat quality (Yost et al. 2008).
A Winding Road to the Best Nesting-Region Model

In a biological sense our research corresponds well with the plethora of other sage-grouse research. Complexities and extremes in topography, tree density and other towering objects in the immediate vicinity, and shrub cover are all becoming well-supported in the literature as critical ecological factors influencing habitat suitability for nesting sage-grouse.

Some exceptions were that for the nesting-region scale of analysis the water and roads variables, at the 1412-m and 1730-m grains, fit our models so well that the models were rendered poorly predictive due to the large effect sizes for these variables. In the literature these variables have not exhibited consistent effect directions or statistical support for their associations with nesting-habitat selection. (Aldridge and Boyce 2007; Aldridge et al. 2012; Dzialak et al. 2011; Kirol et al. 2015). They are, however, less commonly included in analyses than vegetation indices, shrub metrics, topographic metrics, or land cover percentages. We stress that these variables produced the most well-supported models in our initial model sets for the nesting-region scale. They were removed because cross-validation indicated that they did not have biologically reasonable associations with nesting-habitat selection. We reason that these variables were concentrated in a region of the study area adjacent to highly attractive nesting-habitat so they appeared to have a strong influence when smoothing caused them to ‘bleed’ over into regions with the highest abundance of habitat usage samples.

Conclusions

The most salient implication of our research was that shrub cover data, derived from freely and extensively available imagery, was strongly and positively correlated with nesting-habitat
use, at three disparate scales of selection. This reinforces established ecological expectations and is a testament to the methodology that we employed. The RSF models that we developed demonstrated sound predictive potential. The grain sizes for the nesting-site and nesting-region scales of analysis were determined systematically by examining a relatively comprehensive grain-spectrum so we have confidence that particularly important grain sizes were not overlooked.

It is becoming increasingly clear that sage-grouse are attracted to habitat characteristics in a hierarchical fashion. Our research supports the idea that female sage-grouse likely seek out desirable nesting regions within generally attractive habitat patches (zones, fragments). Upon selecting a suitable region the site of the nest is chosen. It appears to be the structure and vigor of the shrubland at potentially any scale that makes a locality attractive for nesting. The evidence certainly points to this dynamic for the Jackson Hole sage-grouse population.

Thanks to our quality-assured high-resolution shrub cover index, and other high-resolution covariates, our nest-site RSF comes close to mapping micro-habitat scale predictions for a landscape extent. This is currently not feasible with the level of detail captured at field plots, but it is a progressive step. The inferences generated from our nest-site and nesting-region RSF are similar to those reported by Doherty et al. (2010), who assessed multiscale multi-grain models for micro-habitat and landscape scales separately and then combined. They were, of course, not able map out the predictions because the micro-habitat variables were only measured at field plots.

Our RSF models and the weighted SRSF model each map out critical information about
the nesting-habitat selection signature that we documented in Jackson Hole. This could not
have been accomplished as rigorously without the high spatial-resolution variables that we
derived from the NAIP imagery. Sagebrush cover specifically, and shrub cover in general,
is truly an important component of sage-grouse functional habitat. Accurate and precise
data regarding the distribution, abundance, and characteristics of sagebrush is as important
to sound inference for sage-grouse nesting ecology as is accurate, properly-sampled, and
abundant demographic data. Topographic ruggedness and tall objects such as trees may
also be fundamental drivers of sage-grouse nesting-habitat selection.

With the appropriate demographic data, statistical models can be fit, important habitat
response signatures can be tested for, and predictions can be mapped using aerial imagery
and software that can be downloaded for free. This process can provide stakeholders and
stewards with some of the answers to the what and where questions that must be asked in
order to account for the fate of the sagebrush-steppe ecosystems and the resident sage-grouse.

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References


REFERENCES


REFERENCES


REFERENCES


REFERENCES


OTB Development Team (2013). *The ORFEO Tool Box Software Guide Updated for OTB-3.18*. CNES.


