Development and evaluation of inductive and deductive models of summer elk (*Cervus elaphus*) resource suitability in Northwestern Ontario.

By

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Abstract

Resource-selection modeling techniques take either a deductive or inductive approach. Deductive methods are a “bottom-up” approach, where individual wildlife-resource relationships are the building blocks that define the suitability of a landscape. Conversely, inductive models imply a “top-down approach”; the suitability of a landscape is predefined by animal use, and statistics are used to identify wildlife-resource relationships. Current modeling caters towards the inductive approach even though a proper comparison between inductive and deductive techniques has yet to identify the superior method.

The Ontario elk restoration project re-introduced 104 elk (*Cervus elaphus*) to the Lake of the Woods (LOW) region in 2000 and 2001. The population diminished substantially over the following four years bringing concern to the successful re-establishment of elk in northwestern Ontario. At present, explanations for this decline are speculative in nature, but one possibility is that the landscape does not contain the resources required to support a viable population. To address this concern, I investigated the ability of the landscape to support elk by creating a series of deductive (HSI) models for the summer season based on published elk-resource relationships. I also created an inductive (RUF) model based on radio-telemetry location data collected weekly throughout 2000-2005 in an effort to improve upon the initial deductive model. Finally, I compared the two modeling approaches to address the growing disparity between modeling methods. Models were validated by comparing model suitability to elk resource use using weighted overlap (WO) and average overlap (AO) indices, and by comparing model suitability to elk space use, utilization distributions (UDs), using the deviation from a ‘no selection’ pattern (DVI Index), a modification of the Volume of Intersection (VI) Index. Comparison to a null model was also used to benchmark each index. I also calculated the VI Index between the predicted suitability’s of RUF and HSI models to compare their overall similarity.

The landscape surrounding the elk release site showed a reasonable suitability, ranging (on a scale of 0 to 1) from 0.57 to 0.69 for the series of HSI models and 0.69 for the RUF model. Predicted HSI relationships for road density and cover width were markedly different than elk use, whereas relationships using the RUF model were similar to elk use. Average elk use ranged in suitability from 0.61 to 0.74 (WO Index) and 0.59 to 0.72 (AO Index) for the HSI models, where 6 of the 7 models performed significantly better than the null model. Average suitability of elk use was 0.77 and 0.86 (AO and WO Indices, respectively) for the RUF model, which performed significantly better than the null model. The HSI model increasingly reflected elk UDs as the relationship between the distance to a forage-cover edge was accentuated. The RUF model identified the proximity to a forage-cover edge as the main factor driving elk selection in northwestern Ontario.

The RUF model showed the greatest predictive ability, as the difference between elk and random W.O. Index scores was greater than for the HSI models. Neither modeling technique predicted elk space use better, but the RUF model showed the greatest difference between elk and the null DVI Indices. Although the RUF model appeared to out-perform the HSI models, the similar DVI pattern for all models and high similarity between predicted suitability of RUF and HSI models suggests that the apparent success of the RUF may be a function of the underlying assumptions of the technique and not an actual improvement on predictive ability.

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General Introduction

Species do not use all resources equally. Different species require a specific set of resources within an environment to survive and reproduce. Because resources are not dispersed equally upon the landscape, organisms seek out areas that have the appropriate combination of resources required; this is termed differential resource selection, and is the basic ecological principle that allows species to coexist (Rosenzweig 1981). Resource selection is generally implied when resources are used in greater proportion than their availability on the landscape (White and Garrott 1990, Garshelis 2000, Manly et al. 2002) and understanding this process aims to explain one aspect of ecology's fundamental question; what determines the distribution and abundance of organisms upon the landscape (Krebs 1985)?

Modeling wildlife-resource relationships gives us insight into the process of resource selection. Models are tools that help us better understand relationships between predictor and response variables (Garton et al. 2001). They can aid in testing our current understanding of wildlife-resource relationships (Morrison et al. 1992) and in predicting the future of wildlife populations in a changing environment. There are many different types of wildlife resource-selection models (see review by Morrison et al. 1992, chapter 6), but they all function with similar underlying assumptions: 1) animal distribution and abundance is related to environmental attributes (Marcot et al. 1983); 2) similar spatial or temporal patterns in environmental attributes will reflect similar patterns in animal abundance (Flather and Hoekstra 1985); 3) animal abundance is positively associated with resource quality (Van Horne 1983); 4) the selection of higher quality resources results in higher fitness (Rosenzweig and Abramsky 1986, Garshelis 2000); and 5) species will select the highest quality resources available to them (Manly et al. 2002).

Resource-selection modeling techniques take either a deductive or inductive approach (Corsi et al. 1986, Stoms et al. 1992). Deductive methods are a “bottom-up” approach to wildlife-resource modeling, where individual wildlife-resource relationships are the building blocks that define the suitability of a landscape. Conversely, inductive models imply a “top-down approach”; the suitability of a landscape is predefined by animal use, and the wildlife-resource relationships are statistically teased out from landscape characteristics.

Deductive models are the simplest form of resource-selection modeling. They are based on a compilation of known or hypothesized relationships between an organism and its environment and are often presented mathematically (Corsi et al. 1986, Morisson et al. 1992). Specifically, layers of environmental variables relevant to a model are merged using a mathematical relationship, often within a Geographic Information System (GIS), with the goal of producing the best estimate of landscape suitability from the combined effects of all environmental variables (Corsi et al. 1986).

