AN ABSTRACT OF THE THESIS OF

Priscilla K. Coe for the degree of Master of Science in Rangeland Ecology and Management presented on March 15, 2007,

Title: Validation of Elk Distribution Models at Sled Springs Wildlife Demonstration Area, Northeast Oregon

Abstract approved:

Martin Vavra

Landscape models for elk distribution developed at Starkey Experimental Forest and Range from 1993-1995 were tested on another landscape during 2003-2005 at Sled Springs Wildlife Demonstration Area. Using location data obtained from 23 wild elk captured and fitted with GPS telemetry collars, 8 spatial resource selection function models representing 8 periods spring through fall were evaluated. Recently published statistical and non-statistical validation methods were used to score models using *a priori* performance criteria. Results showed that 1-month models for early spring, late summer and early autumn scored high, mid-summer models scored medium low and a late fall model scored low. Two 2-month models representing early/late spring and late summer/early autumn scored high. Discussion focuses on understanding both high and low scoring models and recommendations for refinement. Suitability of these spatial models to management planning is also discussed.

Validation of Elk Distribution Models at Sled Springs Wildlife Demonstration Area, Northeast Oregon

by

Priscilla K. Coe

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Master of Science

Presented March 15, 2007

Commencement June 2007

Master of Science thesis of Priscilla K. Coe presented on March 15, 2007

APPROVED:

____

Martin Vavra, representing Rangeland Ecology and Management

____

Head of the Department of Rangeland Ecology and Management

____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

____

Priscilla K. Coe, Author

ACKNOWLEDGEMENTS

I would like to thank Marty Vavra, my major professor, and my committee members Doug Johnson, Mike Wisdom, and John Cook - for their advice, support and help. I thank Bill Boggess for being my graduate representative. Bruce Johnson, Oregon Department of Fish and Wildlife, supported this endeavor and provided invaluable advice and help. I thank my co-workers Scott Findholt and Jim Noyes for their help and patience. Bob Riggs facilitated collection of field data and spent many hours collating GIS data for use in this research. Brian Kernohan and Steve Dodson assisted with GIS data as well. John and Rachel Cook provided substantial field data as did Dahl Damarin and Enkra Darambazar. Norm Cimon provided help in writing SQL code. Technical advice and programs for data analysis were provided by Hawthorne Beyer, Art Rodgers, and Bill Huber. Gary Roloff and Joshua Millspaugh answered many questions concerning kernel estimates. Mike Hansen tested GPS collars in the field. Dave Motanic photo-interpreted canopy cover. Thank you all for your help and support. I thank Rocky Mountain Elk Foundation, Eastern Oregon Agricultural Research Station, and Oregon State University Agricultural Research Foundation for funding. Agencies and corporations that provided data and support for this study were Boise Cascade Corporation, Forest Capital Partners, Oregon Department of Fish and Wildlife, National Council for Air and Stream Improvement, and the US Forest Service Pacific Northwest Research Station Forestry and Range Sciences Laboratory.

Kent Coe and Miriam Coe were supportive and helpful in this research in many ways. I thank them for their continued good cheer and patience in helping me further my education.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

VALIDATION OF ELK DISTRIBUTION MODELS AT SLED SPRINGS WILDLIFE DEMONSTRATION AREA, NORTHEAST OREGON

Introduction

Range and wildlife professionals need tools to help understand wildlife distributions across landscapes and to plan management of wildlife populations. Spatial wildlife distribution models contribute to an understanding of how landscape characteristics influence the quality and quantity of habitat, well-being and productivity of wildlife populations. This research evaluates predictive spatial models of elk (*Cervus elaphus*) distribution in northeast Oregon. It focuses on the need for land managers to understand elk distributions and how land management activities influence them. In the western United States, elk inhabit forests and grassland regions where human habitation is sparse. Elk are of importance in land management both economically and ecologically because elk have high social and economic importance as game and aesthetic species and because they respond to and influence changes in plant communities.

Models that predict wildlife distributions across a landscape help to achieve this understanding. Model evaluation is crucial in understanding how these models may be useful in management planning. My research validated elk resource selection function models, developed at Starkey Experimental Forest and Range (Starkey), on another landscape at Sled Springs Wildlife Demonstration Area (Sled Springs). Both areas are in the Blue Mountains of northeast Oregon (fig. 1).

The goal of my study was to do an "out-of-sample" test of the Starkey models, one step in model validation that should ideally be repeated on several other landscapes. My objectives toward this goal were to 1) obtain elk locations at Sled Springs to use as the observed data, 2) predict elk use across the landscape at Sled Springs using non-standardized coefficients from the Starkey models for 8 monthly periods, and 3) use published model validation methods to evaluate the models.

Justification

Professional land managers are heavily involved in mitigation of impacts to wildlife from land development, road building, timber harvesting, mining and livestock grazing (Jaindl and Quigley 1996). Laws pertaining to environmental impacts of these and other activities on wildlife habitat, such as the National Environmental Policy Act and the Endangered Species Act dictate procedures for ensuring adequate protection or mitigation to wildlife and wildlife habitat. Managers rely on research and technology to help model wildlife distributions and the many factors that determine suitable habitat (Borchers 1996). Managers also must communicate to stakeholders and the public about reasons for land use decisions and the sustainability of wildlife and their habitats. Maps that depict spatial distributions of wildlife are important in that communication.

Models intended to predict wildlife distributions across a landscape often rely on Geographic Information Systems (GIS) technology to predict and display potential habitat (Bissonette 1997). Animal locations for specific time periods are used in combination with landscape data at a specified scale to model distributions. These models must then be validated on other landscapes to evaluate their usefulness in land management decisions. Validation of landscape-based ecological models is an emerging science and approaches to validation of landscape-based wildlife distribution models have only recently been developed (MacNally 2002).

The Blue Mountains of northeast Oregon are typical of forested rangelands that are commonly grazed by elk, mule deer, and cattle throughout the intermountain west (Jaindl et al. 1996). Researchers at Starkey Experimental Forest and Range (hereafter Starkey, Wisdom et al. 2004a) built models for predicting the distribution of elk, mule deer, and cattle (Ager et al. 2004, Johnson et al. 2000). For this study I evaluated the predictive capability of the Starkey elk distribution models (Appendix A) at the Sled Springs Demonstration Area (hereafter Sled Springs, fig. 1) within the Blue Mountains.

To illustrate how my study fits into the larger modeling process, fig. 2 is an overview of the successive steps in model building, calibration and evaluation. My study is step 4 and 5 on the flowchart; an evaluation dataset was used to test the predictive ability of the coefficients developed in the modeling and calibration process. It continues from the point where Johnson et al. (2000) and Ager et al. (2004) completed steps 1 through 3 at Starkey. They modeled elk distributions using a statistical procedure called resource selection functions (RSF). They validated the models within Starkey using observed locations withheld from the initial modeling process and produced models for 8 seasonal time periods for predicting distribution of elk (Appendix A). My study continues on with model evaluation by collecting new data on a different landscape within the Blue Mountains.

Literature Review

Modeling Framework

The elk distribution models developed at Starkey and being validated here were developed using a RSF model (Manly et al. 2002). In this model a RSF is a function of characteristics measured on resource units (landscape features) such that its value for a unit is proportional to the probability of that unit being used by the animal (Manley et al. 2002).

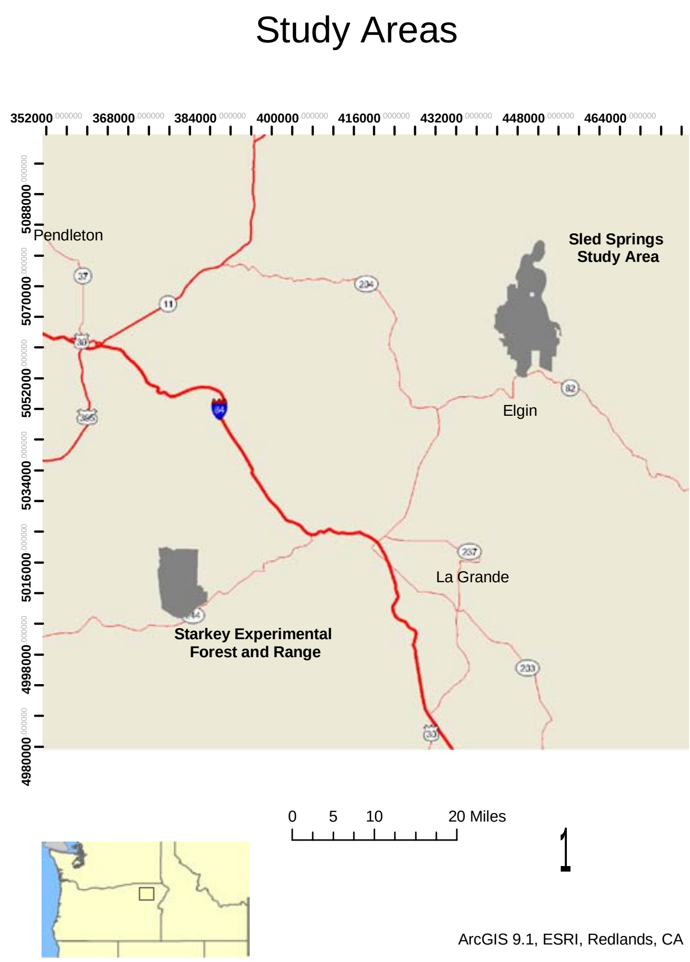


Figure 1 Starkey Experimental Forest and Range, where models were developed and Sled Springs study area where models were validated.

The RSF modeling concept derives from the discipline of landscape ecology (Turner 2005) and from the sub-discipline of spatial statistics. Modeling nature is never truth (Box 1979) and it is helpful to consider how a model was developed and how it relates to modeling approaches. Guisan and Zimmermann (2000), in a paper on predictive habitat distribution models, outlined characteristics of model design and how different approaches affect a model's ability to explain reality (fig. 3).

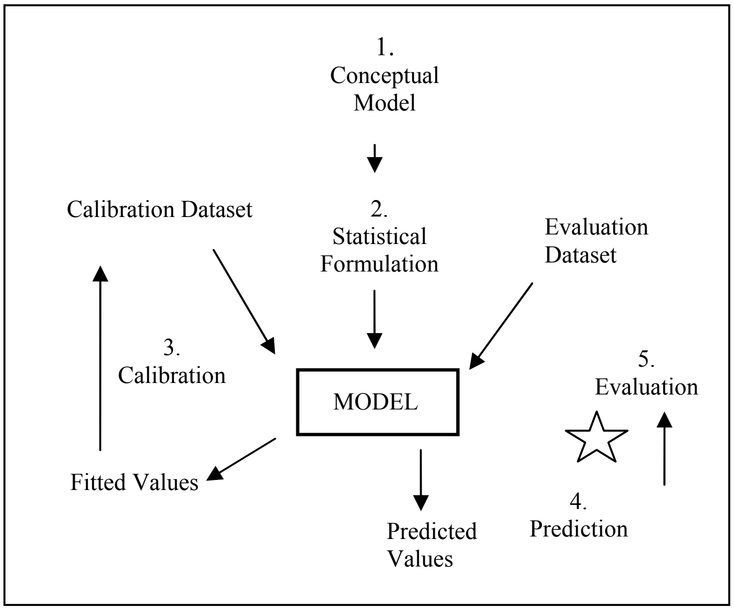


Figure 2 Flowchart (adapted from Guisan and Zimmermann 2000) showing the modeling process. The star shows where this study fits in to that process .

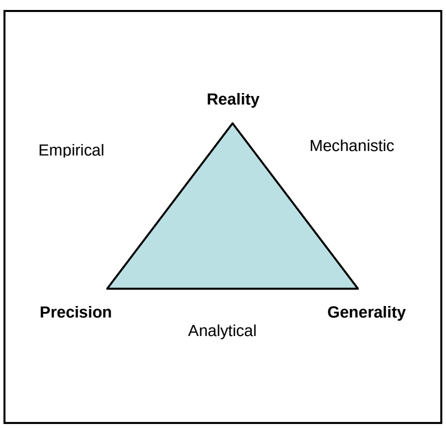


Figure 3 Modeling approaches and their relationship to model characteristics (adapted from Guisan and Zimmerman, 2000).

The 3 model characteristics they identified were precision, reality and generality (some have challenged this view, see Orzack and Sober [1993], and Zeide [1991]). Guisan and Zimmerman (2000) called models that are based on physiological requirements of organisms "mechanistic." This type of model will sacrifice precision for reality and generality – i.e. the model will be applicable to other areas (reality and generality), especially outside the physiographic province where it was developed, but will sacrifice precision. They called model building that is based on ecological characteristics of the habitat of the organism "empirical," and these models will sacrifice generality for reality and precision – i.e. the model will be more accurate but may not apply to areas outside the physiographic province. In "analytical" models that focus on theory and mathematics, such as the Lotka-Volterra population model, generality and precision dominate over reality – this model would apply "everywhere" but may not simulate the real world very well.

Moreover, ecological models may predict the "fundamental" versus "realized" niche of a population. The fundamental niche is a function of physiological performance and ecosystem constraints, while the realized niche additionally includes biotic interactions and competitive exclusion (Guisan and Zimmerman 2000). Strict mechanistic models often have parameters that predict the fundamental niche and may become quite complex, accounting for changes in competitive exclusions, security or habitat succession (Grunbaum 1995). They may employ simulation methods that focus on individual behavior and employ techniques such as random walk analysis (Coughenour 1991). Empirical models predict the realized niche, because they are based on large empirical datasets that describe the organism's actual space use, and thus the additional parameters of biotic interactions and competitive exclusions are inherent in the data (although not extractable).

There is nothing that says that a mechanistic approach to model building cannot be simple (Vanreusel et al. 2007), or that an empirical model might be incorporated into a complex simulation model (Ager et al.2004). But differentiating between the two approaches is important because it distinguishes whether a model is based on theoretical functional responses or on actual use data (Guisan and Zimmerman 2000). In this light, the Starkey models are empirical, reflecting the realized niche of the elk population for which they were developed.

Resource Selection Functions

Definition

Resource selection is the process of how animals select or avoid resources over space and time in relation to the available resources (Johnson 1980). Resource selection analysis is a statistical technique that measures the degree to which resources are selected or avoided (Manly et al. 2002). A RSF is any function that is proportional to the probability of use by an organism.

The general approach in developing RSFs is to define a study area and partition it into discrete units (regular or irregular), and sample or census the resource values within the units. Animal presence in these "resource units" is recorded and summarized over a pre-determined time interval. A statistical method is then used to model the animals' proportionate resource unit use for the entire study area and time period by estimating coefficients for each independent variable (resource). The resulting spatially explicit model can be visually displayed as a map of estimated resource use, expressed as probabilities, across the entire study area. Such spatially explicit models of resource use can be developed for individual animals and for an entire sample of animals, and expressed by season, year, and location. The resulting model coefficients can be applied to other landscapes that contain a similar range of habitat characteristics, resulting in a map of predicted animal use. RSFs have statistical rigor in that they are estimated directly from data (Boyce et al. 2002).

Assumptions

There are several assumptions behind the estimation of RSFs, which, if not recognized and accounted for, can lead to problems in inference. Manly et al. (2002) outlined the key assumptions as follows: "(1) the distributions of the measured X variables for available resources and the resource selection probability function do not change during the sampling period; (2) the population of resource units available to the organisms has been correctly identified; (3) the subpopulations of used and unused resource units have been correctly identified; (4) the X variables influencing the probability of selection have been correctly identified and measured; (5) organisms have free and equal access to all available resources."

Millspaugh et al. (1998) contended that independence of animal locations was a concern because correlation in observations constitutes pseudo replication (Hurlbert 1984). Millspaugh et al. (1998) further characterized the problem in terms of temporal and spatial independence. That is, not only may successive locations be temporally correlated (Swihart and Slade 1985), but animals that also move in the same group may be spatially correlated. However, Millspaugh et al. (1998) thought that this posed a problem only if the 2 animals were biologically dependent on each other, such as a cow and calf pair.

Garton et al. (2001) argues that animal locations are sub-samples that need not be statistically independent but instead need to be unbiased and equally interspersed through time. Further, Garton argued strongly that each radio-collared animal was the sample unit for any telemetry analyses, and that the higher the sample size (animal as sampling unit), the more correlated but less biased the results will be. Rodgers (2001) noted that many authors concluded that sample size is more important than independence of location estimates. Leban et al. (2001) studied sample size in the performance of resource selection analyses for elk. He concluded that at least 20 animals and 50 observations per animal are needed to accurately estimate resource selection for the population and season they studied.

GPS Radio Collar Technology

Definition

The Global Positioning System (GPS) is a space-based radio navigation system that is operated by the U.S. Air Force. It is composed of a constellation of satellites, ground stations, data links and control facilities. GPS permits land, sea, and airborne users to determine their three dimensional position, velocity, and time, 24 hours a day in all weather, anywhere in the world (U.S. Coast Guard 2003). Civilians use the Standard Positioning Service (SPS) without charge or restrictions. The 2001 Federal Radio Navigation Plan (U. S Coast Guard 2001) states that SPS provides a global average predictable positioning accuracy of 13 meters (95 percent) horizontally and 22 meters (95 percent) vertically and time transfer accuracy within 40 nanoseconds (95 percent) of coordinated universal time (UTC).

Radio Collar Performance

Wildlife telemetry systems based on GPS were developed in 1992 (Rodgers 2001). GPS radio collars are now routinely used for estimating animal locations in wildlife research (Garton et al. 2001). Performance of GPS collars for such research is defined as the bias and precision associated with a set of animal locations. Bias and precision each contribute to the accuracy of a set of locations.

GPS collar technology has improved rapidly. Consequently, performance of GPS collars must continually be assessed as new models of collars are developed (Rodgers 2001). However, previous studies have documented a variety of performance issues associated with use of GPS collars to estimate RSFs (Garton et al. 2001). The important accuracy issues involving the use of SPS-GPS devices for resource selection analysis include:

1) positional accuracy (difference in mean GPS compared to true locations),
2) positional precision (spread of locations around the mean),
3) observation rate (number of successful observations/total attempted observations)

which is influenced by:

   a. shrub or tree cover
   b. terrain
   c. animal behavior
   d. individual collar anomalies

and

4) procedures for placing the locations obtained in the correct resource unit (Findholt et al. 2002)

Many studies of GPS collar performance have shown a reduction in position accuracy, position precision and observation rate due to canopy cover (Moen et al. 1996, Moen et al. 1997, Rempel et al. 1995, Rempel and Rodgers 1997, Dussault et al.1999. Recent studies in western Canada and the U.S. have found rugged terrain to be a significant factor in positional accuracy and precision as well (D'Eon et al. 2002, Taylor 2002). In these and other recent studies, terrain has not affected observation rate in raw data (D'Eon et al. 2002, James Biggs, Los

Alamos National Laboratory, Los Alamos New Mexico, pers. comm., Taylor 2002, ODFW unpublished reports on file at Forestry and Range Sciences Lab, La Grande, OR).

An interaction between canopy cover and terrain on observation rate also occurred in the Selkirk Mountains of southeastern British Columbia where slope gradients were greater than 100% and aspects varied from 1 to 360 degrees (D'Eon et al. 2002). This study developed regression equations for adjusting positional accuracy and observation rate using canopy cover and a topographic variable called "available sky."

Each observation from a GPS radio collar carries 2 associated fields called "fix status" and "PDOP." Fix status indicates whether 3 or $\geq$ 4 satellites were used in position estimation. PDOP is an index to satellite geometry where high PDOP reflects poor geometry. Dussault et al. (2001) showed that the number and geometry of satellites used in calculating a GPS location is related to the mean precision of locations. Further, Dussault et al. (2001) found that precision can be improved by discarding some locations that were based on 3 satellites and that had poor satellite geometry. However, accuracy and precision of GPS locations also is related to topography and cover. Consequently, discarding locations with low precision can decrease observation rates in some habitats, which could bias results in resource selection studies (Johnson et al. 1998).

Observation rates can increase by programming the collar to try longer for a fix (for example, increase the time from 60 seconds to 90 seconds) (Moen et al. 1996). The longer the collar is programmed to attempt a fix, however, the more energy is used by the battery per location. Collars must be programmed to balance expected length of use versus attempted fixes in relation to study objectives, to ensure that collars collect data over the needed time period.