Appendices

Appendix A  Shrub Cover Estimation

A.1  Methods

The binary classification of the study area into a region of potential sagebrush and a non-sagebrush region was accomplished by combining a suite of masks that identified non-sagebrush zones. The masks were created using three primary strategies. One method involved calculating Haralick texture metrics from specifically chosen bands of the NAIP imagery and visually inspecting the texture images to determine threshold values that identified particular features in our study area, such as trees or roads. We then performed a boolean classification on the texture image to create a binary mask image for masking out those particular features. The specific NAIP bands were chosen such that they possessed a clear delineation of image texture at a fine scale. In other words, they were relatively sharp images. We produced the Haralick texture images using the Orfeo toolbox module in QGIS (Haralick et al. 1973; OTB Development Team 2013). We produced 6 effective masks in this way. Our next method involved using a multivariate alteration detection algorithm
to identify regions that showed dramatic change from one period of NAIP acquisition to
another (Nielsen 2007). Some examples would be regions that would transition from sand
or gravel bars to water or willows and vice versa, land use changes such as building con-
struction, or differential irrigation and harvest states of agricultural lands between years.

To calculate the change metrics we input multi-band NAIP images from different years into
the multivariate alteration detector algorithm which is implemented as an Orfeo toolbox
module in the Processing toolbox of QGIS. We viewed the output images to ascertain if a
particular range of values of the alteration metrics would uniquely identify areas that were
not sagebrush-steppe. We would then create a binary classification of the image using raster
algebra to specify the range of values that represented between year alteration involving
non-sagebrush cover types. We were able to produce 8 masks to remove regions that would
not be masked out using other methods. This technique leveraged the fact that left undis-
turbed sagebrush-steppe habitat does not change much over the three year NAIP acquisition
frequency.

Supervised image classification was the foundation of the final method that we employed
to create non-sagebrush masks. We experimented with a number of the Orfeo toolbox su-
 pervised classification algorithms implemented in the Processing toolbox in QGIS and found
that support vector machines (SVM) based classification performed well (Oommen et al.
2008). Compared to many of the machine learning classifiers implemented in Orfeo tool-
box, the SVM exhibited strong computational efficiency. This was of great value due to the
volume of data that we had to process. We used an iterative expert knowledge and im-
age interpretation strategy to develop a useful classification that differentiated well between
sagebrush, and all other ground cover types. The analyst used a Orfeo toolbox k-means unsupervised classifier to classify subsets of the study area into spectrally distinct regions. The k-means classifications were then vectorized thereby creating selectable polygons from the imagery subset. Viewing these polygons overlayed on NAIP imagery allowed the analyst to select polygons that corresponded to various ground cover classes and also had somewhat unique spectral signatures. A master set of training polygons was compiled with the intent of assisting the SVM machine learning algorithm with classifying the study area into sagebrush-steppe categories and other land cover categories. Supervised SVM classification was attempted on numerous permutations of image sets, including ancillary data such as vegetation indices or texture indices. Multiple versions of training polygon sets were also employed. Some image classes from these permutations were determined to be useful as the foundation for other covariates. Two examples were a water class and a shadow class, which aided in the generation of habitat variables that were discussed in the Producing Habitat and Landscape Variables section above. Aggregates of classes that identified non-sagebrush areas were binary classified to create 6 additional masks for isolating the sagebrush-steppe cover type.

The non-sagebrush masks developed using all three methods outlined above were used to mask the texture metric that we used to detect shrub cover. To quantify image texture caused by shrubs we used the multi-band variation algorithm of the System for Automated Geoscientific Analysis (SAGA) GIS with the default 1-pixel neighborhood radius and our PCT-1i image as input (SAGA version 2.1.2, www.saga-gis.org, accessed 3 Mar 2016). Using values from all the raster cells in a neighborhood (moving window) the algorithm calculates
distances from the feature space centroid to each individual cell. This distance is the basis for three spectral variation metrics that are calculated and mapped to the center cell in each neighborhood to create three new images. The three outputs are the mean distance of all cells, the standard deviation of distances for all cells, and the distance of the center cell from the centroid. The spectral variation distance metric best seemed to highlight shrubs. Our shrub texture metric was created by binary reclassification of the multi-band variation distance layer such that all pixels representing a multi-band pixel distance greater than 9 would receive a value of 1 and all pixels less than or equal to 9 would receive a value of 0. The multi-band variation distance metric can be thought of as a multivariate spatial residual analysis. This technique relies on the meter scale heterogeneity of sagebrush dominated ecosystems as well as the meter scale patchwork of bright and dark pixels caused by illuminated shrubs and the shadows that they create.

To assess the accuracy of our remotely sensed shrub cover index we collected ground-truthing data at 271 plots throughout the study area. This field work was conducted from 29 May 2012 through 11 August 2012. Data was collected using the line-point intercept method along 6 transects placed inside a 45-m diameter sampling plot (Godinez-Alvarez et al. 2009; Herrick et al. 2009). The criteria used to select plot locations was firstly that the plots lie within potential sage-grouse habitat and secondly that the habitat characteristics be relatively homogeneous within, and next to the plot. Potential sage-grouse habitat was taken to include grassy meadows, relatively barren areas, and abandoned fields. Excluded from sampling were heavily irrigated fields, forested areas, wetlands, willow flats, and extremely rugged or steep regions. Each line-point intercept observation recorded a category of ground
cover, the shrub genus if a shrub was observed, and the plant height if a shrub or vascular
plant was observed. The four cover categories recorded were bare-ground, litter, herbaceous,
and shrub. This field data provided a count of shrub observations for every plot, and our
shrub index provided a binary classification of shrub and non-shrub 1-m pixels for the entire
study area. With a GRASS GIS module in the processing toolbox of QGIS we sampled
the shrub index at each of our plot locations using a 5-m buffer around a vector line file
that approximated the layout of each of the field plots. This was done by summing the
number of shrub pixels within a given plot layout polygon (Michael Shapiro, Glynn Clements,
and GRASS Development Team, 2016 r.neighbors. Geographic Resources Analysis Support
grass.osgeo.org/grass70/manuals/r.neighbors.html). We then performed 271 Fisher
exact tests comparing the count of pixels in our GIS shrub index to the count of shrub
observations in our field data (Vittinghoff et al. 2005) (R version 3.0.2, www.R-project.org,
accessed 9 Sep 2013). As a measure of accuracy we calculated the proportion of of p-values
greater than 0.05. The more incongruent per plot paired counts are the lower the p-values
are. A p-value greater than 0.05 indicates a paired GIS count vs. plot count that was not
extremely likely to be from different populations.

To further assess the accuracy of our shrub index we compared it to USGS sage product
estimates (Homer et al. 2012) and shrub cover estimates derived from Light Detection and
Ranging (LiDAR) data. The LiDAR data was downloaded from the USGS EarthExplorer
website and covered a substantial portion of our study area. This data was obtained in
a semi-processed form and further processing was performed using LAStools production
algorithms combined into a processing pipeline in QGIS model builder (LAStools version 160921, www.lastools.com, accessed 15 Oct 2016). The algorithms used were LAStilePro, LASheightPro, and LAScanopyPro. With the pipeline we produced a 1-m resolution height raster calculated using any vegetation-class LiDAR points over 2 m in height. We also produced a 1-m resolution canopy cover raster. To compare all the independently synthesized estimates we produced a similarity matrix which provided Spearman $\rho^2$ values for all possible correlations between field based, LiDAR based, residual analysis based, and USGS sage product estimates. This similarity matrix is the basis for a hierarchical cluster analysis which uses the similarity metrics to calculate the distance between samples in multivariate space. This distance is then the basis for clustering the samples into similar groups. In this case the samples are all the estimate-target by methodology combinations. We also produced a dendrogram plotted from the results of hierarchical clustering which aids in visualizing the clustering structure. The similarity matrix and the dendrogram were generated with the varclus function from the Hmisc package in R (Harrell 2015).