Bowman et al. (2000) found that behavior of white-tailed deer (*Odocoileus virginianus*) affected observation rate of GPS collars. The behaviors studied were moving, bedded and standing deer. Bedded animals did not acquire a fix on 32.5% of the attempts, while standing and moving deer were 13.5% and 14.3%, respectively. They found that head position did not affect either observation rate or horizontal accuracy.

The accuracy of animal locations has direct bearing on estimation of resource use by radio-collared animals. Findholt et al. (1996, 2002) and Samuel and Kenow (1992) mapped the probability distributions of location errors associated with point estimates of radio-telemetry locations, and mapped these errors in relation to resource values of interest. Both sets of researchers found no difference in the estimation of resource values associated with point estimates of animal locations (i.e., assuming each location was measured without error) versus resource values associated with entire probability distribution of location errors. Both sets of researchers provided convincing documentation as to why this pattern emerged. Specifically, nearly all resource values of interest (e.g., slope, aspect, distance to roads, and canopy closure) are spatially correlated. And second, the probability distribution of location errors is a bivariate normal distribution, with the highest probability of the true animal location associated with the point estimate of the animal location. Consequently, map overlays of point estimates of animal locations with underlying resource values appears to invariably yield the same conclusion about the animal's use of resources as would a spatially-weighted estimate of the animal's resource use based on the entire probability distribution of location errors (with the probabilities used as weights to estimate resource use). Garton et al. (2001) provided a clear and convincing explanation and schematic of these concepts, and concluded that use of point estimates of radio-telemetry locations was an accurate method of estimating the associated resource use.

GPS Collar Tests

In July and August of 2002, ODFW and BCC tested 2 Lotek Inc. model 2200 collars within the Sled Springs study area (Coe 2002). Collars were placed at sites along a north-south transect that bisected a deep east-west canyon, thereby obtaining collar location information from a steep north slope with and without canopy coverage, as well as from south facing slopes and flat terrain. At each site along this transect, the collar was left for at least 24 hours, recording locations at 5-minute intervals. The locations collected for each site were selected to include 1 24-hour day (resulting in 288 locations per site). Observation rate averaged 99.2% for all sites and no site was under 97%. Ninety-five percent of the points were spread over .17 ha. The locations were sorted by fix status and a fairly high percentage (27%) of locations used only 3 satellites (2D locations). I assumed the same percentage or higher when the collars were on moving animals. To test a method for improving accuracy I removed only those 2D locations with a PDOP of greater than 3 as suggested by Dussault et al. (1999). This reduced the size of the 95% area of each site by an average of 27% (to .12 ha) and reduced the number of locations by 6%. With this method the lowest accuracy locations were removed because a 2D location will be highly accurate if the PDOP is low (Dussault et al. 2001). However, by doing this accuracy enhancement, observation bias by habitat was undoubtedly increased by some percentage (because accuracy is associated with slope steepness and tree cover).

Further investigations at Sled Springs in 2004 (Hansen and Riggs in press) revealed that the model 2200 collar locations were more accurate and precise than the model 3300 locations, especially in >60% canopy cover (mean horizontal error was 17.6-24.0 m for the 2200s compared to 49.5 m for the 3300's,[Hansen and Riggs in press]), because the 2200 collars had longer acquisition time, ensuring better satellite geometry. However, the model 2200 collars rejected more possible positions than did the model 3300 collars, resulting in a lower observation rate (successful locations/ attempted locations) for the model 2200 collars. Consequently, the model 3300 collars had lower horizontal accuracy and precision in locations but better observation rate. If the horizontal accuracy in locations is lower than that needed for the study, then the higher observation rates help ensure a non-biased assessment of habitat use (assuming habitat is mapped with similar accuracy). For this study, the model 3300 mean horizontal error of about 50 m in a steep forested draw (Hansen and Riggs in press) was about the same as the overall accuracy of the Loran telemetry system (+ or – 53 m) used at Starkey to model RSFs (Findholt et al. 1996). Therefore, I deemed the overall location accuracy of the GPS collars sufficient for this analysis.

Ecological Model Validation

Definition

Validation of ecological models is a process designed to assess the correspondence between a model and the real system (Power 1992). Debate about whether an ecological model can be validated or only invalidated and whether model validation is impossible or essential (Conroy et al. 1995) occurs in the current literature (Rykiel 1996, MacNally 2002). Practically, predictive validation of ecological models, in which new data is gathered independent of the data used to construct the model itself, is rare because it is expensive, but this type of evaluation is the most robust procedure for evaluating predictive capability (Power 1992).

Validation deems a model acceptable for its intended purpose by meeting specified performance requirements (Rykiel 1996). While there is debate about methods and types of validation, all practitioners agree that a model's purpose ought to be clearly stated.

Power (1992) suggests a two-stage approach to model validation. First, to evaluate whether a model has predictive capabilities and is statistically sound, and second, to assemble all the evaluated models to compare them for best predictive capability.

While studies are few on validating large mammal habitat models, some have occurred. Cook and Irwin (1985) evaluated an HSI model on 29 pronghorn winter ranges in the Intermountain West. Roloff et al. (2001) validated an elk habitat effectiveness model for Rocky Mountain elk in one area of South Dakota. Boyce et al. (2002) tested resource selection models for grizzly bears in Yellowstone National Park.

Use of Prior Expectations to Evaluate Model Performance

The use of *a priori* rules in evaluating a model's performance is important (Johnson 2001). That is, whether a model is "valid" depends on whether the model performs according to a set of expectations in relation to modeling objectives and biological relevance. While statistical tests of validation are the usual method (Mayer and Butler 1993, Roloff et al. 2001, Boyce et al. 2002), unless they are linked to *a priori* expectations about the biological significance of model performance their relation to model performance is unclear (Johnson 2001). And, if one directly states and evaluates the expectations of how a model should perform in terms of its biological significance, then the use of statistical tests may be unnecessary. For example, Wisdom et al. (2002) developed a list of 5 major *a priori* expectations of how a sage-grouse model should perform, based on biological expectations. Results showed that 4 of the 5 expectations were met in relation to modeling objectives and the model's intended uses in management.

A list of biologically-based, *a priori* expectations about model performance of RSFs is stated below. These expectations describe how the resource selection models tested in this study should perform in relation to expected uses of the RSF in management. This list of expectations was used to evaluate model performance in combination with insights gained from the more traditional forms of validation based on statistical significance or other descriptive statistics.

Statistical Tests for Spatial Model Comparison

RSFs may be developed using presence/absence data or presence/availability data (Manly et al. 2002). The models tested here were developed from the latter (Johnson et al. 2000). Statistical techniques developed to validate spatially explicit ecological models include the Kappa statistic (Cohen 1968), the Receiver Operating Characteristic (ROC, Pearce and Ferrier 2000), the volume of intersection Test Statistic (Roloff et al. 2001) and the Ranked Bin Test (Johnson et al. 2000, Boyce et al. 2002).

Two commonly used methods of validation are the Kappa statistic and the ROC. The Kappa statistic is a simple statistic that measures the proportion of all possible cases of presence or absence that are predicted correctly by a model after accounting for chance (Manel et al. 2001). The ROC is a more complex measure of correctly predicted use versus correctly predicted non-use based on threshold probabilities from a logistic regression model (Brooker et al. 2002). The Kappa statistic is most commonly used in remote sensing studies (Pontius 2000), while ecologists only recently borrowed the ROC from the medical field (Boyce et al. 2002). Boyce argues that both the Kappa and ROC are flawed when using presence/availability data because the presence and availability data are from the same population (i.e., a cell that is used will also be included in the list of available cells). Consequently, the categories of observed values and predicted values are not unique and the aforementioned validation techniques will give a falsely poor classification rating. To validate presence/availability models, Boyce et al. (2002) and others (Howlin et al. 2003, Johnson et al. 2000) have successfully used a binning method that compares sums of predicted and observed use. This "Ranked Bin" method ranks proportionate RSFs (RSFPs) values (often >100,000 cells) and bins them into equal area zones of ascending predicted use. Each cell also has an observed proportion of use, which is summed within the predicted use bins or zones. The resulting pairs of sums can then be analyzed with a Spearman-rank correlation test.

The volume of intersection test statistic (Seidel 1992) is a measure of overlap of two utilization distributions. A utilization distribution is a bivariate probability distribution of an animal's use of space over a defined period of time (Van Winkle 1975). Roloff et al. (2001) used the volume of intersection to test overlap between predicted and observed elk habitat use using this method and he and others developed an application for using this test in a GIS (Gary Roloff, pers. comm). The volume of intersection calculation is:

$$\text{V.I. Index} - \iint \min\left(f1(x,y), f2(x,y)\right) dx\,dy$$

where f1 is the utilization distribution from GPS collar data or random data and f2 is the predicted RSF probability distribution. An index of 0 indicates no overlap while an index of 1 indicates perfect overlap. Feiberg and Kochanny (2005) compared the volume of intersection and several other indices of utilization distribution overlap and found that the volume of intersection is a good measure of the degree of similarity between two utilization distributions. However, they also found that the volume of intersection underestimated shared space use by about 30% over the best overlap index. The volume of intersection is most appropriately used with individual animals or sub-herds that use the same space (G. Roloff, pers comm., J. Millspaugh, pers. comm.).

Methods

My study occurred in coordination with a 5-year study being conducted by Oregon Department of Fish and Wildlife (ODFW), National Council for Air and Stream Improvement (NCASI), Boise Cascade Corporation (BCC), and Oregon State University (OSU) (ODFW 2001, Riggs et al. 2004). In spring of 2003-2005 cow elk were captured and fitted with global positioning system (GPS) telemetry collars. These elk were re-captured fall of each year to remove the collars and download GPS-collected locations to a computer. These locations provided the observed data needed to test the Starkey models on the Sled Springs landscape.

Study Area

Description

The Sled Springs study area (45.6° N, 117.5°W), Wallowa County, Oregon, consists of rolling upland plateaus bisected by steep canyon riparian systems. The area is bounded on the south and west by the Wallowa and Grande Ronde River systems. The area encompasses approximately 181 km^2 and varies in elevation from 741 to 1323 meters. Sled Springs is underlain by a basaltic formation that characterizes the surrounding Columbia River plateau region. An ash layer occurs on north slopes and flat areas. The climate is characterized by cold, snowy winters and warm, dry summers. Annual precipitation ranges from 43 to 63 cm, falling mainly as snow in winter and rain in spring. Average annual temperature is approximately 7° C (Sheehy et al. 1999). Soils are minimally developed but relatively deep due to the ash layer that underlies much of the area.

The vegetation is coniferous forest interspersed with grasslands. Both the forests and grasslands are actively managed through logging, recreation, and livestock grazing. Forests occur on flat and north facing aspects and consist of grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menzesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and Englemann spruce (*Picea englemanii*). Grasslands and meadows occur where soils are too shallow or wet for trees, predominantly south facing slopes, and are dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudorogneria spicata*), Sandberg's bluegrass (*Poa secundai*), onespike oatgrass (*Danthonia unispicata*), and Kentucky bluegrass (*Poa pratensis*). Forest understories are grass-, forb-, or shrub-dominated, depending on plant community and post-disturbance regimes. Understory biomass declines as overstory canopy cover increases.

The study area is on corporate land, owned by Gallatin Land and Timber Co. and managed by Forest Capital Partners (FCP). However the land was owned and managed by BCC at the start of the study. The study area was defined by the extent of the summer distribution of elk. Timber production is the primary management use of the area and cattle-grazing is a secondary use. The area was designated a Cooperative Wildlife Management Area and hosts several on-going wildlife studies by a team of inter-agency researchers (Riggs 2002).

Study Area Boundary Definition

RSFs are estimated using use/availability ratios. Consequently, the "available" resources must be carefully quantified because the amount of resources available to the animal can easily influence the expected proportion of use (Garshelis 2000). Porter and Church (1987) concluded that where habitats occurred in aggregated patterns, the size of the study area changed inferences of habitat use by wildlife. However, in areas where the habitat features were regularly dispersed study area size had no effect. They recommended letting the animals define the study area through home range analysis in non-aggregated habitats. Fig. 4 shows a digital image of a portion of the study area, portraying the habitat as being non-aggregated in relation to the foraging range of an elk.

A preliminary study area boundary was identified using data collected between March and October of 2001 by ODFW. That year 20 cow elk from the resident herd of about 400 elk at Sled Springs were captured and collared with VHF radios (Johnson 2002). The 20 elk that were collared were selected randomly from a helicopter. Twenty sites were randomly selected before catch day and the first elk seen after arriving at a site was caught. After 20 elk were collared they were subsequently aerially located (estimated accuracy of + or – 250 m) 7 times throughout the season. To define the preliminary study area boundary I estimated the combined home range area using an adaptive kernel method (Seaman et al. 1999) for the 137 elk locations obtained from the aerial flights (fig. 5). I used the kernel method because it has been generally accepted as an unbiased home range estimator (Powell 2000). Rodgers and Carr (1998) developed software called Home Range Extension (HRE) for Arcview, which used points in a GIS coverage to define the home range boundary. I used the default parameters in HRE for Arcview (Environmental Systems Research Institute (ESRI), Redlands, CA) to calculate home range area for the 20 collared elk, using an adaptive kernel estimate and the “User” option for smoothing parameter. From the locations collected over the summer on the 20 radio-collared elk, I removed one animal from the estimation because it left the area (fig. 5).

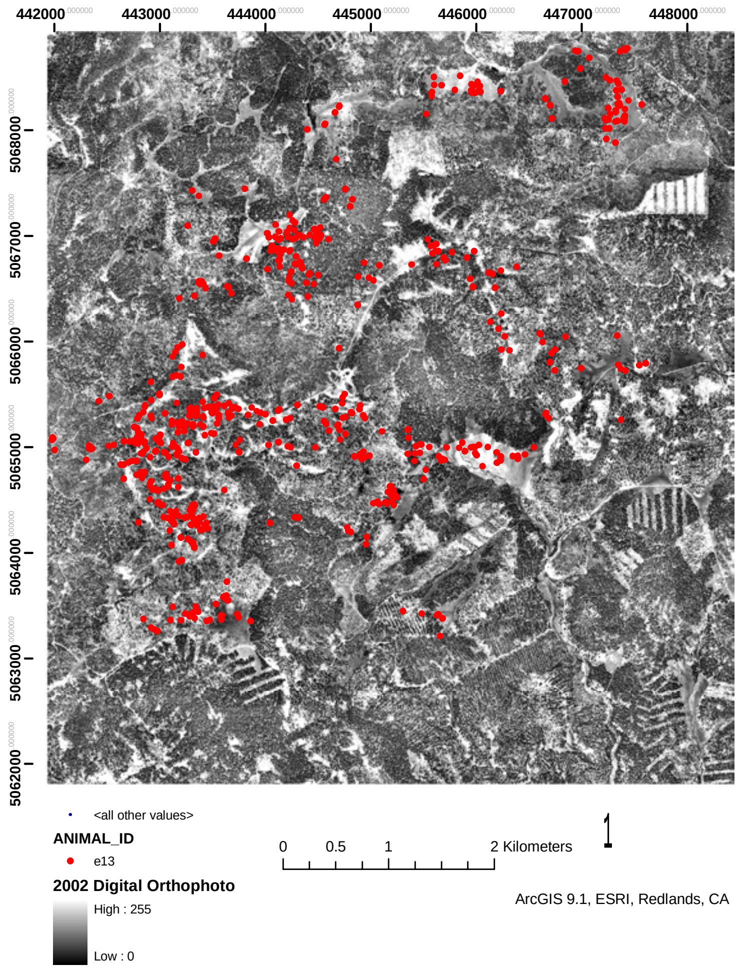


Figure 4 Elk "e13" during foraging periods May 15 - June 14 in 2003 and 2004. This illustrates regular dispersal of vegetation patches relative to the elk's foraging area and justifies using elk locations to define available resources.

After data were collected from the GPS-collared elk, I calculated the final study area boundary using a random sample of all the GPS locations obtained and the method described above. I calculated a 90% kernel home range area for all elk used in the validation analysis. Finally, I removed areas within the boundaries of the kernel home range that were not corporately owned and managed (fig. 6).

The justification for this boundary was that the lands excluded were not managed similarly to the corporately-owned lands. For example, the Smith Ranch in the southern portion of the study area attracts elk in unusually high numbers. In addition, I could not obtain resource data from three other entities (Oregon Dept of Forestry, U. S. Forest Service, and Bureau of Land Management) in a cohesive and timely manner for the analysis. In the final analysis I included observed locations collected during the 2005 grazing season but I did not re-estimate the study area boundary. I included the 2005 locations if the majority of the elk locations collected that year were within the study area.

Scale of Research

It is important to use similar scales in comparing RSF models (Boyce et al. 2006). Spatial and temporal grains and extents used during validation were similar to those used during model development except for spatial extent. The spatial extent of the Sled Springs study area was 181 km^2 while the study area at Starkey was 77 km^2. Temporal grain for both areas was 1-month and temporal extent was 4 years at Starkey and 3 years Sled Springs. For both areas the minimum mapping unit used to characterize model variables was < or = 2 ha. Resolution of raster maps used in model development and model validation was .09 h (30 X 30 m cell).

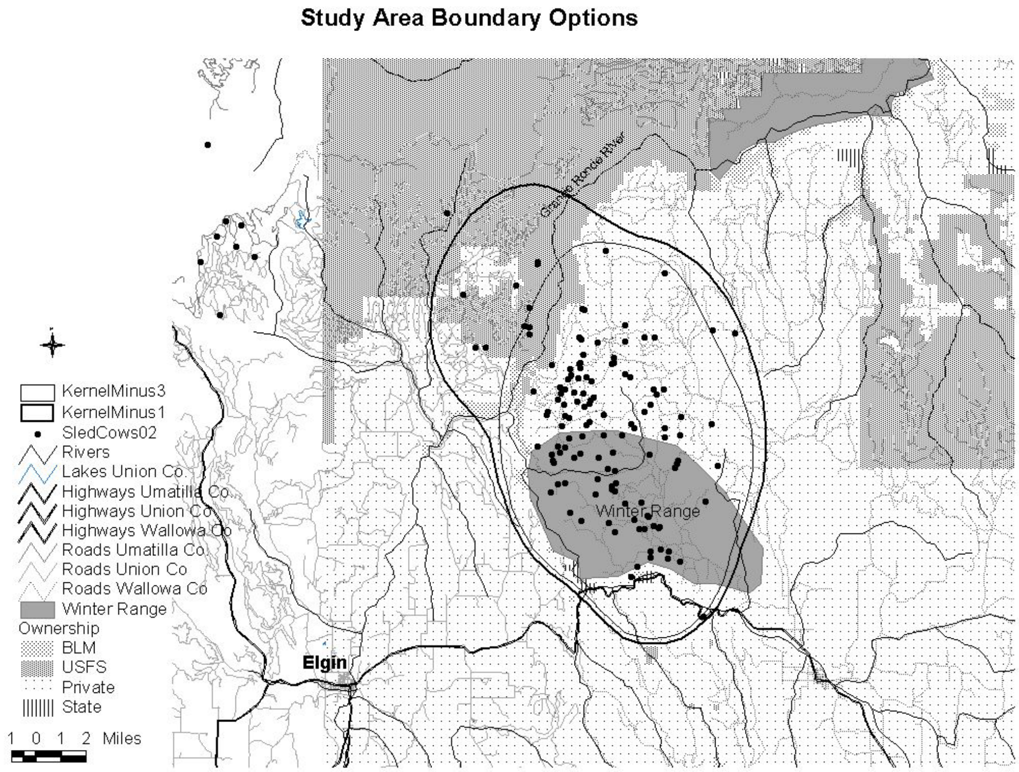


Figure 5 Home range boundaries for summer locations of 21 (outer polygon) and 19 (inner polygon) cow elk. Cow elk were captured randomly on winter range. Kernel estimator (Seaman et al.1999) was used to define 95 percent home range area (ArcGIS 9.10, ESRI, Redlands, CA).