To improve the accuracy of the sagebrush index we regressed our field measured shrub-proportions on the texture index based proportions and then used the fitted relationship to correct the shrub index counts. The relationship between the GIS and field proportions was not linear so we tried a log and square root transformation of the GIS proportions. We did this for multiple versions of the sagebrush-steppe mask which was a composite of numerous texture, alteration detection, and classification derived masks. The choice of which version of sagebrush index to use in our resource selection analysis took into account multiple aspects of the accuracy assessment results. One assessment was to display the index layer
in a GIS and compare it to NAIP data and sagebrush height and cover metrics calculated from LiDAR data. Our field sampling protocol targeted cover types and variation within the sagebrush-steppe but a few landscape-image contexts were not sampled and were not well discriminated by our methods. The final choice regarding which of the masking methods to use took this into account. Specifically we used a masking method that provided slightly lower values of our multiple-paired testing assessment but appeared to somewhat alleviate the masking out of sagebrush covered slopes. Steep slopes combined with the aspect of some sagebrush covered areas creates differential lighting and therefore alters the magnitude of image digital numbers. This confounds some components of our methodology and introduces potential error that was not targeted by our field sampling methods.

A.2 Results

The percent of Fisher exact tests where \( p > 0.05 \) was true among 271 paired tests comparing plot samples of field based sagebrush cover counts to regression adjusted GIS based shrub texture counts was between 40% and 50% prior to adjustment (Table 6). Overall our estimates show decent correspondence with field sampled proportions of shrub cover. The methodology we utilized was relatively insensitive to variations in the suite of non-sagebrush masks used and whether or not we targeted estimates of sagebrush cover specifically or shrub cover in general. Both log and sqrt transformations of the GIS derived cover estimates notably improved the fit of the regression model thereby providing a degree of calibration for our shrub index. We chose to use the regression model where our field estimates were regressed on a log transformed texture-based shrub cover index, adjusted \( R^2 = 0.55 \). The
Fisher exact tests indicate that \((1 - 0.565) \times 100 = 0.435 \times 100 = 43.5\%\) of the paired counts are unlikely to be coming from the same distribution. Examination of the distribution of differences between our field estimates and our GIS texture-based estimates indicates that our GIS estimates are relatively unbiased overall, but not extremely precise. There is a degree of overestimation for field values 0\%–22\% and an increasing degree of underestimation as actual cover increases from 22\%–62\% (Fig. 16). Our estimates are substantially more accurate than the USGS sage product shrub estimates with similar but less extreme patterns of bias (Fig. 16).

The comparison with LiDAR based estimates of height and shrub cover indicates that the LiDAR based estimates have a good correspondence to our plot sampling field based estimates. In turn the LiDAR estimates of shrub height and shrub cover show a good correspondence to our spatial residual analysis (texture-based) estimates. These relationships provide further confidence in the accuracy and biological relevance of our shrub cover surface (Table 7, Fig. 17).

The USGS sage products consistently cluster together but not with our field based measurements. This is further evidence of severe local inaccuracies in the USGS sage products and illustrates that minimal additional information is contained between separate variations of the USGS shrub metrics, for the Jackson Hole region. The basal split from the more accurate LiDAR-based and texture-based shrub metrics helps justify our decision to exclude these metrics from our RSF model sets.
Table 7: Similarity matrix giving Spearman $\rho^2$ values indicating the degree of correlation between plot-based field measurements of shrub height and shrub cover compared to our LiDAR estimates, our texture derived estimates, and USGS sage product estimates, for Jackson Hole, Wyoming, USA. Field data was collected in 2012; GIS texture-based estimates are derived from imagery captured in 2007, 2009, and 2012; LiDAR data was captured in 2014.

<table>
<thead>
<tr>
<th>SSM</th>
<th>H.las$^1$</th>
<th>H.fld$^2$</th>
<th>H.gs$^3$</th>
<th>S.fld$^4$</th>
<th>S.las$^5$</th>
<th>S.gs$^6$</th>
<th>At.gs$^7$</th>
<th>Atb.gs$^8$</th>
<th>Atw.gs$^{10}$</th>
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<td>0.058</td>
<td>0.274</td>
<td>0.670</td>
<td>0.359</td>
<td>0.013</td>
<td>0.011</td>
<td>0.007</td>
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<td>0.032</td>
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<td>0.087</td>
<td>0.178</td>
<td>0.119</td>
<td>0.244</td>
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<td>0.012</td>
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<td>0.004</td>
<td>0.028</td>
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<td>0.020</td>
<td>0.406</td>
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$^1$ shrub height LiDAR estimated  
$^2$ shrub height field measured  
$^3$ USGS shrub height estimates  
$^4$ shrub cover field measured  
$^5$ shrub cover LiDAR estimated  
$^6$ shrub cover texture based estimates  
$^7$ USGS sagebrush species cover estimates  
$^8$ USGS shrub cover estimates  
$^9$ USGS big sagebrush cover estimates  
$^{10}$ USGS Wyoming sagebrush estimates

Table 6: Proportion of Fisher exact test p-values > 0.05 derived from 271 paired tests implemented for each of 40 GIS methodological variations of our shrub index accuracy assessment, for Jackson Hole, Wyoming, USA, 2007-2012. Heading label numbers represent specific masking methods and letters represent estimation targets. Higher values indicate a greater proportion of tests where observed (GIS) and expected (field) values did not differ at the 0.95 confidence level.

<table>
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<tr>
<th>method</th>
<th>1$^a$</th>
<th>1$^b$</th>
<th>2$^a$</th>
<th>2$^b$</th>
<th>4$^a$</th>
<th>4$^b$</th>
<th>5$^a$</th>
<th>5$^b$</th>
<th>6$^a$</th>
<th>6$^b$</th>
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<td>0.395</td>
<td>0.428</td>
<td>0.406</td>
<td>0.421</td>
<td>0.446</td>
<td>0.480</td>
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<td>0.410</td>
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<td>0.410</td>
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<td>0.494</td>
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<td>0.568</td>
<td>0.561</td>
<td>0.568</td>
<td>0.554</td>
<td>0.587</td>
<td>0.565</td>
<td>0.587</td>
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<tr>
<td>sqrt</td>
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<td>0.601</td>
<td>0.565</td>
<td>0.598</td>
<td>0.565</td>
</tr>
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</table>

$^a$ Shrub estimates targeted.  
$^b$ Sage specific estimates targeted.
Figure 16: Density plots showing distributions of differences between remotely sensed and field measured estimates of shrub cover, for Jackson Hole, Wyoming, USA, 2007-2012. The heavy lines indicate our estimates and thin lines indicate USGS sage product estimates, both compared to our field measurements. The plot in the upper left hand corner uses the total field truthing dataset and the rest of the plots use a subset from the indicated range of field measurement values. The subset size is indicated on the y-axis where n = 271 represents the total dataset.
LIDAR: shrub height (H.las)
FIELD: shrub height (H.fld)
LIDAR: shrub cover (S.las)
FIELD: shrub cover (S.fld)
TEXTURE: shrub cover (S.gis)
USGS: height (H.gs)
USGS: Wyoming sagebrush (Atw.gs)
USGS: shrub (S.gs)
USGS: sagebrush general (At.gs)
USGS: big sagebrush (Atb.gs)

Figure 17: Dendrogram depicting the results of hierarchical clustering of various shrub metric targets by methodology combinations to assess our shrub index accuracy, for Jackson Hole, Wyoming, USA, 2007-2012. Squared Spearman correlations $\rho^2$ were used as the similarity measures. The text in parentheses corresponds to the shortened labels in Table 7.
B.1 Methods