Data Collection and Preparation

Model Time periods

The Starkey elk models (Appendix A) consist of 8 models that predict proportion of use by elk during daily peak foraging times for 1-month periods beginning on April 15 and ending on November 15 (Ager et al. 2004), with the eighth model predicting a 2-month spring period from April 15 – June 15 (Johnson et al. 2000). Monthly time periods for the Starkey RSF models were based on considerations of plant phenology and cattle management. May 15, June 15, and July 15 are the flowering midpoint dates for elk sedge (*Carex geyeri*), Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudorogneria spicata*), respectively (Coe 1997, Skovlin 1967), which are important foraging species for elk.

Figure 6 Study area is intersection of 90% kernel home range and BCC ownership

.

Phenology is the main factor influencing changes in nutritive value of plants (Cook 2002), which influences seasonal changes in foraging distribution of elk (Skovlin et al. 2002). Cattle begin grazing on forest allotments in the Blue Mountains generally on June 15 and end on October 15 each year, with cattle often moved among pastures on a monthly time step. Cattle presence may influence distribution of elk, depending on season of use (Coe et al. 2001).

Daily Observation Intervals

The observation interval needed for the observed use to match the frequency used during development of the Starkey RSF models was 2 hours during foraging periods (defined as 2 hours before and after sunrise and sunset). However, animal location data was collected at 30-min (2003), 20-min (2004) and 15-min (2005) intervals to accommodate other studies being conducted at Sled Springs (Riggs 2002). Animal locations were subsequently sub-sampled to provide a similar number of locations per elk per time step.

Animal Locations

A sampling schedule on elk GPS collars was developed using software provided by Lotek, Inc. The schedule was developed for the period between expected collar releases (March of each year) until the expected collar retrievals (December of each year).

In 2003, the schedule began on April 15 at 30-minute fix intervals for 8 hours per day during foraging periods (2 hours before and after sunrise and sunset), and 1-hour fixes for the rest of the 24 hours (Green and Bear 1990). A moving window following the nearest hour of sunrise and sunset was used to keep the more-frequent fixes within the foraging period. In 2004 the newer model collars allowed a constant 20-min 24-hr fix schedule and in 2005 a 15-min 24-hr schedule was used.

Twenty cow elk were randomly selected in fall 2001 and fitted with traditional radio-tracking collars. In 2003, 10 of the traditional collars were replaced with Lotek GPS model 2200 collars with a sampling interval of 30 minutes. In 2004 the 10 collars were upgraded to model 3300 collars to accommodate other studies. In addition to these collars, 14 more collars were purchased and these 24 collars were deployed in March of 2004 and programmed at a 20-minute sampling interval. In March of 2004, 7 of the 2003 cow elk retained a GPS collar and 17 more were placed on new animals.

Leban et al. (2001), who studied sample size of elk in relation to the resource variables estimated at Starkey, concluded that 20 animals were the minimum number needed to sample for "adequately determining resource selection for a population during a season at one time of day. Final observed data include 5 cow elk with 3 years of locations (e14, e2, e22, e23, e3), 11 with 2 years (e13, e16, e164, e167, e4, e5, e52, e53, e54, e55, e59), and 8 with 1 year (e17, e19, e24, e253, e254, e257, e58, e9), for a total of 24 elk. There were 10, 17 and 18 elk used in analysis in 2003, 2004 and 2005, respectively.

I displayed each collar file individually on a map. Two elk (e165 and e167) took excursions for several days outside their usual area whereas most elk maintained fidelity to one area. Elk e165 in 2004 traveled linearly the last half of April 2004 in Sled Springs and then crossed the Grande Ronde River and went to the Umatilla National Forest for the rest of the year. She stayed outside the study area through 2005. I deleted this elk from the analysis. Elk e167 traveled linearly outside her usual area during the hunting season (first part of November). I deleted these locations from the analysis. In 2005 I selected collars that were mostly inside the study area defined by the 2003 and 2004 locations.

I calculated observation rate as records with a valid GPS fix divided by the total number of records in the data file (attempted plus successful fixes). To equalize 2003 (with 30-min sampling interval) , 2004 (with 20-min sampling interval), and 2005 (15-min sampling interval) I randomly selected percentage of the locations based on number of locations per elk in 2003 (6168). This was 41% in 2004 and 34% in 2005 (Hawth's Tools extension in ArcMap). Next, I selected records that were within 2 hours before and after sunrise and sunset for the date. Finally, I withheld a random 20% of the remaining locations for use in model refinement. No data was censored from the GPS files as our accuracy and observation rate tests showed that this was not warranted (see GPS Collar Tests, above).

In 2003 all 10 Lotek 2200 collars functioned during the entire time period in the field. In 2004 there were 24 collars in the field and one collar stopped taking locations on 8/10/2004. In 2005, of the 24 GPS collars that were deployed in April, there were 5 collars that failed during part of the year. Observation rate ranged from 88.00% to 99.46% (Table 1).

Friar et al. (2004) investigated the effect of GPS collar observation rate bias on estimating RSFs. She found Type II error rates (a coefficient was not identified as being important when in fact it was) of 30-40% given an observation rate bias of as little as 10%. However, this was with a GPS sampling intensity of 6 h. At a sampling intensity of 1 h she did not find any Type II errors. Sampling intensity for my study was 0.5 h. Consequently, it is unlikely that the <90% observation rate in the location data significantly affected observed proportion-of-use for the validation tests.

Table 1. Observation rate for GPS collars by year.

Time Period	2003	2004	2005
Apr 15 to May 15	92.09	97.13	99.46
May 15 to Jun 15	93.15	97.06	99.32
June 15 to July 15	90.12	97.84	99.47
July 15 to Augt 15	88.48	97.99	99.00
Aug 15 to Sep 15	88.00	95.25	98.79
Sep 15 to Oct 15	87.34	90.71	98.80
Oct 15 to Nov 15	89.88	97.05	98.92
Average for year	**89.02**	**97.78**	**99.11**

The number of locations in September and October was lower than in other months (fig. 7). Further investigation revealed that several individual cow elk were outside the 90% kernel home range study area during those 2 months, probably because of disturbance during the hunting seasons (September and October). Over 200 locations remained for these elk during those 2 months, inside the study area boundaries.

Predictor Variables

Development of a predicted elk distribution map for the Sled Spring study area required habitat variables estimated over the landscape for each monthly time step. These were either obtained from existing sources or developed for this analysis. Categories of GIS layers needed to calculate RSFs over the Sled Springs landscape were:

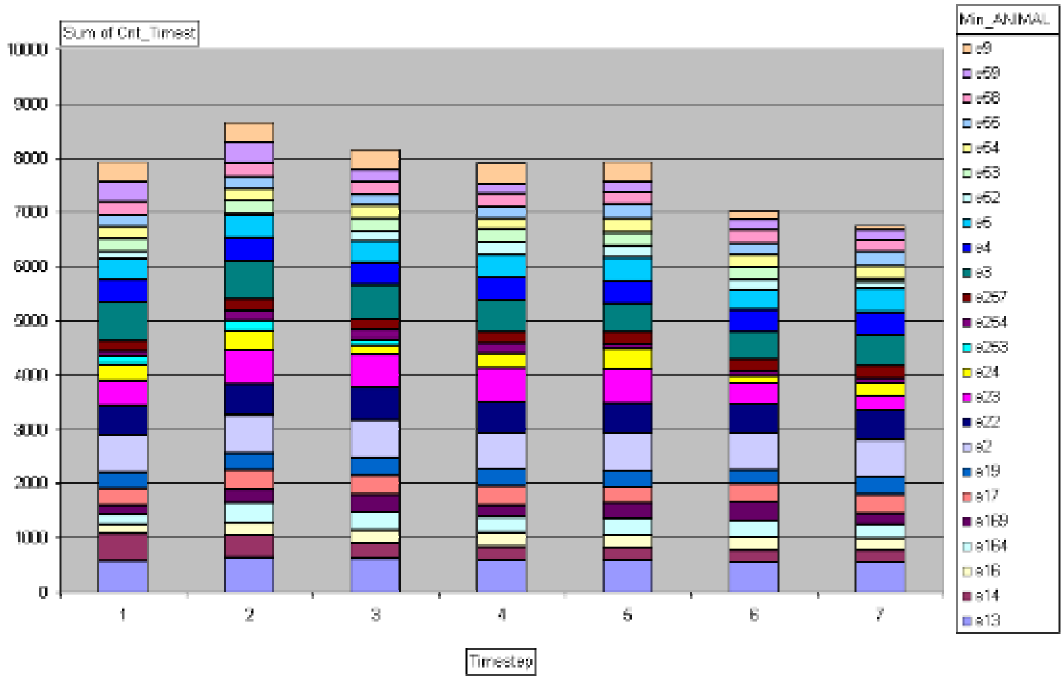


Figure 7 Cow elk locations by monthly time step. 1 = Apr 15 – May 14, 2 = May 15 – Jun 14, 3 = Jun 15 – Jul 14, 4 = Jul 15 – Aug 14, 5 = Aug 15 – Sep 14, 6 = Sep 15 – Oct 14, 7 = Oct 15 – Nov 14.

- topographic (sine of aspect, cosine of aspect, percent slope, and convexity)
- vegetation (large tree canopy cover, distance to edge of stand boundary, distance to large tree canopy cover >40%, circularity of forest and grassland polygons, and forage production)
- soil (depth)
- traffic (distance to high, medium, and low traffic)

Topographic Layers **-** The topographic variables were derived from 10-m resolution digital elevation models (DEMs) available from USGS Earth Resources Observation and Science (EROS) Center. I used ArcGIS 9.1 tools “slope,” “aspect,” and “curvature” to generate slope, sine and cosine of aspect, and convexity layers, respectively (Fig. 8). Each variable was calculated using a

3 x 3 window of neighboring cells. Slope was calculated in degrees. Sine and cosine of aspect were generated by using the ArcGIS tools "sin" and "cos" with the aspect layer as the input layer. Calculation of sine of aspect results in values of -1.0 – 0.0 for westerly and 0.0 – 1.0 for easterly aspects. Calculation of cosine of aspect results in values of -1.0 – 0.0 for southerly and 0.0 – 1.0 for northerly aspects. Accuracy of USGS DEMs is documented well. Ninety percent of 7.5-minute DEMs derived from a photogrammetric source, have a vertical accuracy of 7-meter root mean square error (RMSE) or better and 10 percent are in the 8- to 15-meter range. (U.S. Geological Survey Fact Sheet 040-00, April 2000).

Vegetation Layers - Vegetation variables were developed using two methods. Canopy cover and the associated distance-to-cover, distance-to-edge, and circularity-of-forest-stand layers were derived from a forest stand polygon layer obtained from BCC (minimum polygon size 2 ha). Forage production was derived from a grid map of Potential Natural Vegetation and field estimates of forage production.

Canopy cover (% tree canopy of trees greater than 12 cm dbh) was completed by photo-interpretion of a digital orthophoto (resolution 1 m) with overlayed forest stand polygons and ocular estimation of percent large-tree canopy cover across forest stands. The photo-interpreter was the same person who provided canopy cover estimates for the Starkey GIS layers during model development. Canopy estimates for each month of each year were adjusted based on logging information supplied by BCC. Boundaries of harvest polygons were edited to conform to actual cut boundaries shown on a digital orthophoto. Canopy cover decreased over the three validation years as logging activities took place each year (fig. 9).

Photo-based canopy cover estimates were compared to ground estimates obtained during summer of 2005 (John Cook, NCASI). The ground estimates were from tame-elk pen sites used in another study at Sled Springs and were not randomly selected. The comparison between stand estimates and selected pen sites is not ideal because the scale of the pen site was smaller than the scale of the photo-interpretation. Consequently it was possible that a pen site could have been placed in a small, anomalous patch of the associated forest stand polygon. However, the comparison does provide an independent verification of the data from ground estimates (fig. 10).

The distance-to-cover variable was constructed by selecting areas with >40% canopy cover from the canopy cover layer (fig. 11). These polygons were then rasterized as a cover/no cover classification. Then a distance-to-cover map was generated within the study area buffer using "eucdistance" in ArcGIS Raster Calculator.

The distance-to-edge variable was constructed by selecting all the polygons < 11% canopy cover and all polygons $\geq$ 11% canopy cover as a forest/non-forest classification (fig. 11). Hawth's Tools, an independent analysis extension program for Arc 9.1, was used to extract the edge of the forest/non-forest layer. A distance calculation ("eucdistance", ArcGIS Raster Calculator) was then run for each cell in the study area from the edge lines of the forest/non-forest layer.

Circularity of forest and non-forest areas was calculated using the forest polygon table in a new field called "Circular":

4 * 3.1415 * [Shape_Area] / ([Perimeter] * [Perimeter])

Where [Shape_Area] is the area of the polygon (m^2) and [Perimeter] is the length of the polygon perimeter (m). The resulting circularity measurement is a number between 0 and 1, with 1 indicating a circle and lower values indicating longer, narrower shapes (fig. 11).

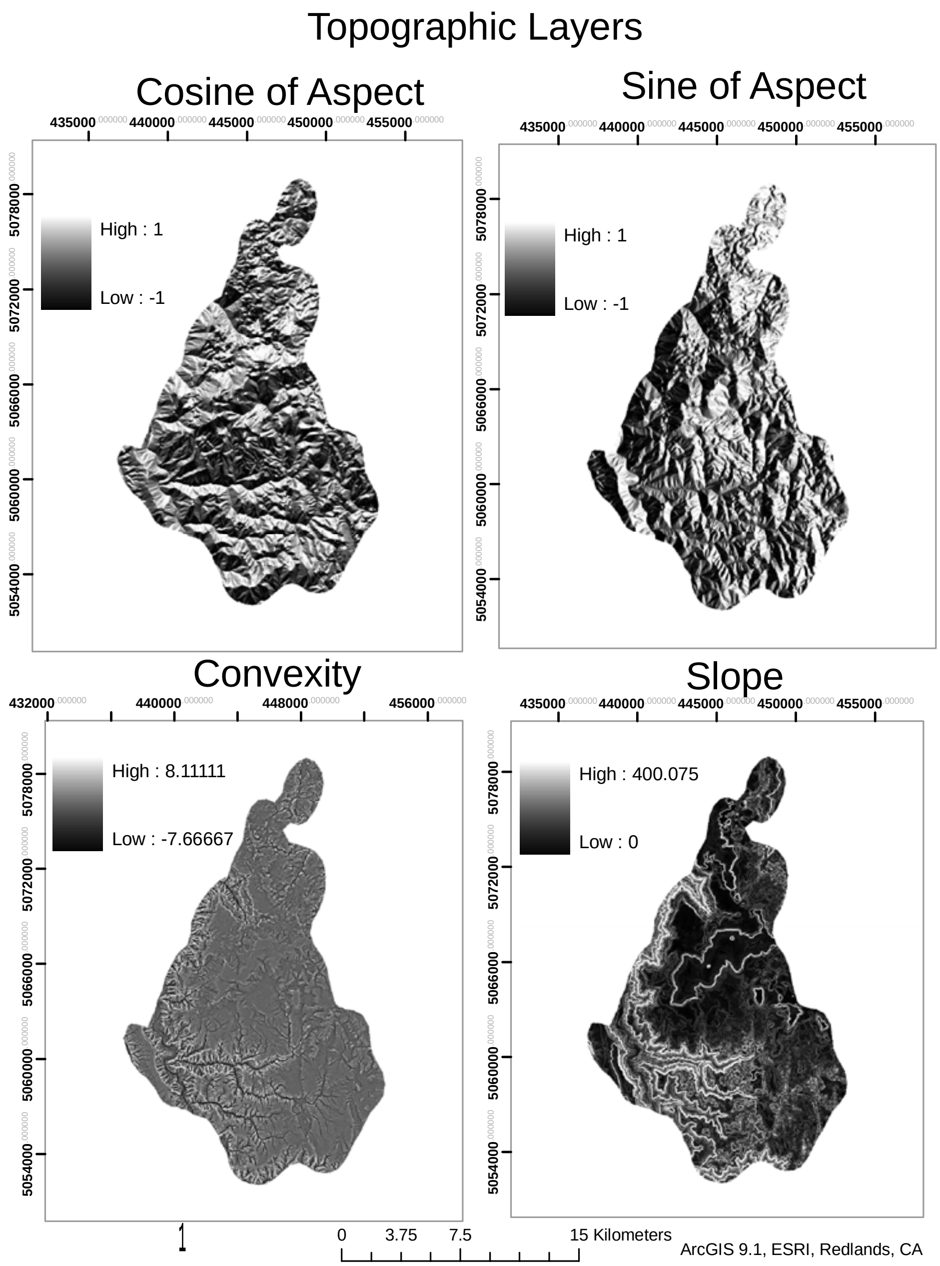


Figure 8 Topographic layers for Sled Springs used in calculating prediction maps from Starkey models. See text for explanation of development of each layer.

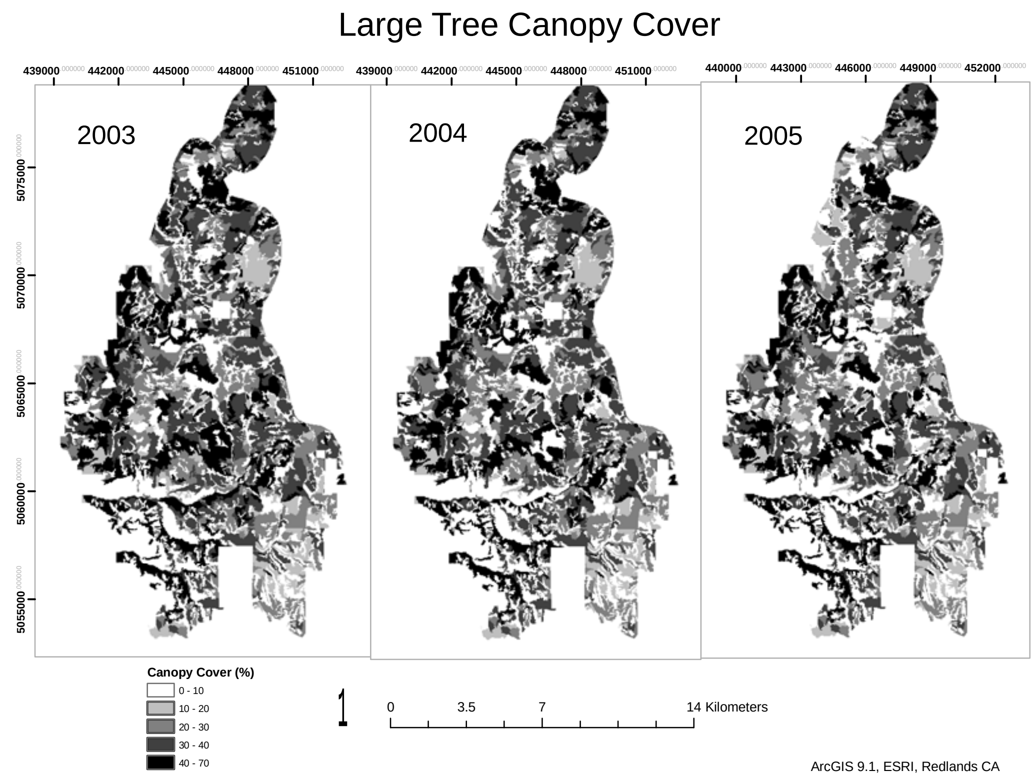


Figure 9 Canopy cover estimates for 2003 – 2005 at Sled Springs. Canopy cover decreased over the 3 years due to logging.