The initial data for the patch variable was our shrub texture metric. First our availability
mask was applied to zero out trees, water bodies, and willow flats. The next step was to
smooth the binary image using the Orfeo Toolbox smoothing algorithm with the Gaussian
smoother and the default 2-pixel radius. The resulting image was then binary reclassified
using a threshold value that split all pixels into a habitat class and a non-habitat class. Any
smoothed texture-metric pixels greater than 16 were given class 1 and all other values were
given class 0. This threshold was selected via trial and error using the criteria that shrub-
habitat patches not be eroded, and incorrectly classified non-habitat patches be minimized.
In some areas this had the effect of creating fringes around shrub-habitat that extended into
marginal habitat such as fallow fields, meadows, or relatively barren areas. This specification
of habitat is realistic in the sense that open areas and meadows adjacent to and within
sagebrush regions are utilized by sage-grouse and are a minimal barrier to movements. A
reasonable definition of sage-grouse structural habitat would include meadows, open patches,
and abandoned fields as long as sagebrush stands of substantial area are in the immediate
vicinity. In order to remove small holes in the patches resulting from fine-scale variation in
the texture metric we applied the GDAL sieving filter in QGIS with a threshold of 700 pixels
and the pixel connection parameter set to 8. To exercise some control over how the patches
were specified we hand digitized a vector layer that could be used to stitch or sever the
separate clumps of pixels that would become patches. This was done by drawing individual
lines that had an attribute of 1 if the line was intended to bridge a gap between patches.
and a zero if it was intended to separate 1 clump of pixels into 2 clumps. This vector file was converted to a raster file and then multiplied by the binary classified image of the pixel clumps. For the most part the clumps were separated by water bodies, forested areas, wetlands, legacy or active agricultural fields, developed areas, and roads. In some cases our method did not resolve clumps in a biologically reasonable manner. A separation of clumps by a low traffic or restricted travel dirt road would not be reasonable as the road would present little to no inhibition to the movement of sage-grouse. As another example, a small section of sagebrush flats extending into a forested area may not be identified as a unique patch. This is questionable because a sage-grouse is not likely to venture into the involution and is all the more unlikely to extensively utilize or nest on such a peninsula of habitat engulfed in forest. In both cases we altered the pixel based links between patches as we deemed appropriate. Converting the pixel clumps into individual patches was accomplished with the GRASS GIS r.clump algorithm. The area of individual patches was then calculated with the r.statistics algorithm. This resultant image provided a delineation of sagebrush habitat patches composed of 1-m pixels whose values were either zero for non-sagebrush zones or the area in km$^2$ for patches.

B.2 Results

See figure 18.
Figure 18: Illustration of the patch area variable, for Jackson Hole, Wyoming, USA, 2007-2012. The area variable had units of km². It was log transformed; 1 was added to prevent negative values and undefined values for non-patches with a size of 0 (not shown).
Appendix C  Bitterbrush Cover Estimation

C.1 Methods

We manually digitized all regions where we could identify bitterbrush presence with good confidence. This was done by viewing the 2012 NAIP image which was acquired in mid-August when much of the herbaceous vegetation had become dessicated. Bitterbrush is a drought tolerant evergreen shrub which visually stands out in these conditions. As an auxiliary image source we relied on the ArcGIS webpage map viewer (http://www.arcgis.com/home/webmap/viewer.html) which allows the viewing of sub-meter DigitalGlobe imagery.

To provide an initial foundation for our Antelope bitterbrush vector digital data layer we selected polygons from the Spatial Vegetation Data for Grand Teton National Park Vegetation Mapping Project geo-spatial database (USBR Remote Sensing and GIS Group, Denver, Colorado, http://biology.usgs.gov/npsveg/ftp/vegmapping/grte). We only selected polygons that contained substantial amounts of bitterbrush. We then manually edited the polygons as we deemed appropriate based upon image viewing. We also digitized many polygons not included in the GTNP vegetation map. Next we created a SVM supervised classification of the bitterbrush ground cover using a method analogous to that which we used for classifying sagebrush dominated regions. To calculate the cover index we used the vector layer and a binary classified bitterbrush layer to mask our shrub texture metric. We then applied a GRASS GIS r.neighbors average smoothing filter with a 43-m diameter. To assess the accuracy we regressed our field measurements on our GIS based estimates. To enhance the accuracy we used the fitted relationship to calibrate the bitterbrush index, just as we did with our shrub index, except that no transformation of the GIS estimates was
C.2 Results

Our bitterbrush index was highly correlated with our field based estimates \( (n = 271, r = 0.9) \). The correlation between the index and the field measurements was still high even when restricted to field values greater than 0 \( (n = 40, r = 0.82) \). This provides evidence that both the categorical and continuous-scale accuracy is good for these estimates. A linear regression based calibration of the estimates hardly changed the correlation between index and field measurements; the calibration was deemed unnecessary.