Forage production (fig. 12) was estimated over the study area using annual peak production (non-grazed) field estimates from 2003-2005 (Darambazar et al. 2007). I overlaid 497 plots from the field estimates on a GIS layer of plant association groupings (Kelly et al. 2005) and calculated mean forage production where the field estimate habitat definition matched the habitat definition in the GIS classifications for wet Douglas-fir, wet grand fir, ponderosa pine, and dry grand fir. I then re-classed the plant association grassland types for Idaho

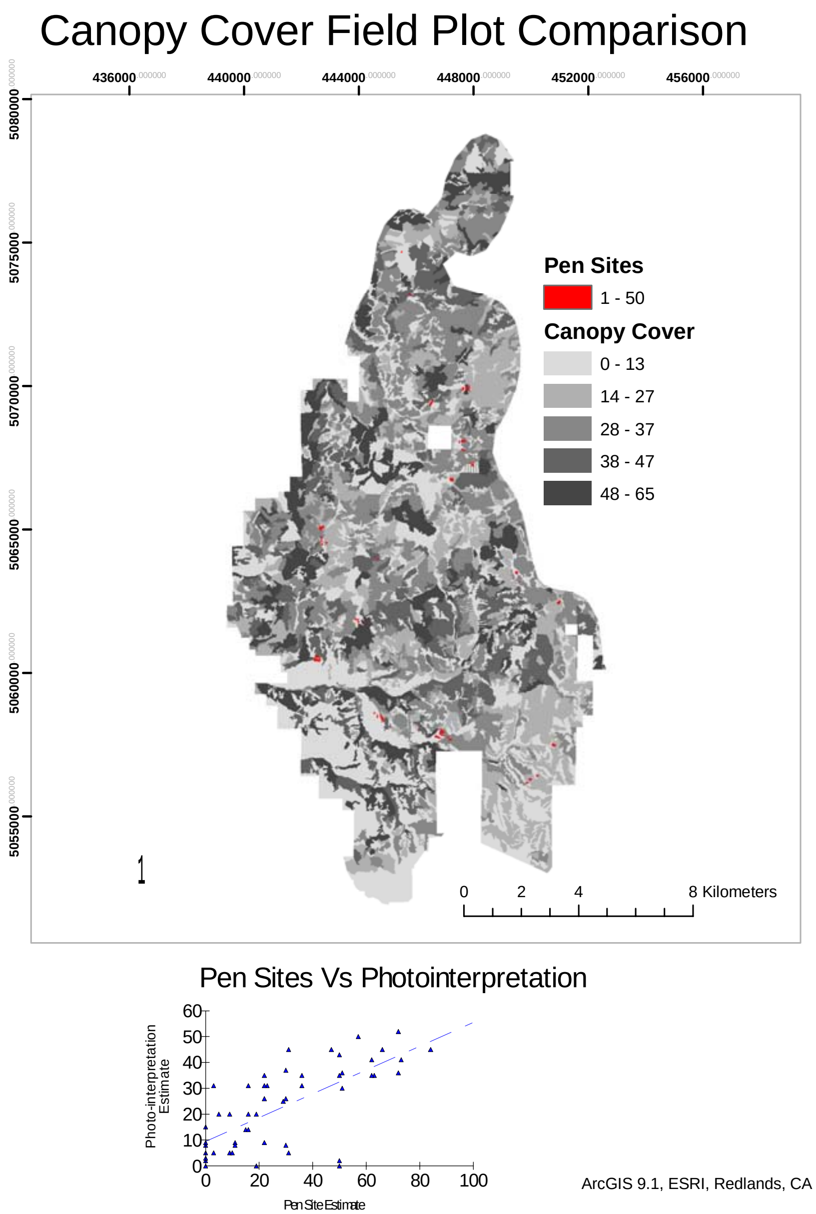
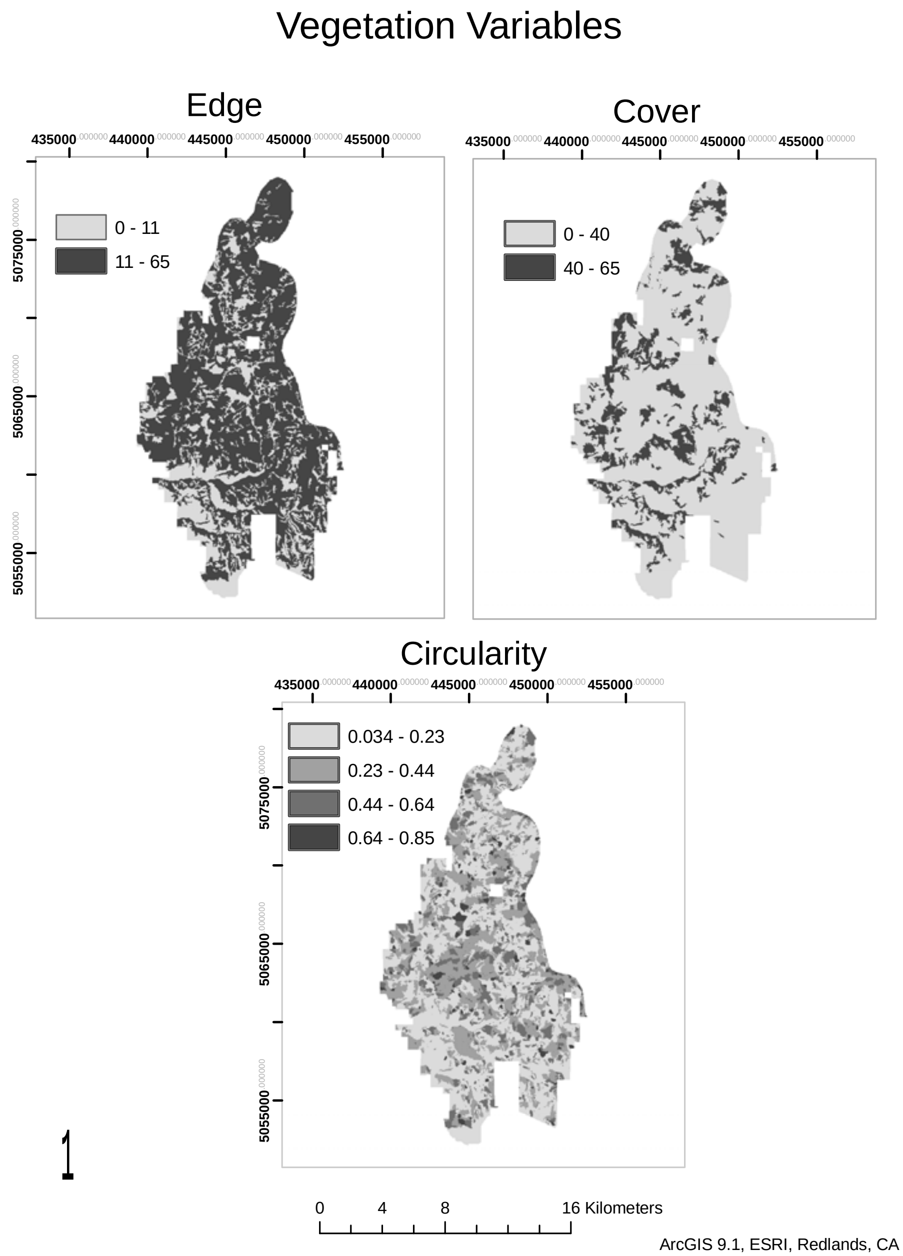


Figure 10 Canopy cover photointerpretation comparison to field checks at Sled Springs.

fescue/prairie junegrass, Idaho fescue/bluebunch wheatgrass, bluebunch wheatgrass/Sandberg's bluegrass, and Sandberg's bluegrass/one-spike oatgrass to one classification and matched the polygons to the field plots classified as grassland. I overlaid National Wetlands Inventory polygons that identify wetlands and wet meadows onto the plant association layer and matched field plots that were within the wetland boundaries and were described as wetlands, scablands, or riparian grasslands (Table 2). The accuracy of the plant grouping layer was 63%, based on a previous assessment (Kelly et al 2005).

Soil Layers - The soil layer and the associated depth variable was obtained from the Natural Resources Conservation Service (NRCS). The NRCS Soil Survey Geographic Database (SSURGO) was accessed online (http://soildatamart.nrcs.usda.gov) and the soils polygons for Wallowa and Union Counties obtained. An additional database and macro were obtained from the Portland Office of the NRCS (Steve Campbell), which calculated soil depth of the polygon based on the most prevalent soil type in the polygon. This produced a soil depth layer (fig. 13) that I rasterized. According to NRCS metadata the positional accuracy of the soil meets "National Map Accuracy Standards at a scale of 1 inch equals 1,000 feet…Soil delineation boundaries and special soil features generally were digitized within 0.01 inch of their locations on the digitizing source… All attribute data conform to the attribute codes in the signed classification and correlation document and amendment(s)." (http://soildatamart.nrcs.usda.gov/Metadata.aspx?Survey=OR670&UseState=OR#7).

Traffic Layers -The landowner in 2003 (BCC) provided a GIS roads layer (fig. 14) that included a road type attribute. Traffic levels at Starkey were calculated from an extensive network of traffic counters but no counters were used at Sled Springs. I estimated traffic rates based on road type and familiarity with the road system, gained from extensive field work in the area. I developed traffic estimates by model time step by initially ranking the roads based on road type.



t

Figure 11 Example of vegetation layers (July 2003) from which distance to edge, distance to cover, and circularity predictor variables were derived.

Table 2 Peak production (non-grazed) forage estimates for plant associations and their associated standard deviations and sample sizes.

Plant Association Group	Kg DM /ha	SD	Sample Size (field estimates)
Wet Douglas-fir	581	329	22
Wet grand fir	894	423	38
Ponderosa pine	943	453	19
Dry grand fir	1010	590	34
Grassland	2058	924	3
Wet meadow and scablands	3454	1249	14
Total Sample Size			**130**

Then the rankings were increased or decreased based on activities (logging, research, road closures, hunting). All-weather roads were assigned a categorical value of High (greater than 4 vehicles per day), conditional roads were assigned Medium (1 – 4 vehicles per day), unimproved roads were assigned Low (0.1 – 1.0 vehicle per day) and abandoned, closed, and blocked roads were assigned Zero (no vehicles). Traffic rates correspond to traffic rates used at Starkey in model development, which were based on road counter data analysis (Wisdom et al. 2004). I used road type as a surrogate for traffic rate because there were no traffic counters at Sled Springs. The resulting traffic estimate map was then examined visually and edited according to the following rules:

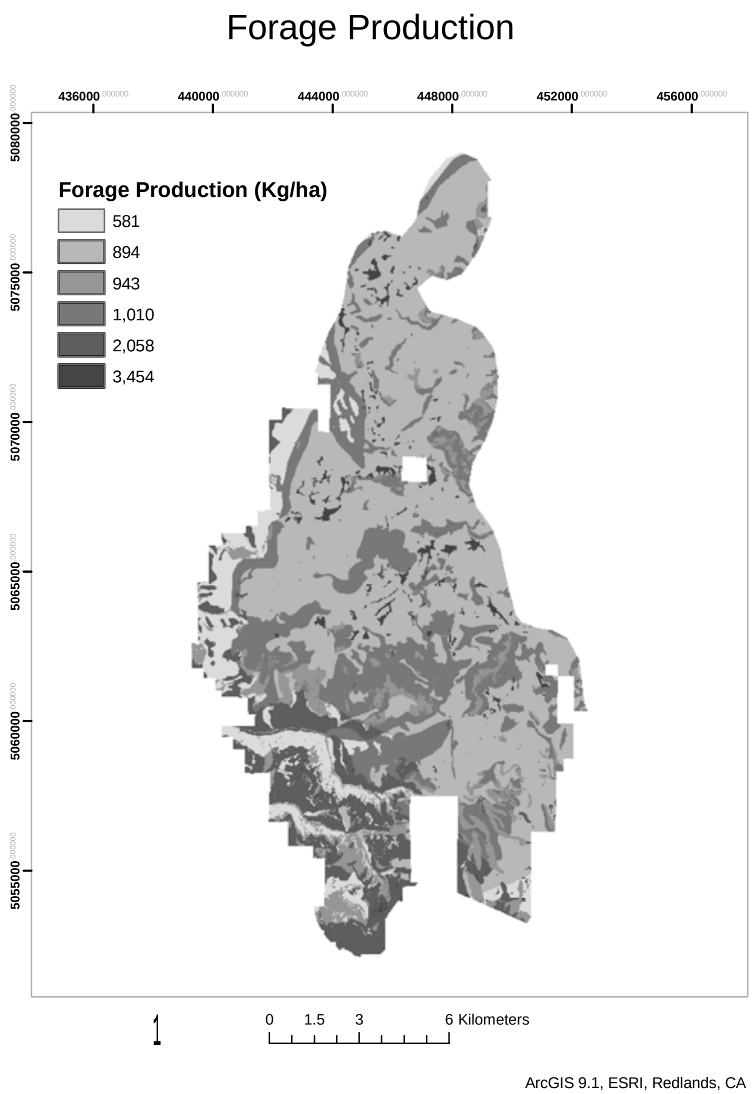


Figure 12. Forage production layer used in June and July models.

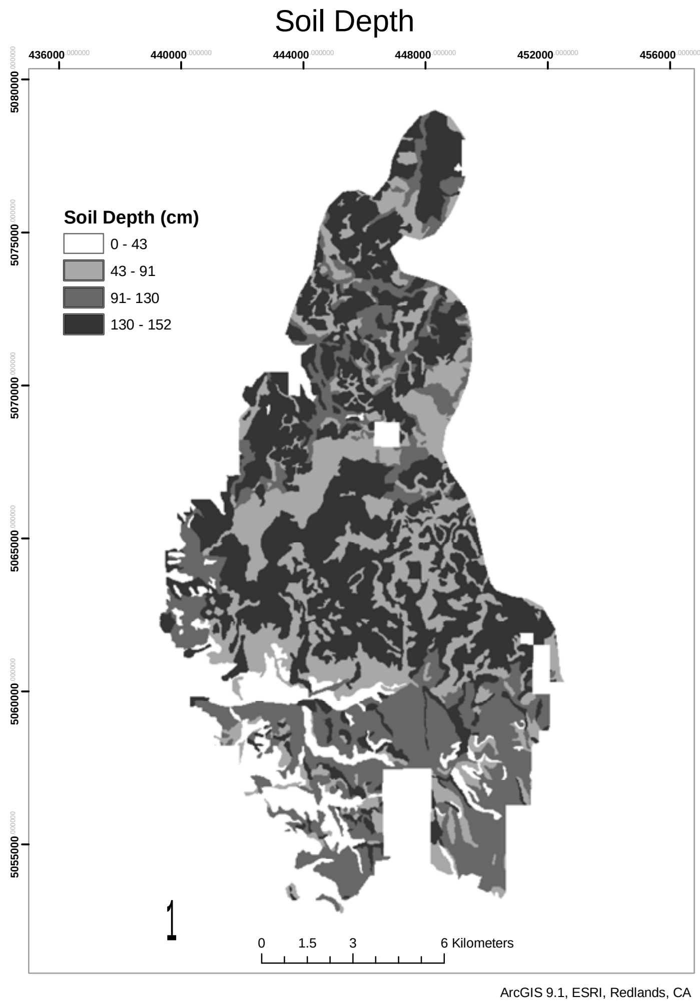


Figure 13. Soil depth layer used in prediction models.

a. If a segment was isolated from the same or next higher rank then I either re-ranked the isolated segment or the segment leading back to a higher ranked segment.

b. If there was a lower-rank segment between two higher-ranked roads and all segments were open to traffic, then I upgraded the lower-ranked road to be the same rank.

c. I downgraded by one rank all roads behind permanently locked gates.

d. I downgraded by one rank roads that were inside private ranches, unless they were public roads.
e. I downgraded by one rank level 3 roads that dead-ended and were little used.
f. I upgraded by one rank all roads affected by logging activities based on the harvest polygons during logging months.
g. I upgraded roads by one rank if they were used by researchers during elk calf capture periods.
h. I downgraded by one rank all roads closed by the Norgaard Travel Management Area restrictions and designated all roads that were open within the Norgaard management area as level 3.
i. I reset rankings lower than 0 to 0. I reset rankings higher than 3 to 3.

Roads affected by harvest activities were identified by selecting all roads within 100 meters of harvest polygons plus the haul routes leading back to the main roads. Roads affected by research activities were identified by selecting all roads that were commonly used by ODFW research staff to search for calves. Traffic rankings for every time period and year (6 models * 3 years for 18 time periods) were assigned to fields.

Next, the roads layer was rasterized for the 18 time periods including a 2-k buffer around the study area so that edge cells would get assigned the proper distance from traffic, when a traffic level occurred closer on the outside than on the inside of the study area. Then each ranking was selected and a distance to traffic layer calculated for each time period (12 predictor variables (see Appendix A)* 3 years for 36 traffic predictor variable maps.

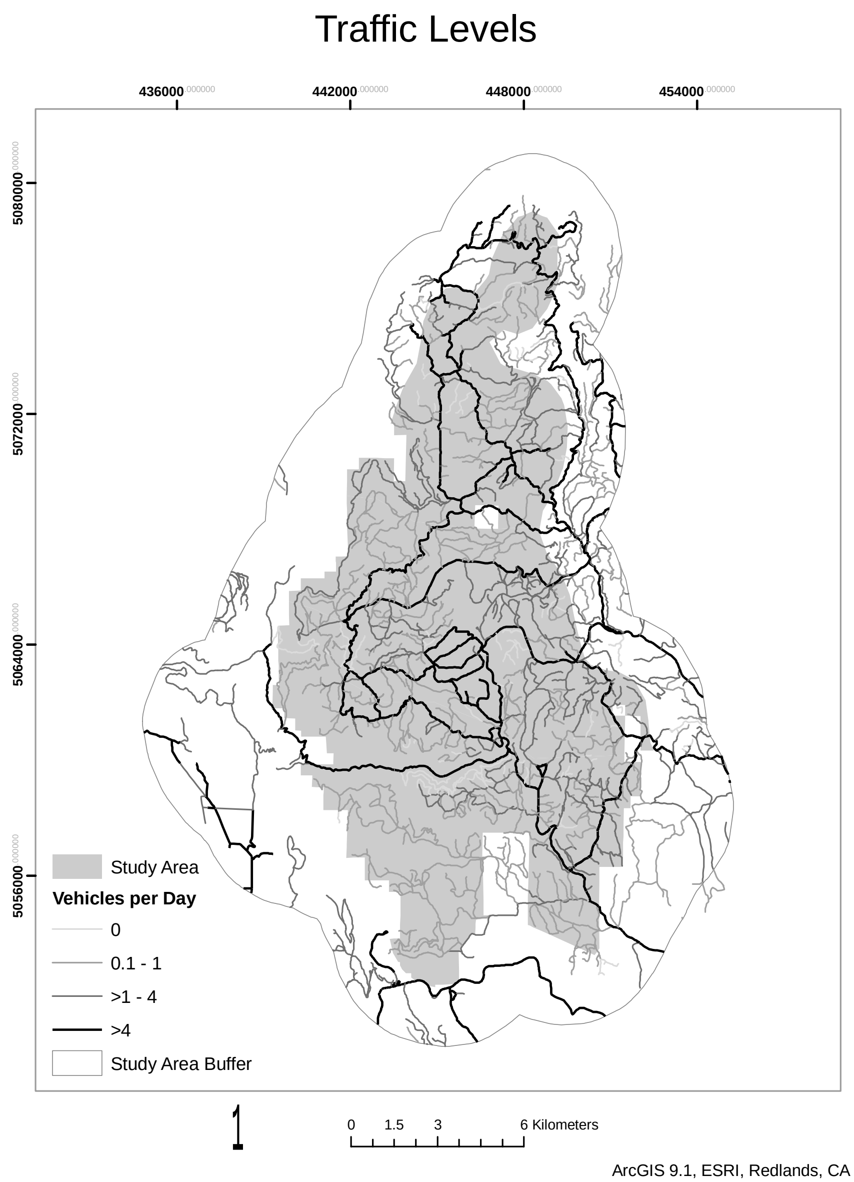


Figure 14 Traffic levels at Sled Springs based on road type. These were adjusted for each season and year as explained in the text to account for road closures, logging activities, and research activities.

Observed Proportion of Use

To calculate observed-proportion-of-use, I selected locations by month and year from the GPS locations database and summed them by 30-meter cell (fig. 15).