Appendix D Creating the Availability Mask

D.1 Methods

The availability mask was created by calculating the visual vegetation index (VVI) using the 2009 NAIP imagery (Ponti 2013). This served to highlight trees and shadows. The VVI was then binary reclassified such that all pixels with a value greater than 70 received a 1 and all pixels less than 70 became zero. In essence this extracted the trees and shadows. In order to mask out water bodies we overlayed our water bodies vector file and then used a vector-to-raster algorithm to ‘burn in’ the water bodies to the tree and shadow mask. A SAGA morphological filter with a radius of 3 was then applied to the binary image; the search mode of the algorithm was set to square. This expanded the tree and shadow pixel clumps. Next we applied a SAGA closing morphological filter with a radius of 3 and the search mode set
to circle. This was used to fill in the gaps between pixels representing trees and shadows.

From here we applied an Orfeo mean smoothing filter with the radius set to 3. The final step was to binary reclass the smoothed image into regions available and not available to sage-grouse. A threshold value that provided sufficient masking of forested regions, water bodies, and willow flats was determined by setting various transparency thresholds while viewing the smoothed mask layer on top of a NAIP image.

D.2 Results
Figure 19: Illustration of the mask used to partially define availability within the study area for all scales of analysis. Availability was restricted to the white regions within the black study area bounding polygon.
Appendix E  Roads and Water Covariate Removal

Figure 20: Boxplots each illustrating the distribution of $\Delta AIC_c$ values of 111 nesting-region models at each of 24 grain sizes, for Jackson Hole, Wyoming, USA, 2007-2012. No models have been excluded from the initial model set.

Figure 21: Boxplots each illustrating the distribution of $\Delta AIC_c$ values of 67 nesting-region models at each of 24 grain sizes, for Jackson Hole, Wyoming, USA, 2007-2012. All models containing roads have been excluded from the initial model set.
Figure 22: 5-fold cross-validation of the top model with all variables included. This model was of the 1730-m grain size, for Jackson Hole, Wyoming, USA, 2007-2012. The expected proportions are based on bin utilization values, as defined here: $U(x_i) = w(x_i)A(x_i)/\sum_j w(x_j)A(x_j)$ where $w(x)$ is the midpoint value for a bin interval and $A(x)$ is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0–1.

Regression (expected vs. observed)
$y = 0.067 + 0.135(x)$
$R^2 = 0.354$

Chi squared goodness−of−fit test
$\chi^2 = 4758637306$, df = 12, $p = 0$

Spearman's rank−based correlation
$r_s = 0.582$, $p = 0.02$

Random: use = availability

Perfect fit

Random: use = availability
Figure 23: 5-fold cross-validation of the top model with roads excluded. This model was of the 1730-m grain size, for Jackson Hole, Wyoming, USA, 2007-2012. The expected proportions are based on bin utilization values, as defined here: $U(x_i) = w(x_i)A(x_i)/\sum_j w(x_j)A(x_j)$ where $w(x)$ is the midpoint value for a bin interval and $A(x)$ is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0–1.
Figure 24: 5-fold cross-validation of the top model with roads and water excluded. This model was of the 1730-m grain size, for Jackson Hole, Wyoming, USA, 2007-2012. The expected proportions are based on bin utilization values, as defined here: $U(x_i) = w(x_i)A(x_i)/\sum_j w(x_j)A(x_j)$ where $w(x)$ is the midpoint value for a bin interval and $A(x)$ is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0–1.
Figure 25: 5-fold cross-validation of the next best 1730-m grain size model with roads and water excluded, for Jackson Hole, Wyoming, USA, 2007-2012. The expected proportions are based on bin utilization values, as defined here: 

\[ U(x_i) = \frac{w(x_i)A(x_i)}{\sum_j w(x_j)A(x_j)} \]

where \( w(x) \) is the midpoint value for a bin interval and \( A(x) \) is the area of a particular bin. The numbers on the plotted points are the midpoint values for the raw RSF bins, rescaled from 0–1.
### Appendix F  Nesting-Site 90% Confidence Set


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<th>RSF Structure</th>
<th>AIC</th>
<th>k</th>
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Appendix G 3-D Wireframe Plot for Nesting-Patch Model

Figure 26: Nesting-patch 3-D wireframe plot indicating the interaction between the area of patches and the average shrub cover index for the patches, for Jackson Hole, Wyoming, USA, 2007-2012.