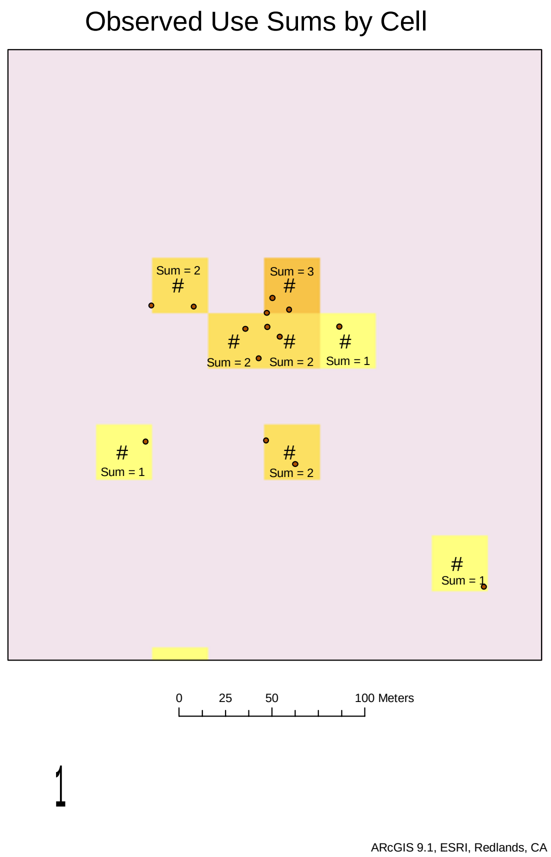


Figure 15 Example of centering of locations into a cell, giving the cell value the summed locations (cell size = 30 x 30 m).

Next observed proportion-of-use by cell was calculated:

$$Ouse_{isy} = Obs_{isy} / ObsSum_{sy}$$

Equation 1. Calculation for observed proportion of use.

where $Ouse_{isy}$ is the observed proportion of use at cell *i* and during season *s* and year *y*, Obs_{isy} is the sum of the observations at cell *i* during season *s* and year *y*, and $ObsSum_{sy}$ is the sum of all observations in the study area during season *s* and year *y*. Observed proportion of use was averaged across years for mean observed proportion of use by season.

Predicted Proportion of Use

Non-standardized coefficients from the Starkey RSF models (Appendix A) were used to estimate predicted proportion of use at Sled Springs, using the resource layers described above. For each time period and year each cell in the GIS was assigned a prediction value based on the following logistic formula:

$$\mathbf{Puse_{isy} = exp(\beta_0 + \beta_1 x_1 + \beta_2 x2 + \ldots + \beta_p \tilde{x}_{p.}} / \mathrm{Sum}[\exp(\beta_0 + \beta_1 x_1 + \beta_2 x2)]$$

Equation 2. Calculating predicted use using non-standardized model coefficients.

Where Puse $_{isy}$ is the expected proportion of use at cell *i*, during season *s* and year *y*, *ß* is the Starkey non-standardized model coefficient (Appendix A) for habitat variable *x* at cell *i* , and *p* is the number of habitat variables in the model. This resulted in 24 predicted-proportion-of-use GIS raster layers (8 seasons x 3 years). Mean predicted proportion of use was obtained by season by averaging predicted proportion of use across years.

Validation Tests

Using methods suggested by Boyce et al. (2002), Johnson et al. (2000), Johnson (2001), Roloff et al. (2001), and Wisdom et al. (2002), the 8 seasonal models were evaluated comprehensively, using a "performance matrix" to rate the models' overall success. Five evaluation criteria were used to test the Starkey models at Sled Spring: (1) a priori objectives and expectations, (2) percentage location, (3) ranked bin, (4) volume of intersection, and (5) use/availability.

A Priori Objectives and Expectations

The model objectives described below were identified or assumed by Johnson et al. (1996, 2000), Johnson (1999) and Ager et al. (2004) when they built models of RSFs for elk at Starkey. These objectives include the following:

- To identify and use predictor variables in elk distribution RSF models for which there is a prior, empirical basis established from past elk studies and which managers can relate directly to land use strategies.

- To use predictor variables in RSF models that are widely available to public land managers, and that are less costly to measure and assess for accuracy.

- To use predictor variables in RSF models that can easily be updated to increase accuracy, and that can be updated in a consistent manner among a variety of public land managers.

- To use a minimal set of predictor variables in RSF models that provides maximum predictive value of resource selection for elk, so as to avoid "over-parameterization" of models (Johnson et al. 2000). That is, to develop and use the most parsimonious (fewest variables with highest predictive capability) models possible.

- To develop models of RSFs for elk for each season of elk use on spring, summer and fall ranges specifically encompassing spring (15 Apr – 15 May, 15 May – 15 Jun), summer (15 Jun – 15 Jul, 15 Jul – 15 Aug, 15 Aug – 15 Sep), and fall (15 Sep – 15 Oct, 15 Oct – 15 Nov).

- To develop models of RSFs for elk spring through fall that specifically focus on the times of day that elk are most likely to be foraging (dawn and dusk, as defined by Johnson et al. 2000), thus capturing the most important selection patterns associated with nutrition.

Expectations for model validation that follow from these objectives include the following:

1. More observed locations should occur in areas of higher predicted use than in areas of lower predicted use. This simple test checks to see if >50 percent of observed locations are found in predicted use areas that have predicted values > 50 percent.

2. Observed proportional use within ranked predicted RSF equal area zones should be positively related in a linear or curvilinear fashion that is obvious when graphed. A Spearman rank correlation coefficient should be > 0.50 with a significance probability of < 0.10.

3. Home range utilization distribution grids of observed locations should show higher overlap with the prediction utilization distribution for models that perform better. A volume of intersection index of 0.50 or higher (Roloff et al. 2001, Feiberg and Kolchanny 2005) would be expected for utilization distributions that are similar.

4. Use/availability for model variables should be consistent with model coefficients, especially if a predictor is affected by land management (typically non-topographic variables). For example, if a predictor coefficient such as canopy cover is negative, a graph of use/availability within canopy cover categories should indicate higher selection in the lower values of canopy cover.

Percentage of Locations within High Prediction Areas

Mean predicted proportion of use cells (>200,000) were sorted from low to high and the upper 100,000 cells selected. Mean observed proportion of use within these cells was summed.

Ranked Bins Test

Predicted proportion-of-use for each 30 x 30 m cell in the study area was ordered from low to high and placed into 20 equal area bins. To determine the number of bins, I examined the RSF scores (not proportions) on a frequency histogram (Boyce et al. 2002). I noted the histogram often flattening out on the right side where high RSF values occurred, indicating many high RSF scores in few cells. I calculated the number of validation points occurring in 20 (I selected 20 based on past work of Johnson et al. [2000] and Boyce et al. [2002]) equal-area bins to make sure that bins were well represented (Hawth's Tools Point-in-Polygon in ArcGIS). Results showed that each of 20 bins were represented by at least 100 observed locations – indicating a sufficient number of location to adequately represent each of 20 prediction bins. For each bin the predicted proportions and the observed proportions were summed, resulting in 20 pairs of predicted and observed sums-of-proportions. This was done for 8 models for 2003, 2004, and

2005 individually. The seasonal RSFP grids and observed proportion-of-use grids were then averaged and the averaged proportions summed by bin and combined.

I used ArcGIS 9.1 Model Builder to sequence operations for the Ranked Bin tests. The resulting tables of predicted and observed sums by zone were exported to SAS 9.0 and Spearman's Rank Correlation test was run for each season/year combination and for seasons averaged across all years.

Volume of Intersection Index

For each season and year I calculated a fixed kernel utilization distribution for the combined elk locations. For the April 2003 time period I calculated utilization distributions for each individual elk as well. I used Hawth's Tools Kernel Estimator extension for ArcGIS 9.1 to construct utilization distribution grids. I used a fixed bivariate normal kernel option and a single smoothing factor of 1000 m. I examined smoothing factors between 90 and 1000 m and settled on 1000 because it was usually the size where the resulting 90% utilization distribution remained a single unit (pers. comm. A. Rodgers). I used all locations for each animal in the estimates. Swihart and Slade (1985) and DeSolla et al. (1999) recommend using all locations (as opposed to sub-sampling to eliminate auto-correlation), if the time intervals between each location is consistent. The volume of intersection index was executed using Arc Macro Language (AML). This macro used 2 input utilization distribution grids and calculated the 3-D area of 2 utilization distributions where they intersect (see Validation Methods, above), reporting an index between 0 and 1.

Habitat Selection Test

Prediction models may perform well, but unless observed locations are investigated for response to each habitat variable individually, it is unknown whether each predictor variable elicited the expected response in elk use. If a non-responsive variable in an otherwise highly predictive model is one that can be manipulated by management, such as vegetation and traffic variables, then it would impact planning decisions that may affect road use and timber management. Similarly, if a model performed poorly, an investigation will help elucidate poorly performing model variables.

Observed locations were summarized by variables that may be affected by management (canopy cover, distance to levels of traffic, distance to edge, and distance to cover) if they occurred in the model. A use/availability ratio was calculated (area of observed locations within a habitat category/ area of available habitat category). These ratios were graphed and evaluated for trend according to model coefficients.

To summarize observed habitat locations within available habitat categories, I used ArcGIS to combine the centered summed locations for a model time step and year (see Ranked Bin Test above), with each habitat variable grid map reclassified into 5-7 categories. I exported the combined pixel location sums and habitat categories to Access where I summed the locations by habitat category and then divided the used habitat by the available habitat to create a final table of use/availability ratios by habitat category. This table was then brought into Excel to graph patterns. Each year's selection ratio was then averaged across three years for mean monthly use/availability.

Performance Matrix

Each of the 8 models was rated according to performance criteria (Table 3). Points were summed for each model, giving an overall rating for that model. The rationale for the criteria in each rating category is as follows. For the locations within predicted use zones, it is intuitive to suspect that greater than half the observed locations should fall within the upper half of the predicted values. For the ranked bin test, a Spearman rank correlation coefficient of greater than 0.50 and a probability of 0.10 would show a positive trend in observed and predicted elk use. The minimum volume of intersection test statistic was chosen based on the scores obtained in Roloff et al. (2001) and the findings of Feiberg and Kochanny (2005). Finally, use/availability within the model predictor categories that are affected by management actions help make the model relevant to land managers. The more management variables that are responsive to model predictions (trend in the predicted direction), the more confidence a manager has in using the model for management.

Results

Over the 3 years of validation 47,588 elk locations were obtained for model periods (8 hours each day during peak foraging periods) from a total of 73 elk years (5 elk * 3 years, 14 elk * 2 years, and 30 elk * 1 year).

April 15 – May 15

Percentage of elk locations within the upper half of mean predicted use for this period was 67.06 (Table 4). Mean observed elk use increased in proportion to increasing mean predicted use ($R_s = 0.717$, $p = 0.0004$, Table 5, Fig. 16). Mean volume of intersection was 0.5693 (Table 6). Mean use/availability within vegetation and traffic variables was consistent for medium traffic and canopy and for high traffic up to 250 m (Appendix B). Elk use trends were for areas farther from high and medium traffic and for lower canopy cover. Performance matrix score for April was 14 (Table 7).

Table 3 Performance matrix identifies criteria for rating overall model performance. Each monthly model was scored based on 1) percentage of observed locations falling within upper half of predicted use areas, 2) results of Spearman correlation of ranked bins, 3) volume of intersection index, and 4) and percentage of model variables related to management (cover and traffic) that were consistent with model predictions (e.g., if a model coefficient was negative then use/availability should have been negative as variable value increased). After models were assigned a score for each test, scores were tallied. Models scoring 1-4 = Low, 5-8 = Med Low, 9-12 = Med High, 13 – 16 = High.

Test	**Score**			
	1	2	3	4
1) Locations within upper half of predicted use zones (%)	< 50	50 – 54	55 – 60	> 60%
2) Ranked Bin: (R_s) (p)	< 0.50 > 0.10	0.50 – 0.59 ≤ 0.10	0.60 – 0.69 ≤ 0.10	> 0.70 ≤ 0.10
3) Volume of Intersection test (Index 0 – 1)	≤ 0.50	0.50 – 0.54	0.55 - 0.59	≥ 0.60
4) Use/availability By elk within model variables related to management (% consistency)	< 25	25 – 49	50 - 75	> 75

Table 4 Results of Test 1(Table 3). Locations (%) within upper half of predicted use values in Sled Springs, northeast Oregon.

One-month Models	Year			Mean (2003 – 2005)
	2003	**2004**	**2005**	
Apr 15 – May 15	65.31	67.14	68.74	67.06
May 15 – Jun 15	49.67	40.11	47.57	45.78
Jun 15 – Jul 15	44.19	50.35	57.93	48.84
Jul 15 – Aug 15	58.68	48.61	49.02	52.10
Aug 15 – Sep 15	56.94	61.04	62.16	60.05
Sep 15 – Oct 15	55.22	62.37	55.65	57.75
Oct 15 – Nov 15	41.54	48.72	40.34	43.53
Two-month Models				
Apr 15 – Jun 15	61.89	57.70	56.46	58.68
Aug 15 – Oct 15	55.18	60.23	57.21	57.30

May 15 – June 15

Percentage of elk locations within the upper half of mean prediction values was 45.8% (Table 4). Mean observed elk use decreased in proportion to increasing mean predicted use (R_s = -0.388, p = 0.0910, Table 5, Fig. 16). Mean volume of intersection was 0.5530 (Table 6). Mean use/availability within vegetation and traffic variables was consistent for medium traffic to 250 m, for high traffic, and for canopy cover (Appendix B). The performance matrix score was 9 (Table 7).

Table 5 Results of Test 2 (Table 3). Spearman rank correlation coefficient and probabilities for Ranked Bin test at Sled Springs, northeast Oregon.

One-month Model s	**Year**			
	2003	**2004**	**2005**	**Combined Observed Vs Mean Predicted**
Apr 15 – May 15	0.6932 0.0007	0.7845 <0.0001	0.8015 <0.0001	0.7172 0.0004
May 15 – Jun 15	0.0218 0.9273	-0.65312 0.0018	-0.2460 0.2957	-0.388 0.0910
Jun 15 – Jul 15	-0.5879 0.0064	-0.0007 0.9975	0.7649 <0.0001	-0.3594 0.1196
Jul 15 – Aug 15	-0.0588 0.8226	-0.3740 0.1392	-0.3774 0.1353	-0.3431 0.1775
Aug 15 – Sep 15	0.4806 0.0319	0.7897 <0.0001	0.7792 <0.0001	0.7824 <0.0001
Sep 15 – Oct 15	0.5834 0.0069	0.8270 <0.0001	0.7118 0.0004	0.7578 0.0001
Oct 15 – Nov 15	0.0271 0.9094	-0.6696 0.0012	-0.3969 0.0831	-0.5308 0.0160
Two-month Models				
Apr 15 – Jun 15	0.80857 <0.0001	0.84381 <0.0001	0.79248 <0.0001	0.91880 <0.0001
Aug 15 – Oct 15	0.72143 0.0024	0.81429 0.0002	0.78571 0.0005	0.87218 <0.0001

June 15 – July 15

Percentage of elk locations within the upper half of mean predicted use values was 52.77% (Table 4). Mean observed elk use decreased in proportion to increasing mean predicted use (R_s-0.3594, p = 0.1196, Table 5, Fig. 16). Mean volume of intersection was 0.5592 (Table 6). Mean use/availability within vegetation and traffic variables was consistent for low traffic and for edge but not for medium traffic (Appendix B). The performance matrix score was 6 (Table 7).

July 15 – August 15

Percentage of elk locations within the upper half of mean predicted use values was 52.01% (Table 4). Mean observed elk use was not related to mean predicted use (R_s = -0.343, p = 0.1775, Table 5, Fig. 16). Mean volume of intersection was 0.5036 (Table 6). Mean use/availability within vegetation and traffic variables was consistent for traffic variables but not for vegetation variables (Appendix B). The performance matrix score was 8 (Table 7).

August 15 – September 15

Percentage of elk locations within the upper half of mean predicted use values was 60.05% (Table 4). Mean observed elk use increased in proportion to mean predicted use (R_s = 0.782, p < 0.0001, Table 5, fig. 16). Mean volume of intersection was 0.5761 (Table 6). Mean use/availability within traffic and vegetation variables was consistent for low and high traffic but not related to distance to cover and canopy cover variables (Appendix B). The performance matrix score was 14 (Table 7).

September 15 – October 15

Percentage of elk locations within the upper half of mean predicted use values was 57.75% (Table 4). Mean observed elk use increased in proportion to increasing predicted use (R_s =0.758, p = 0.0001, Table 5, fig. 16).

Mean was 0.5780 (Table 6). Mean use/availability within traffic and vegetation variables was consistent for all variables (Appendix B). The performance matrix score was 14 (Table 7).

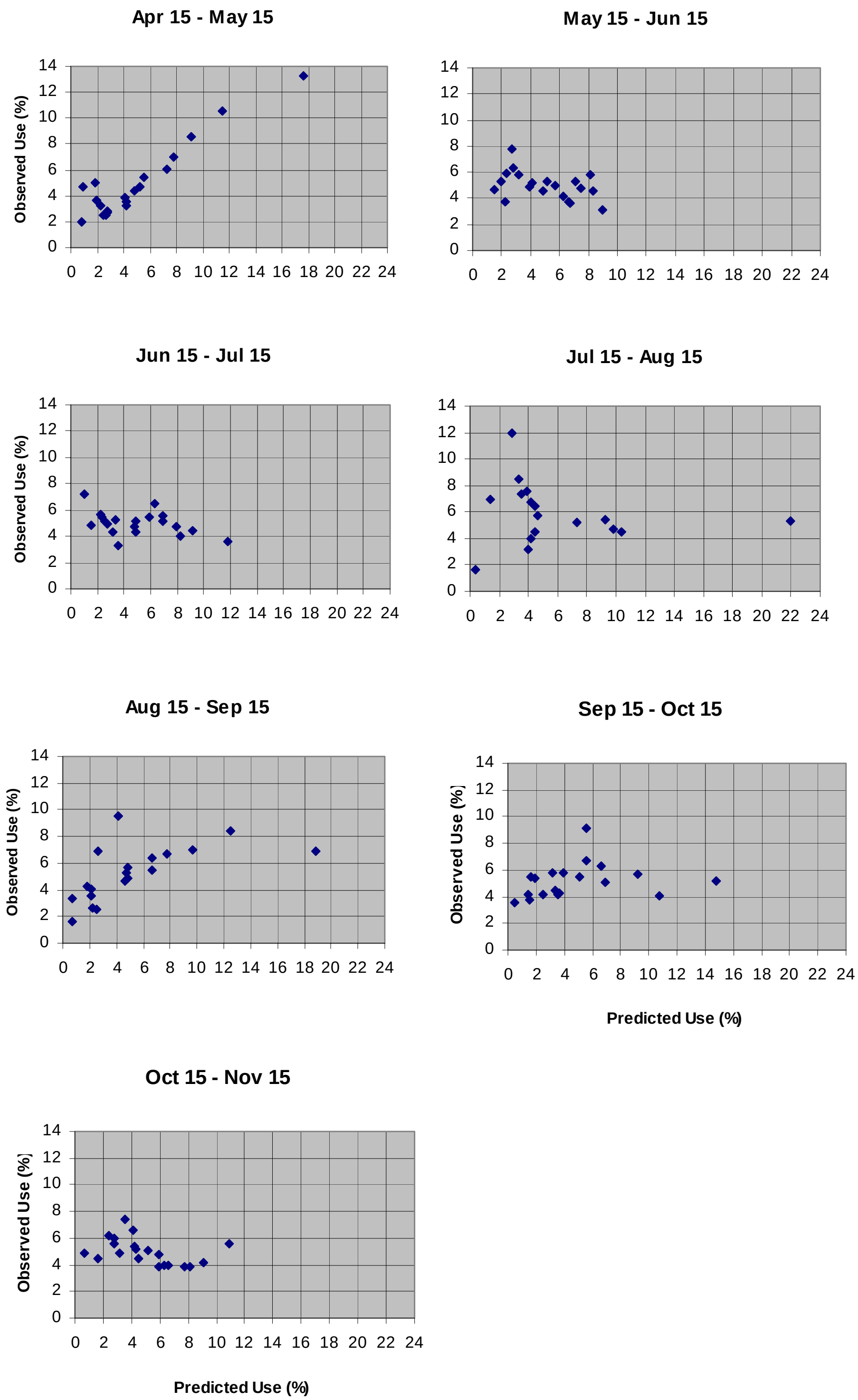


Figure 16 Mean predicted proportion of use sorted by equal area bins vs observed proportion of use within predicted bins for 1-month models.

October 15 – November 15

Percentage of elk locations falling within the upper half of mean predicted use values was 43.53% (Table 4). Mean observed elk use decreased in proportion to increasing predicted use areas (R_s = -0.53083, p = 0.0160, Table 5, fig. 16). Mean volume of intersection was 0.5865 (Table 6). Mean use/availability vegetation variables was inconsistent for canopy cover and non-responsive for distance to cover (Appendix B). The performance matrix score was 6 (Table 7).

Table 6 Results of Test 3 (Table 3). Volume of Intersection Index for observed and predicted elk use, Sled Springs, northeast Oregon. Index ranges 0 to 1 with 0 indicating no overlap and 1 perfect overlap.

One-month Models	**Year**			**Mean**
	2003	**2004**	**2005**	
Apr 15 – May 15	0.5450	0.5556	0.6073	0.5693
May 15 – Jun 15	0.5266	0.5497	0.5828	0.5530
Jun 15 – Jul 15	0.4760	0.5463	0.6553	0.5592
Jul 15 – Aug 15	0.4490	0.5233	0.5385	0.5036
Aug 15 – Sep 15	0.5080	0.5979	0.6224	0.5761
Sep 15 – Oct 15	0.5405	0.5819	0.6116	0.5780
Oct 15 – Nov 15	0.5417	0.5902	0.6275	0.5865
Two-month Models				
Apr 15 – Jun 15	0.5893	0.6060	0.6221	0.6058
Aug 15 – Oct 15	0.5556	0.6243	0.6420	0.6073

April 15 – June 15 (Two-month spring model)

Percentage of elk locations within the upper half of the mean predicted distribution was 58.68 % (Table 4). Observed elk use increased in proportion to increasing mean predicted use (Spearman rank correlation coefficient (R_s) = 0.918, probability (p) < 0.0001, Table 5, fig.16). Mean volume of intersection was 0.6180 (Table 6). Mean use/availability within vegetation and traffic variables was consistent for all management variables - elk use was consistent for canopy cover, high traffic, and for medium traffic (Appendix B). Overall score of the model based on the performance matrix score was 16 (Table 7).

Table 7 Performance of models based on a priori performance criteria (listed in Table 3).

One-month Models	**Score**				
	Test 1	**Test 2**	**Test 3**	**Test 4**	**Total**
Apr 15 – May 15	4	4	4	4	16 (High)
May 15 – Jun 15	1	1	3	4	9 (Med High)
Jun 15 – Jul 15	1	1	3	1	6 (Med Low)
Jul 15 – Aug 15	2	1	2	3	8 (Med Low)
Aug 15 – Sep 15	4	4	3	3	14 (High)
Sep 15 – Oct 15	3	4	3	4	14 (High)
Oct 15 – Nov 15	1	1	3	1	6 (Med Low)
Two-month Models					
Apr 15 – Jun 15	4	4	4	4	16 (High)
Aug 15 – Oct 15	3	4	4	4	15 (High)

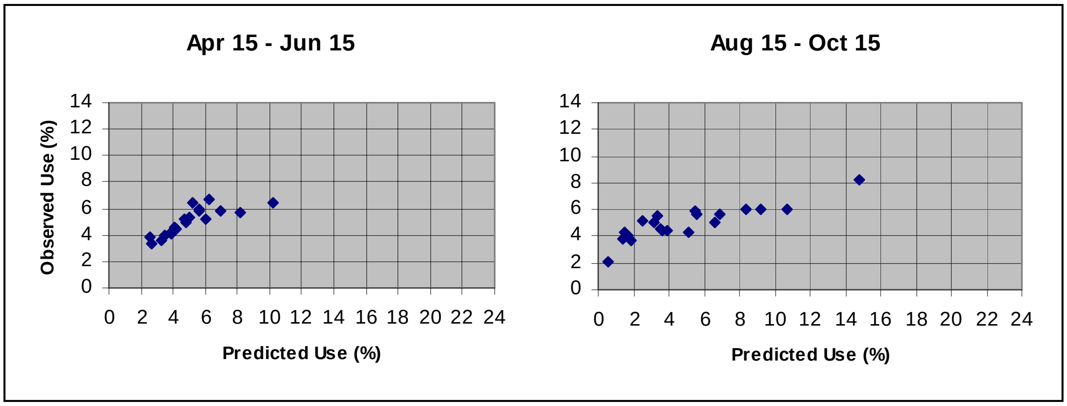


Figure 17 Mean predicted proportion of use sorted by equal area bins vs observed proportion of use within predicted bins for 2-month models.

Discussion

Volume of Intersection Test

Performance of the volume of intersection test was less variable than expected and contributed to inflating the performance scores (Table 7). Several of the models that scored low in the other tests scored higher in the volume of intersection test. Eliminating the volume of intersection test from the performance criteria resulted in lower overall rating of several models (Table 8 compared to Table 3). The May 15 – Jun 15, Jun 15 – Jul 15, and Oct 15 – Nov 15 models were each demoted one rank. This is more realistic given the much lower individual scores in the other tests. Feiberg and Kolchanny (2005) found that the volume of intersection compared to other home range overlap indexes was low in estimating shared space use. It may be that the performance criteria should have had a smaller range, which would result in a more sensitive test. Or it is likely that the volume of intersection is not an appropriate test for RSFs. RSFs are modeled on point estimates while home range utilization distributions are modeled on density estimates. Millspaugh et al. 2006 developed resource utilization functions (RUF) using utilization distributions. The volume of intersection may be much more appropriate for testing these predictions, because they are based on the same underlying theory of space use by animals.

A 9th Model: August 15 – October 15

I noticed the Sep 15 – Oct 15 model was very similar to the Aug 15 – Sep 15 model. I tested the Sep 15 – Oct 15 model predictions to 2 months of observations (Aug 15 – Oct 15). This model performed well across the 2-month period. Percentage of elk locations falling within the upper half of mean predicted use values was 57.30% (Table 4). Mean observed elk use increased in proportion to increasing predicted use areas (R_s = 0.87218, p <0.0001, Table 5, fig. 17). Mean volume of intersection was 0.6073 (Table 6). Mean use/availability was consistent for canopy cover and traffic variables (Appendix B). The performance matrix score was 15 (Table 7).

Factors in Model Performance

Landscapes in the Blue Mountains vary in topographic complexity, precipitation regime, and management. These differences may account for low performance scores of some models. Equally interesting is that some models had high performance in spite of these differences. I will discuss differences as they relate to model performance and offer insight into model refinement.

Starkey differs from Sled Springs in elevation range (Starkey = 1120 – 1500 m, Sled Springs = 741 – 1323 m), precipitation (Starkey = 37.2 and Sled Springs = 49.6 cm from Mar-Nov of 2003-2005, respectively), extent of elk distribution

Table 8 Performance of models when volume of intersectionis eliminated.

One-month Models	**Score**			
	Test 1	**Test 2**	**Test 4**	**Total**
Apr 15 – May 15	4	4	4	12 (High)
May 15 – Jun 15	1	1	4	6 (Med Low)
Jun 15 – Jul 15	1	1	1	3 (Low)
Jul 15 – Aug 15	2	1	3	6 (Med Low)
Aug 15 – Sep 15	4	4	3	11 (High)
Sep 15 – Oct 15	3	4	4	11 (High)
Oct 15 – Nov 15	1	1	1	3 (Low)
Two-month Models				
Apr 15 – Jun 15	4	4	4	12 (High)
Aug 15 – Oct 15	3	4	4	11 (High)

(Starkey = 77.6 km^2, Sled Springs = 181 km^2), elk density (Starkey = 6 elk / km^2, Sled Springs = 1 elk / km^2), and management (Starkey is managed by the U. S. Forest Service as a research forest and range, Sled Springs is managed by a timber corporation).

Precipitation Differences

Precipitation differences between Starkey and Sled Springs may account for where elk foraged during some model periods. Table 9 shows precipitation for the years during model development (1993-1995) and for the years of model validation (2003-2005). Sled Springs had consistently higher precipitation Mar-May and Sep-Nov than Starkey. This probably resulted in forage staying greener longer into summer and in earlier forage green-up in the fall after summer drought dried forage (Skovlin 1967, Westenskow et al. 1994).

Table 9 Seasonal precipitation (cm) at Starkey Experimental Forest (top) during years of model development and Sled Springs (bottom) 2003 – 2005 (model validation years). Data from weather station at Starkey (www.nadp.sws.uiuc.edu) and from Oregon Climate Service (www.mistral.oce.orst.edu).

Season		1993	2003	1994	2004	1995	2005	Season Mean 93-95 (sd)	Season Mean 2003-2005 (sd)
Mar-May	Starkey	22.1	19.3	11.5	18.4	19.5	18.9	15.3 (5.5)	18.9 (0.4)
	Sled	25.0	31.8	14.0	24.6	25.0	22.8	21.3 (6.3)	26.4 (4.8)
Jun-Aug	Starkey	20.1	5.0	7.0	12.2	14.8	5.2	14.0 (6.6)	7.5 (4.1)
	Sled	19.8	2.8	5.6	12.0	12.3	6.0	12.6 (7.1)	6.9 (4.7)
Sep-Nov	Starkey	3.9	11.4	16.0	12.4	18.4	10.1	13.8 (7.8)	11.3 (1.1)
	Sled	7.1	18.7	24.3	15.8	30.5	14.3	30.8 (12.1)	16.3 (2.2)
Year Total	Starkey	46.1	35.4	34.6	42.0	52.7	34.2	**44.5 (9.2)**	**37.2 (4.2)**
	Sled	51.9	53.3	43.9	52.4	67.8	43.1	**54.5 (12.2)**	**49.6 (5.6)**

Two models that had lower validation scores and for which precipitation may have been a factor were Jul 15 – Aug 15 and Oct 15 – Nov 15. In both models the canopy cover coefficient is positive, indicating elk were expected to use higher canopy. At Starkey, elk foraged under canopy cover in late summer and fall probably because forage in the open was dried out. However, in both these periods at Sled Springs, use/availability for canopy cover was negative, that is, elk selected for areas with lower canopy cover (Appendix B). This likely was due to higher precipitation at Sled Springs compared to Starkey. In July, forage in open areas would have stayed greener longer because more water was available in the soil. In October, green-up of previously dry forage species such as Idaho fescue (*Festuca idahoensis*), one-spike oatgrass (*Danthonia unispicata*), Sandberg's bluegrass (*Poa secunda*), and bluebunch wheatgrass (*Pseudorogneria spicata*) would have occurred earlier due to more precipitation occurring in fall (Skovlin [1967], Westenskow et al. [1994], John Cook [pers. comm.]).

High scores for the Apr 15 – June 15 and Aug 15 – Oct 15 models occurred despite differences in precipitation between Sled Springs and Starkey. For the early spring periods the forage available is concentrated on open southwest facing slopes. The canopy cover coefficient was negative, indicating that elk were predicted to be in low canopy cover areas. Precipitation may not be an important factor during this period because forage availability is driven by solar radiation warming and drying the soil, and not by soil moisture. For the Aug 15 – Oct 15 period canopy cover variables had positive coefficients, indicating predicted elk use to be in higher canopy cover. Use/availability in both these months showed elk using both low and high canopy cover (Appendix B). Despite these differences, the models performed well, probably due to topographic and traffic variables overwhelming cover variables.

Model refinement for periods when canopy cover is a predictor variable could include building RSFs using a greenness index from satellite imagery. Greenness images at a resolution of 100 m for 1- or 2-week intervals are now routinely available for public agency use (www.wfas.us) and could easily be incorporated into model building. If a greenness variable were in a model in place of or in addition to canopy cover it would likely solve the problem of variable drying and greening of forage.

Traffic Differences

Traffic management was different between Starkey and Sled Springs due to differences in management of the areas. Starkey management reflected typical National Forest management practices during model development years (1993-1995). All-weather roads were open to public use April – November and secondary roads were limited to administrative use or closed. Sled Springs, owned by a private corporation, allowed public access on all non-barricaded roads May – August, then closed all roads in most of the study area to public use as a part of a cooperative agreement to allow for quality hunting. Logging traffic, however, continued August-November. Despite these differences in traffic management elk use/availability followed predicted traffic variables in every model except one (Jun 15 – Jul 15 showed little response to medium traffic), although in a few cases the predicted trend occurred to 250 m from traffic and then reversed (Appendix B). Elk response to traffic on public lands has been well documented in literature (Rowland et al 2000) and extensively tested at Starkey (Wisdom et al. 2004b). This study shows that elk response to traffic held up even under different traffic types (logging traffic versus recreational traffic).

Hunting differences

Rifle elk hunting occurred late October and early November at Sled Springs during all three years of validation (ODFW 2003, ODFW 2004, and ODFW 2005), with about 1000 tags for the Sled Springs Wildlife Unit. Evidence of disturbance was seen, as discussed earlier, in several animals leaving the area during September and October (fig.7). During model building at Starkey hunting did not occur Oct 15 - Nov 15 and this may be another reason for poor model performance at Sled Springs in the late fall period. Research at Starkey showed that RSF predictions broke down when tested during an elk hunting season there (Johnson et al. 2004a). Hunting disturbance, as a variable, could be included in model refinement, perhaps represented as hunter density.

Density differences

The extent of the study area at Starkey was restricted by an elk proof fence to 77 km^2, and elk at Sled Springs used a 226 km^2 (90% kernel home range estimate of all GPS collared elk). Elk density was estimated to be 5-6 elk / km^2 at Starkey (Johnson et al. 2000) and Sled Springs elk herd density estimates were 1 elk / km^2 (Bruce Johnson, pers. comm). Density differences may have more effect on model performance when forage is abundant and available across the study area because elk are not limited to concentrated areas of forage. Forage production and nutritive value of forage is annually highest on native ranges in northeast Oregon during June and July (Vavra and Phillips 1980). Evidence of the difficulty in predicting elk use during this period is shown in the models themselves. The models for Jun 15 – Jul 15 and Jul 15 – Aug 15 had 11 predictor variables, as compared to 5-9 variables in the other periods (Appendix A). When elk distribution becomes more complex to predict, elk density may become important when applying out-of-sample RSFs. I investigated use/availability for all the variables in these 2 models to find out which variables were not performing as predicted. For Jun 15 – Jul 15 I found that, in addition to elk not responding to the medium traffic variable (Appendix B), elk use did not follow predicted trends for westerly and northerly aspects. However, elk did follow model predictions by using more convex topography, flatter terrain, deeper soils and higher forage production. The Jul 15 – Aug 15 model predicted use of higher canopy cover but elk selected for lower canopy cover and further from cover, as discussed above (Appendix B). Elk response to traffic variables, however, was consistent with predictions. Mid-summer prediction of elk distribution is more complex than it is in spring and late summer and model refinement will likely include predictor variables that are more expensive to obtain than what is typically available currently in public agency GIS databases.

Conclusions

Three out of 7 monthly models rated high on the performance matrix (Table 6): Apr 15 – May 15, Aug 15 – Sep 15, and Sep 15 – Oct 15. The 2-month model for Apr 15 – Jun 15 also rated high. In addition, a 1-month model tested on 2 months of observations, Aug 15 – Oct 15, rated high and I added this 9th model option as a possible 2-month model to consider.

The 2-month models are well suited to management applications because predictions can be calculated using GIS layers currently existing in most land management agency databases: DEMs, roads, and large tree cover. The Apr 15 – Jun 15 model encompasses an important life stage (parturition) for elk. The Aug 15 – Oct 15 period constitutes another important life stage for elk – the breeding period. Recent research has shown that the late summer/autumn period is critical for elk nutrition and reproduction (Cook et al. 2004). Maps of the predicted and observed use at Sled Springs for these time periods are in Appendix C.

Models that performed well were those for forage-limited periods, when topography and canopy cover were good predictors of forage availability, and traffic variables helped to further limit where high elk use occurred. Further refinement of models should include a greenness variable derived from available satellite imagery and a hunting density variable.

Validation tests used in my study were a mixture of published and unpublished methods. The first test was simple and intuitive – did more locations occur in the upper ranked predicted areas? The second test was the ranked bin test, which has been used in recent years to validate RSFs (Johnson et al. 2000, Boyce et al. 2002), although they used withheld locations from model development to validate models in the same study area. The third test, was published by Roloff et al.(2001), and, as discussed above, I concluded would be more suited to validating resource selection models that are built from home range utilization distributions. The fourth test I designed in order to help managers decide suitability of a model. I wanted to test elk use of model variables that are most affected by management.

Applying landscape models in management planning requires programs that can input the resource layer data, perform map algebra, and output digital maps of predicted use. The KRESS Modeler developed at the Department of Rangeland Ecology and Management at Oregon State University is such a system that does not require an expensive GIS package (Johnson et al. 2004b, http://kress.us/index.htm). I performed the model validation in ArcGIS because it is the standard software used in the Forest Service and BLM.

Validation of wildlife distribution models on landscapes other than where the models were developed is important if models are to be used for management applications. Validation on other landscapes has been rare because of the expense involved in obtaining adequate samples of animal locations. However, with the continued development and affordability of GPS collars this opportunity will be available. My research used a suite of possible methods for evaluating wildlife distribution model performance over a landscape.

Literature Cited

Ager, A. A., B. K. Johnson, P. K. Coe, M. J. Wisdom. 2004. Landscape simulation of foraging by elk mule deer and cattle on summer range. In: Transactions of the 69th North American Wildlife and Natural Resources Conference, 69: 687-707.

Bissonette, J. A. 1997. Wildlife and Landscape Ecology, Effects of Pattern and Scale, Springer-Verlag, N. Y.

Borchers, J. G. 1996. A hierarchical context for sustaining ecosystem health. In: Jaindl, R. G. and T. M. Quigley, Editors, Search for a Solution, American Forests, Washington DC.

Boyce M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157: 281-300.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12 (3), 269-276.

Bowman, J. L., C. O. Kochanny, S. Demarais, and B. D. Leopold. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28(1): 141-145.

Box, G.E.P. 1979. Robustness in the strategy of scientific model building. In Robustness in Statistics, R.L. Launer and G.N. Wilkinson, Editors. Academic Press: New York.

Brooker S., S. I. Hay, and D. A. P. Bundy. 2002. Tools from ecology: useful for evaluating infection risk models? Trends in Parasitology Vol 18 No. 2, 70-74.

Coe, P.K. 2002. Unpublished notes and powerpoint presentation reporting the results of GPS collar testing. On file at La Grande Forestry and Range Sciences Laboratory, La Grande, OR.

Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001a. Responses of elk and mule deer to cattle in summer. Journal of Range Management 54: 205, http://uvalde.tamu.edu/jrm/mar01/coe.htm

Coe, P. K. 1997. Unpublished data on 6 years of phenology measurements of understory plants at Starkey Experimental Forest, on file at Forestry and Range Sciences Laboratory, La Grande, OR.

Cohen, J. 1968. Weighted Kappa: nominal scale agreement with provision for scaled disagreement or partial credit. Psychological Bulletin 70: 213-200.

Conroy, M. J., Y. C. Cohen, F. C. James, Y. G. Matsinos, B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications, 5(1): 17-19.

Cook, J. G. 2002. Nutrition and food, in Elk of North America, by D.E. Toweill and J.W. Thomas, Eds. Smithsonian Institution Press, Washington, D.C., p 259-349.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs No. 155: 61 pages.

Cook, J. G. and L. L. Irwin. 1985. Validation and modification of a habitat suitability model for pronghorns. Wildlife Society Bulletin 13: 440-448.

Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. Journal of Range Management 44(6), 530-542.

Darambazar, E., D. Damiran, B. Riggs, M. Vavra, and J. Cook 2007. Understory production of transitional forested rangelands in the Blue Mountains of Eastern Oregon [abstract], In: Abstracts for the 60th Annual Meeting of the Society for Range Management, 9-16 February 2007, Reno-Sparks, Nevada.

D’Eon, R. G., R. Serrouya, G. Smith, and C.O. Kochanny. 2002. GPS radio-telemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30(2):430-439.

De Solla, S. R. R. Bonduriansky, R. J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68, 221-234.

Dussault, C., R. Courtois, J. Ouellet, and J. Huot. 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildlife Society Bulletin 27(4): 965-972.

Dussault, C., R. Courtois, J. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy, Wildlife Society Bulletin 29(1):171-179

Fieberg, J. and C. O. Kochanny. 2005. Quantifying home-rage overlap: the importance of the utilization distribution. Journal of Wildlife Management, 69(4): 1346-1359.

Findholt, S. L, B. K. Johnson, L. D. Bryant, and J. W. Thomas. 1996. Corrections for position bias of a LORAN-C radio-telemetry system using DGPS. Northwest Science, Vol. 70, No. 3.

Findholt, S. L., B. K. Johnson, L. L. McDonald, J. W. Kern, A. Ager, R. J. Stussy, and L. D. Bryant. 2002. Adjusting for radio-telemetry error to improve estimates of habitat use. USDA Forest Service General Technical Report, PNW-GTR-555, October 2002.

Friar, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41, pp 201-212.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection and importance. In: Boitani, L. and T.K. Fuller, Editors, Research Techniques in Animal Ecology, Columbia University Press, New York.

Garton. E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radio-telemetry studies. In: J. J. Millspaugh and J. M. Marzluff, editors: Radio Tracking and Animal Populations, Academic Press, San Diego, CA.

Green, R. A., and G. D. Bear. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. Journal of Wildlife Management 54(2): 272-279.

Grunbaum, D. 1998. Using spatially explicit models to characterize foraging performance in heterogeneous landscapes. The American Naturalist 151(2).

Guisan, A. and N. E. Zimmermann 2000. Predictive habitat distribution models in ecology. Ecological Modeling 135: 147 – 186.

Hansen, Michael C. and R. A. Riggs. Accuracy, precision, and observation rates of GPS telemetry collars in the Blue Mountains of northeast Oregon. Journal of Wildlife Management, in press.

Howlin, S., W. P. Erickson, and R. M. Nielson. 2003. A validation technique for assessing predictive abilities of resource selection functions. Proceedings on the First International Conference on Resource Selection Functions, Laramie, Wyoming, Jan. 13-15, 2003. West, Inc., Laramie, Wyoming.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54(2).

Jaindl, R. G. and T. M. Quigley, 1996. Search for a Solution, American Forests, Washington, D. C.

Jaindl, R. G., T. M. Quigley, and R. Harrod. 1996. Forest health issues and resources of the Blue Mountains. In: Search for a Solution, by R. G. Jaindl and T. M. Quigley, Editors, American Forest, Washington D. C.

Johnson, B. K. 1999. Development and validation of 7 empirical models of elk and mule deer resource selection in spring at Starkey Experimental Forest and Range – draft manuscript. Unpublished report on file at La Grande Forestry and Range Sciences Lab, La Grande, OR.

Johnson, B. K. 2002. Unpublished records on file at La Grande Forestry and Range Sciences Lab, La Grande, OR.

Johnson, B. K., A. A. Ager, S. A. Crim, M. J. Wisdom, S. L. Findholt, and D. Sheehy. 1996. Allocating forage among wild and domestic ungulates –a new approach. In: Proceedings of a Symposium on Sustaining Rangeland Ecosystems, by W. E. Edge and S Olson-Edge, Editors, Oregon State University Extension Service, Corvallis, Oregon.

Johnson, B. K. A. A. Ager, J. H. Noyes, N. Cimon. 2004a. Elk and mule deer responses to variation in hunting pressure. Transactions of the Sixty-ninth North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington DC.

Johnson, B. K., A. A. Ager, S. L. Findholt, M. J. Wisdom, D. B. Marx, J. W. Kern, and L. D. Bryant. 1998. Mitigating spatial differences in observation rate of automated telemetry systems. Journal of Wildlife Management 62: 968-967.

Johnson, B.K., J.W. Kern, M.J. Wisdom, S.L. Findholt, and J.G. Kie. 2000. Resource selection and spatial separation of mule deer and elk in spring. Journal of Wildlife Management 64:685-697.

Johnson, D.E., Johnson, M.D., Harris, N.R., M. Louhaichi, and D.C. Ganskopp. 2004b. KRESS Modeler Version 1.12 User's Manual. The KRESS Project, Department of Rangeland Resources, Oregon State University, Corvallis, OR.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Johnson, D.H. 2001. Validating and evaluating models. Pages 105-119 in T.M. Shenk and A.B. Franklin, editors. Modeling in natural resource management: development, interpretation and application. Island Press, Washington, D.C.

Kelly, A., D. C. Powell, R. A. Riggs 2005. Predicting potential natural vegetation in an interior northwest landscape using classification tree modeling and a GIS. Western Journal of Applied Forestry, 20 (2): 117-127.

Leban, F. A., M. J. Wisdom, E. O. Garton, B. K. Johnson, and J. G. Kie. 2001. Effect of sample size on the performance of resource selection analyses. Pages 293-309. In: Millspaugh, J. J. and J. M. Marzluff, eds. Radio Tracking and Animal Populations, Academic Press, San Diego, CA.

Mac Nally, R. 2002. Improving inference in ecological research: issues of scope, scale, and model validation. Comments on Theoretical Biology 7: 237-256.

Manel, S, H. C. Williams, S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38 (5), 921-931.

Manly, B.F.J., L.L. McDonald and D.L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Kluwer Academic Publishers, London.

Mayer, D. G. and D. G. Butler. 1993. Statistical validation. Ecological Modelling 68, 21-32.

Millspaugh, J. J., J. R. Skalski, B. J. Kernohan, K. J. Raedeke, G. C. Brundige, and A. B. Cooper. 1998. Some comments on spatial independence in studies of resource selection. Wildlife Society Bulletin 26(2): 232-236.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70(2): 384-395.

Moen, R., J. Pastor, and Y. Cohen. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60(3):659-668.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61(2): 530-539

ODFW 2005. Oregon Big Game Regulations 2005. Oregon Dept of Fish and Wildlife, Salem Oregon.

ODFW 2004. Oregon Big Game Regulations 2004. Oregon Dept of Fish and Wildlife, Salem Oregon.

ODFW 2003. Oregon Big Game Regulations 2003. Oregon Dept of Fish and Wildlife, Salem Oregon.

ODFW. 2001. Environmental assessment – research on the effects of nutrition and predation on elk recruitment. U.S. Dept of Interior Fish and Wildlife Service http://www.dfw.state.or.us/ODFWhtml/InfoCntrWild/ODFWEA.pdf

Orzack, S. H., and E. Sober. 1993. A critical assessment of Levins's the strategy of model building in population biology (1966). Quarterly Review of Biology 68, No. 4: 533-546.

Pearce, J. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modeling 133: 225-245.

Pontius, R.G. Jr. 2000. Quantification error versus location error in comparison of categorical maps. Photogrammetric Engineering & Remote Sensing, 66: 1011-1016.

Porter, W. F. and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. Journal of Wildlife Management 51(3): 681-685.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. In: Boitani, L. and T.K. Fuller, Editors, Research Techniques in Animal Ecology, Columbia University Press, New York.

Power, M. 1992. The predictive validation of ecological and environmental models. Ecological Modeling 68: 33-50.

Rempel, R.S., A.R. Rodgers, and K.F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59(3):543-551.

Rempel, R.S. and A.R. Rodgers. 1997. Effects of differential correction on accuracy of a GPS animal location system. Journal of Wildlife Management 61(2):525-530.

Riggs, B. A. 2002. Opportunities for Cooperative Elk Research in the Sled Springs Game Management Unit, 2002-2006. On file at Boise Building Solutions, La Grande, OR.

Rodgers, A. R. 2001. Recent telemetry technology. In: J. J. Millspaugh and J. M. Marzluff editors, Radio Tracking and Animal Populations, Academic Press, San Diego.

Rodgers, A.R. and A. P. Carr. 1998. HRE: the home range extension for ArcViewTM, Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. Journal of Wildlife Management 65: 613-1076.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Managmenet 65(3): 672 – 684.

Rykiel, E. J. Jr. 1996. Testing ecological models: the meaning of validation. Ecological Modeling 90: 229- 244.

Samuel, M. D., and K. P. Kenow 1992. Evaluating habitat selection with radio-telemetry triangulation error. Journal of Wildlife Management 56: 725-734.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:(2), p. 739.

Seidel, K. S. 1992. Statistical properties and applications of a new measure of joint space use for wildlife. Masters Thesis, University of Washington, Seattle, WA.

Sheehy, D., P. Schreder, and R. Lewis. 1999. Transitory habitat in eastside industrial forests. Blue Mountain Natural Resources Institute, La Grande Oregon.

Skovlin, J. M., P. Zager, and B. K. Johnson 2002. Elk habitat selection and evaluation. In: Elk of North America, by D.E. Toweill and J.W. Thomas, Eds. Smithsonian Institution Press, Washington, D.C.

Skovlin, J. M. 1967. Fluctuations in forage quality on summer range in the Blue Mountains. U.S. Forest Service Research Paper PNW-44, U. S. Dept. of Agriculture, Portland OR (20 pages).

Swihart , R. K., and N. K. Slade. 1985. Testing for the independence of observations in animal movements. Ecology 66, pg 1176-1184.

Taylor, S. D. 2002. Addressing observation bias in a GPS-telemetry study of coastal mountain goats. Master's Thesis. University of British Columbia.

Turner, M. G. 2005. Landscape ecology: what is the state of the science? Annual Review of Ecology, Evolution, and Systematics (36: 319 – 344).

U.S. Coast Guard. 2003. Navigation Center, http://www.navcen.uscg.gov/gps/default.htm

Vanreusel, W., D. Maes, and H. Van Dyck. 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. Conservation biology 21 (1), 201-212.

Van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39(1) 118 – 123.

Vavra, M. and R. L. Phillips 1980. Drought effects on cattle performance, diet quality and intake. Proceedings of Western Section, American Society of Animal Science, Oregon State Agricultural Experiment Station Technical Paper No. 5503.

Westenskow, K. J., W. C. Krueger, L. D. Bryant, D. R. Thomas. 1994. Nutrient quality of bluebunch wheatgrass regrowth on elk winter range in relation to defoliation. Journal of Range Management 47(3): 240-244.

Wisdom M. J., B. C. Wales, M. M. Rowland, M. G. Raphael, R. S. Holthausen, T. D. Rich, and V. A. Saab 2002. Performance of greater sage-grouse models for conservation assessment in the interior Columbia basin, U. S. A. Conservation Biology, 16(5) 1232-1242.

Wisdom M. J., M. M. Rowland, B. K. Johnson, B. L. Dick. 2004a. Overview of the Starkey Project: mule deer and elk research for management benefits. In: Transactions of the Sixty-ninth North American Wildlife and Natural Resources Conference, 69: 455-474.

Wisdom, M. J., N. J. Cimon, B. K. Johnson, E. O. Garton, and J. W. Thomas. 2004b. Spatial partitioning by mule deer and elk in relation to traffic. In: Transactions of the Sixty-ninth North American Wildlife and Natural Resources Conference, 69: 509-530.

Zeide, B. 1991. Quality as a characteristic of ecological models. Ecological Modeling 55, no. 3-4: 161-174.

APPENDICES

Appendix A

Coefficients of RSFs for elk during eight monthly time steps in Main Study Area 1993-1996, Starkey Experimental Forest, northeastern Oregon. Coefficients are standardized (top) and non-standardized (bottom) (from Ager et al. 2004).

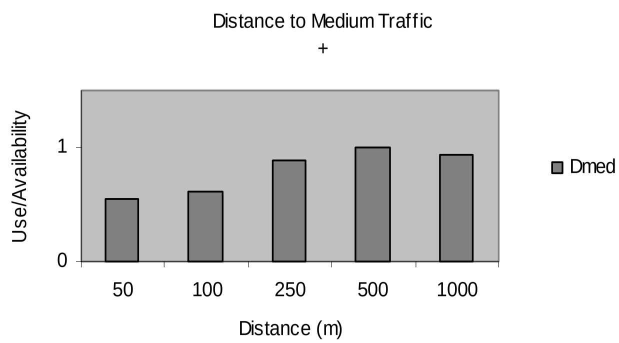
One-Month Models	Intercep	Dist. Edge of Patch	Forage Prod.	Shape of Patch	Dist. Traffic Zero	Dist. Traffic Low	Dist. Traffic Med.	Dist. Traffic High	Slope %	Aspect East West	Aspect North South	Topog Convex	Soil Depth	Dist. Cover	Can. Cover
Apr 15 – May 15	-2.588 -12.7926						0.2085 0.0002	0.2785 0.0003	-0.3404 -0.0273	-0.0569 -0.0779	-0.1504 -0.2232	0.1085 0.0209	-0.1086 -0.0089	-0.0486 -0.0003	-0.1528* -0.0069*
May 15 – Jun 15	-2.4546 -14.0412						0.1191 0.0001		-0.1119 -0.0089			0.1181 0.0226	0.1470 0.0121		-0.0552 -0.0025
Jun 15 – Jul 15	-2.8329 -21.2643	-0.0378 -0.0008	-0.0568 -0.0003	-0.0455 -0.2897	-0.1228* -0.0004*	-0.2775 -0.0004	0.0741 0.0001		0.1075 0.0086	-0.0442 -0.0607	0.1034 0.1543	0.1944 0.0371	0.1384 0.0114		
Jul 15 – Aug 15	-3.6208 -20.3917	0.1038 0.0022	0.0377 0.0002	-0.0681 -0.4333			0.1237 0.0002	0.2306 0.0002	0.1190 0.0095		0.2491 0.3722	0.1617 0.0309	0.1851 0.0153	-0.1919 -0.0015	0.1776 0.0081
Aug 15 – Sep 15	-3.0575 -20.4503	0.0992 0.0021			0.1182 0.0005	0.0984 0.0002		0.1946 0.0003			0.1946 0.2900	0.1706 0.0326	0.1527 0.0126	-0.1558 -0.0012	0.1709 0.007
Sep 15 – Oct 15	-3.1617 -19.0188	0.0463 0.0010				0.0822 0.0001					0.2379 0.3556	0.1598 0.0305	0.1212 0.0100	-0.1813 -0.0014	0.1874 0.0085
Oct 15 – Nov 15	-3.2960 -20.4223								0.0978 0.0078		0.1396 0.2073	0.1757 0.0336	0.0915 0.0075	-0.1612 -0.0012	0.0580 0.0026
Two-month Model															
Apr 15 – Jun 15	-1.777 -12.264						0.160 0.0002	0.149 0.0002	-0.212 -0.017	-0.050 -0.0673					-0.099 -0.0045

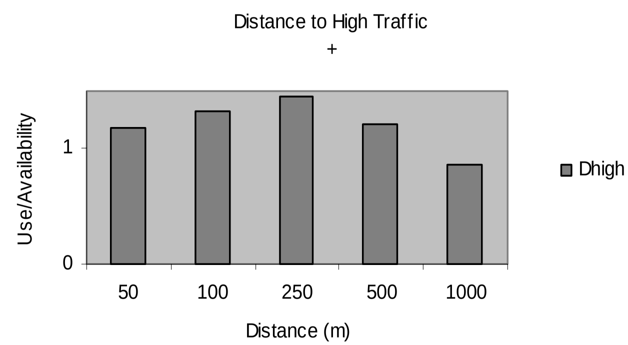
* *Values with *'s were misprinted in Ager et al. 2004. These are the correct values.*

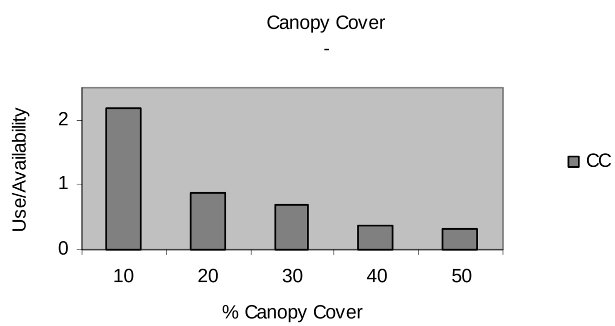
Appendix B

Use/availability (percent observations divided by percent habitat availability) of model variables affected by management (cover and traffic variables). Use/availability greater than 1 indicates selection. Plus (+) or minus (-) signs for each variable indicate expected trend of use by elk according to model coefficients . Pluses mean that use/availability is expected to relate to increasing variable value positively, and minuses mean that use/availability should relate negatively to increasing variable value.

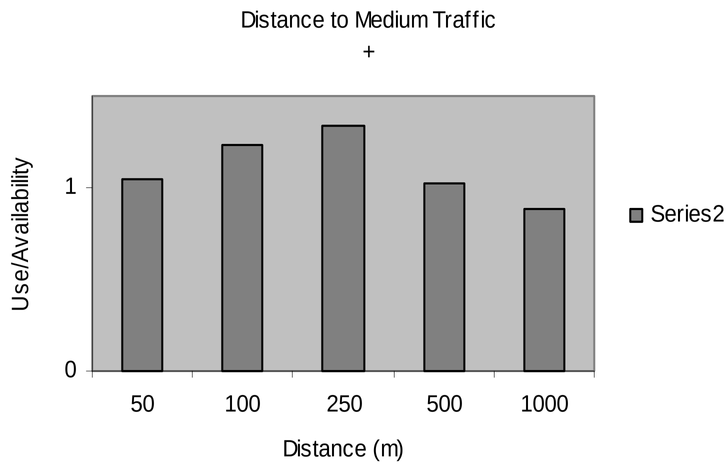
Apr 15 - May 15

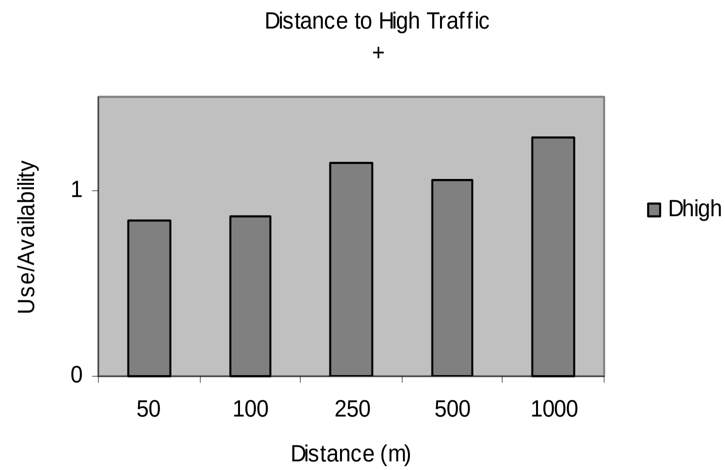


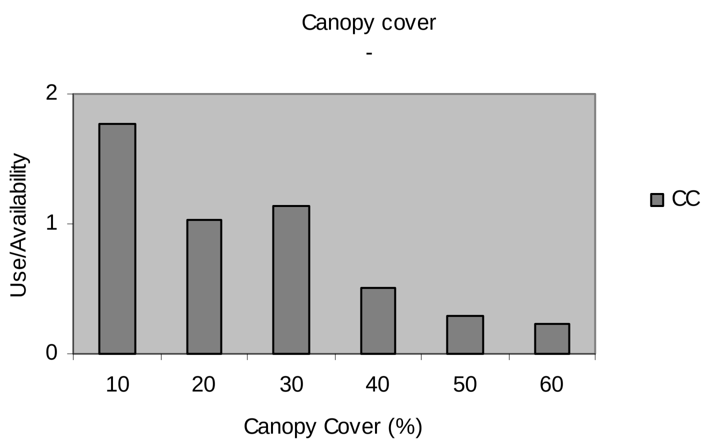




May 15 - Jun 15

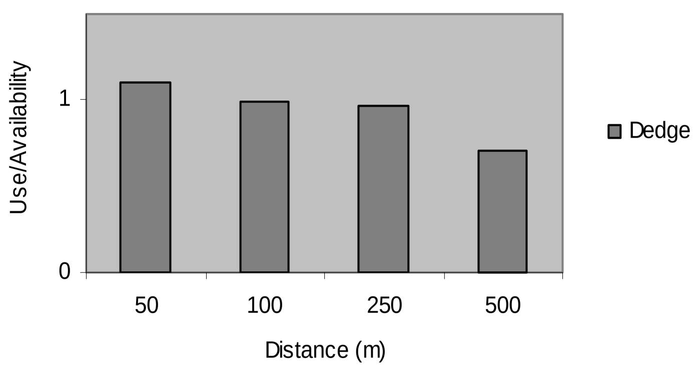

Distance to Medium Traffic
+
Use/Availability
0
1
50
100
250
500
1000
Distance (m)
Series2


Distance to High Traffic
+
Use/Availability
0
1
50
100
250
500
1000
Distance (m)
Dhigh

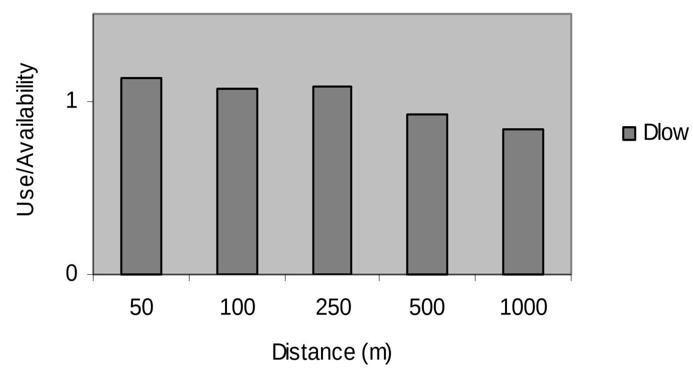

Canopy cover
-
Use/Availability
0
1
2
10
20
30
40
50
60
Canopy Cover (%)
CC

Jun 15 - Jul 15

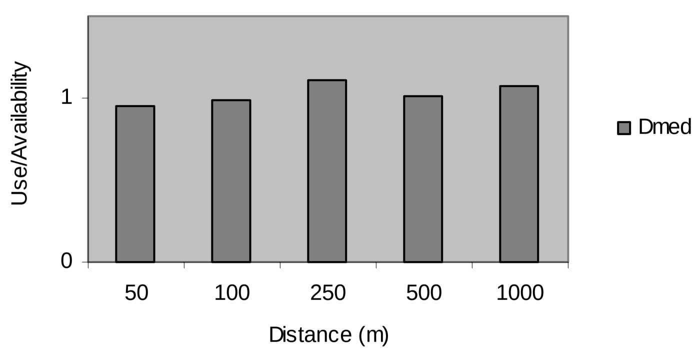
Distance to Edge
-



Distance to Low Traffic
-

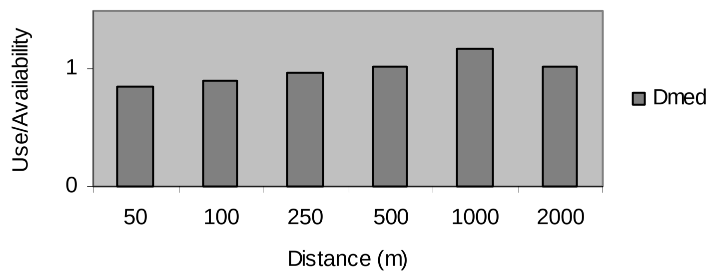


Distance to Medium Traffic
+

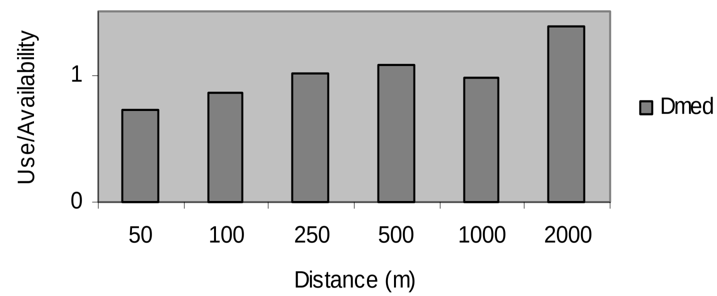


Jul 15 - Aug 15

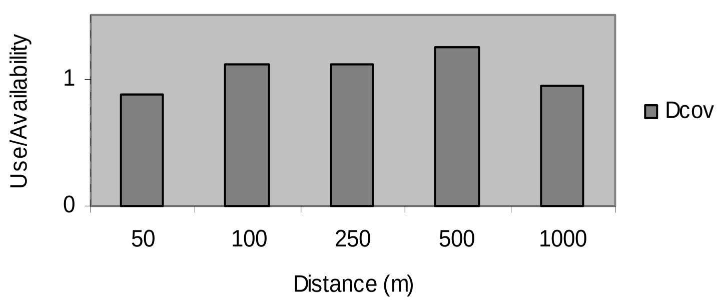
Distance to Medium Traffic
+



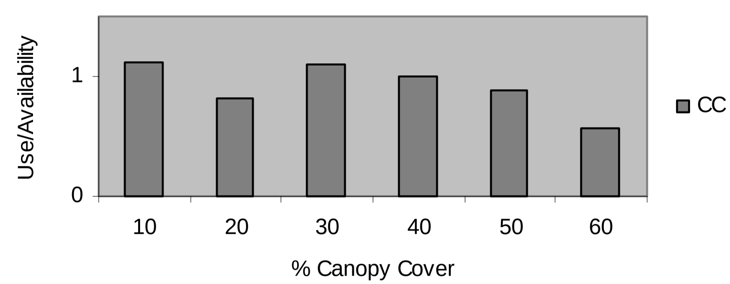
Distance to High Traffic
+



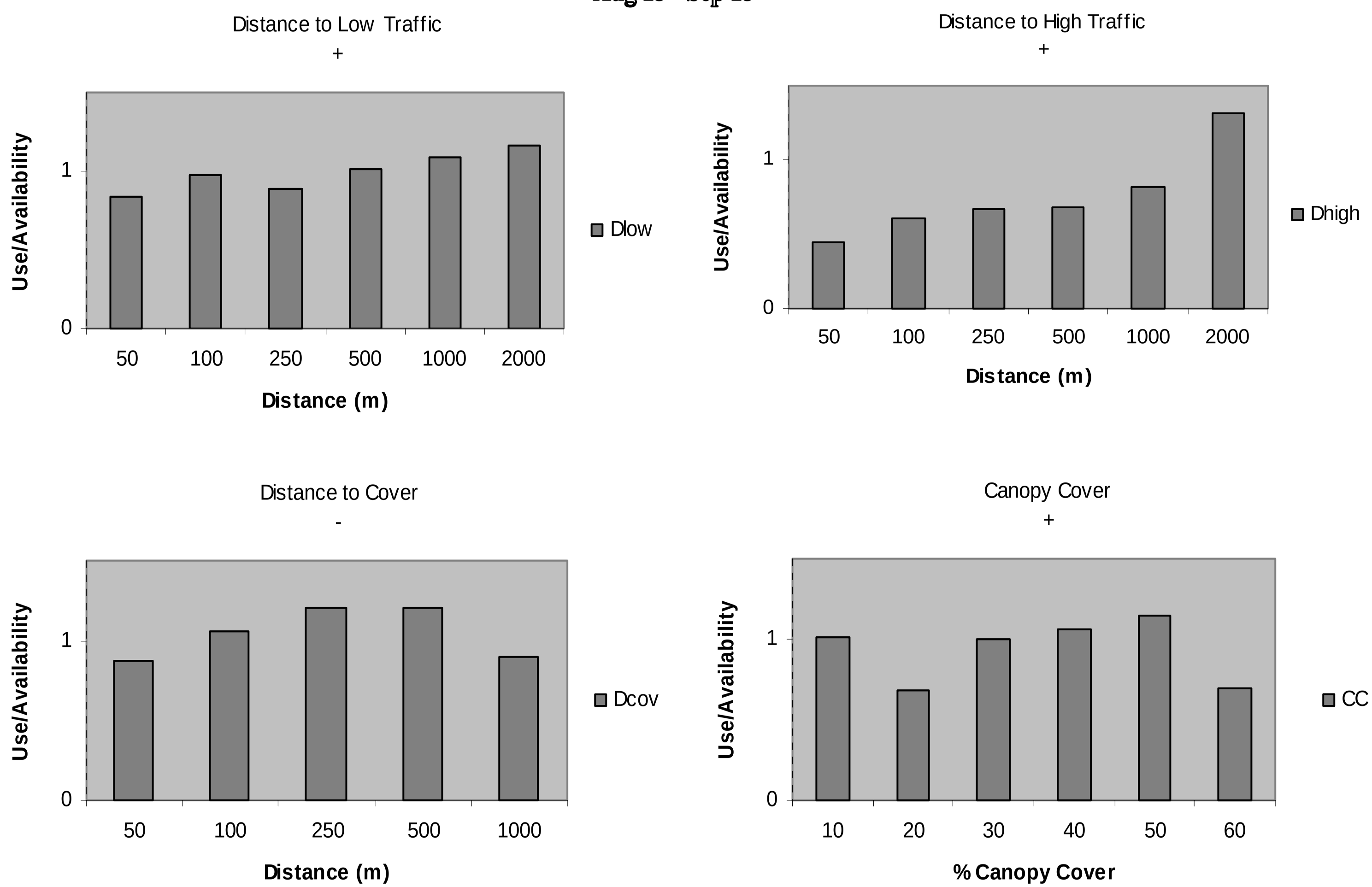
Distance to Cover
-



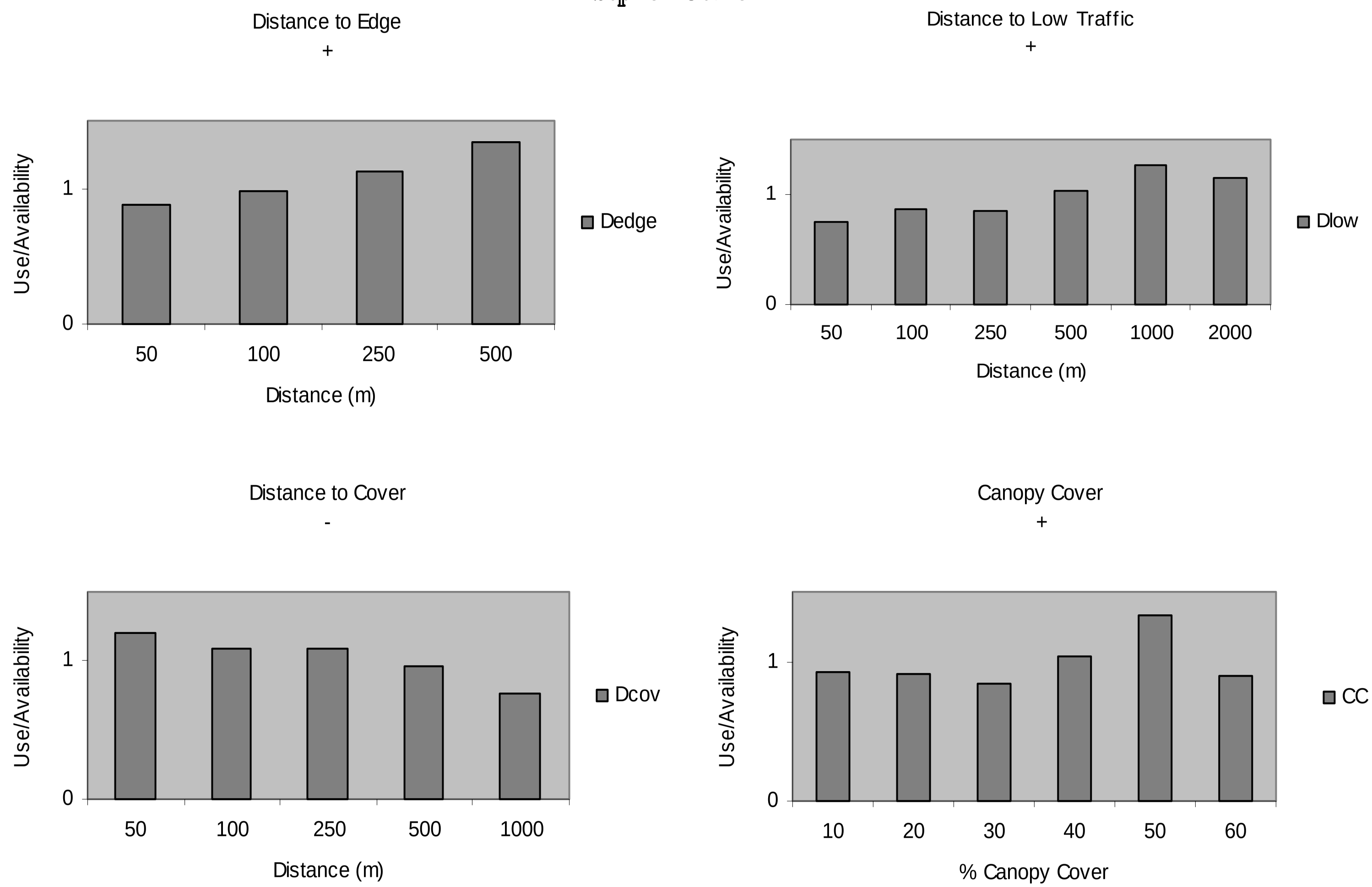
Canopy Cover
+



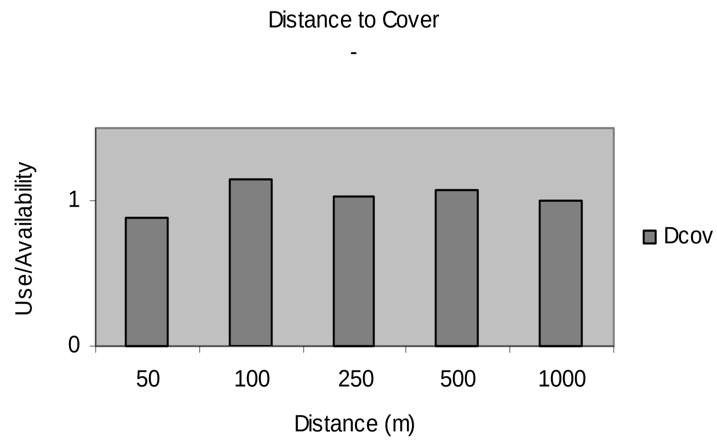
Aug 15 - Sep 15

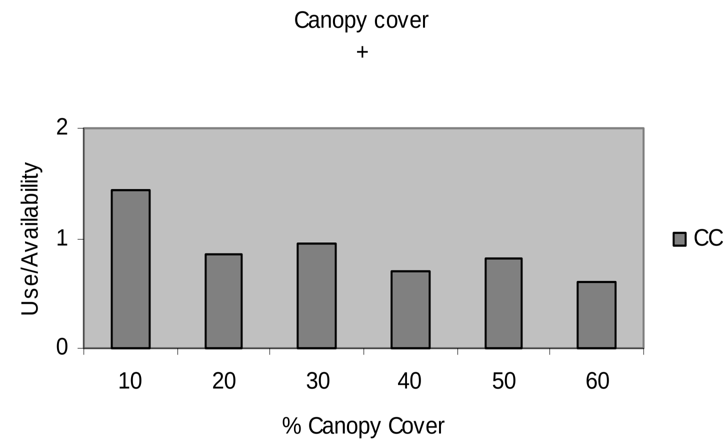

Distance to Low Traffic
+
Use/Availability
1
0
50
100
250
500
1000
2000
Distance (m)
Dlow
Distance to High Traffic
+
Use/Availability
1
0
50
100
250
500
1000
2000
Distance (m)
Dhigh
Distance to Cover
-
Use/Availability
1
0
50
100
250
500
1000
Distance (m)
Dcov
Canopy Cover
+
Use/Availability
1
0
10
20
30
40
50
60
% Canopy Cover
CC

Sep 15 - Oct 15


Distance to Edge
+
Use/Availability
1
0
50
100
250
500
Distance (m)
Dedge
Distance to Low Traffic
+
Use/Availability
1
0
50
100
250
500
1000
2000
Distance (m)
Dlow
Distance to Cover
-
Use/Availability
1
0
50
100
250
500
1000
Distance (m)
Dcov
Canopy Cover
+
Use/Availability
1
0
10
20
30
40
50
60
% Canopy Cover
CC

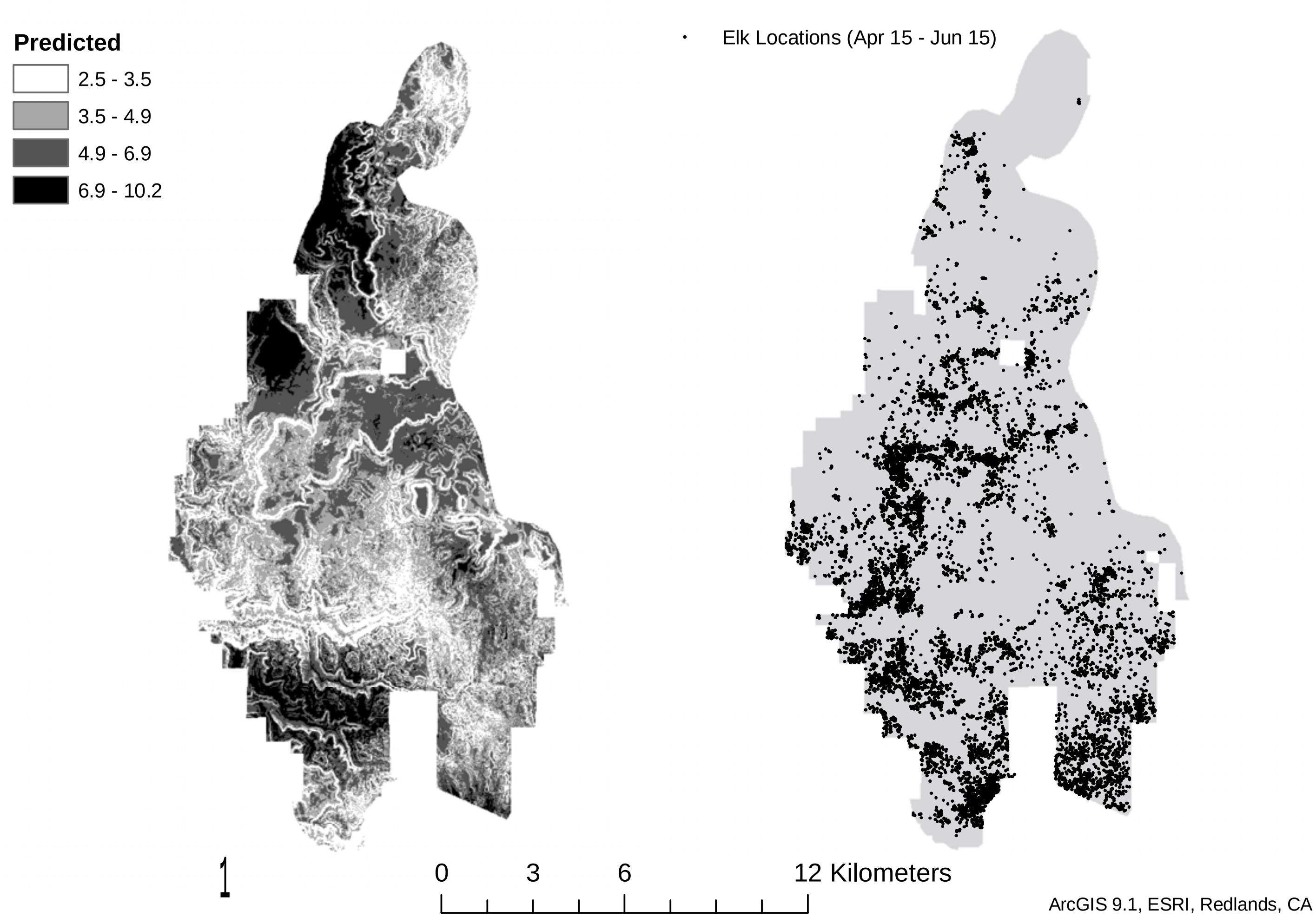
Oct 15 - Nov 15


Distance to Cover
-
Use/Availability
0
1
50
100
250
500
1000
Distance (m)
Dcov


Canopy cover
+
Use/Availability
0
1
2
10
20
30
40
50
60
% Canopy Cover
CC

Appendix C

Predicted Proportion of Use and Observed Locations
April 15 - June 15



Predicted Proportion-of-Use and Observed Locations
August 15 - October 15