An example of a deductive approach to resource-selection modeling is the Habitat Suitability Index (HSI) model, formulated by the United States Department of Agriculture Fish and Wildlife Service (USFWS*;* 1981). A HSI model is a compilation of *a priori* and empirically derived wildlife-resource relationships that are compiled by an expert (Marcot et al. 1983). These relationships describe the predicted use of an area, generally expressed as the relative proportion of time that the area is used relative to optimal use (Marcot et al. 1994). The simplest form of this type of model estimates the overall landscape suitability by taking the geometric mean of *n* environmental variables that are thought to affect species abundance, distribution or presence (Morisson et al. 1992). The individual wildlife-resource relationships (e.g. effects of road density on animal resource use or effects of quality of nesting sites on bird use) are usually studied independently and their individual relationship to animal resource use (suitability) is well understood, but the cumulative effect of all variables on suitability is not empirically derived from field data.

Habitat capability (HC) and habitat effectiveness (HE) models are additional deductive techniques, and are similar to HSI models, but can vary in their structure. Generally, HC models incorporate an estimate of the total area that has suitable landscape (often denoted as habitat units) or rank an area based on its potential for supporting a given species (Morrison et al. 1998). They do not necessarily represent current habitat conditions, as does the HSI. HE models rank an area based on the degree to which it can support a species to its environmental carrying capacity (Morrison et al. 1998) or cultural carrying capacity (McClafferty 2000), the latter defined as the tolerance level of the local human population to a nuisance situation brought on by the study species.

An inductive modeling approach is used when the wildlife-resource relationships are not known a priori (Corsi et al. 1986) but field observations of the animal's landscape use are available. In this case, environmental predictor variables are chosen based on the known ecology of the organism (Burnham and Anderson 2001), while the cumulative effect of all variables on the animal's landscape use is derived statistically. Because these models do not test explicit independent hypotheses about resource use, they provide little information on the underlying ecology driving the relationship between the predictor variables and resource use (Morrison et al.1992). However, they can give insight into the relative importance of the predictor variables on an individual's or population's use of a landscape (Dettki et al. 2003).

Resource selection function (RSF) models are constructed using an inductive modeling approach. A RSF model is a compilation of resource selection functions; being any function that is proportional to the probability of use by an organism (Manly et al. 1993) that can predict the relative probability of occurrence of an individual (or population) upon a landscape (Johnson 1980). Therefore, areas with higher resource suitability values should have a higher degree of animal usage than areas of lower resource suitability. RSF's are often estimated from relocation point data (e.g. Nielson et al. 2003, Johnson et al. 2004) using a multivariate analysis (Boyce et al. 2002). RSF models can follow either multiple regression or binary logistic regression models, where a set of environmental variables are often used to describe variation in an animals' space use, distribution or abundance. When data are in the form of used/available or used/unused resource units, then RSF models are created with binary logistic regression (Boyce et al. 2002). Used resources are often represented in the form of telemetry or GPS animal relocation points upon a landscape, whereas unused/available resources are represented by a set of random relocation points upon the landscape. Binary logistic regression is used to differentiate between used and available sites based on the presence or absence of the suite of predictor variables.

When data are in the form of probability of space use, such as a utilization distribution (Silverman 1986), then multiple regression can be employed to calculate RSFs (Marzluff et al. 2004). The resulting model is termed a resource utilization function (RUF) model. The utilization distribution is draped over a landscape and a set of predictor variables are measured throughout the landscape and used to explain variation in animal space use.

Deductive models have been used extensively throughout the United States and Canada since the 1980s but they are seldom validated. Specifically, many habitat and resource models have been developed for elk (*Cervus elaphus*) in North America (Leege 1984, Wisdom et al. 1986, Edge et al. 1987, Roloff 1998, TAEM consultants 1998, Thomas et al. 1988, Buckmaster et al. 1999, Benkobi et al. 2004) but only a few of these models have been validated (Roloff et al. 2001, Jones et al. 2002, Benkobi et al. 2004). Many assumptions made in un-validated HSI models have been questioned and often proven false (Laymon and Barrett 1986), such as the typical assumption of linear relationships between wildlife density and environmental parameters (Meents et al. 1983), or that density is an appropriate measure of habitat quality (Van Horne 1983). Validation of a model is extremely important as it initiates the process of adaptive management; specifically, to pinpoint weaknesses in a model, compensate for the weaknesses and adjust the model to a particular environment (Roloff et al. 2001).

A model is most useful when it can accurately predict the locations of wildlife (Marcot et al. 1983, Boyce et al. 2002), but that rarely happens. Validation helps to assess how well a model fits the data (reliability), and how well it can predict the distribution and abundance of a species in other places and times (robustness: Marcot et al. 1983, Boyce et al. 2002). Untested models are of little use because they simply lack credibility (Laymon and Barrett 1986), as do management decisions made using unvalidated models (Roloff et al. 2001).

In recent years, the advancement in both data analysis techniques and computational power has led to a proliferation of species-environment modeling techniques (Guisan and Zimmermann 2000). As a result, traditional deductive modeling techniques that rely on a bottom-up approach have become less desirable than statistical-based (top-down) inductive models. There has been little effort to compare deductive and inductive resource selection modeling techniques. Currently, it appears as though the scientific community has fully embraced high powered statistical analysis and GIS-based modeling approaches (Corsi et al. 1986, Boyce and McDonald 1999, Boyce et al. 2002, Manly et al. 2002, Marzluff et al. 2004) without comparing the limitations and benefits of both techniques.

Elk Restoration in Ontario

Elk (*Cervus elaphus*) were once the most widespread member of the deer family (Cervidae), occupying most of North America, Europe, Scandinavia and Asia, and were also present in North Africa and South America (O’Gara and Dundas 2002). However, overhunting, settlement and habitat destruction in North America are thought to be the main reasons for the reduction in numbers and extirpation throughout much of their historic range (Peterson 1957, Bryant and Masser 1982). At present, there are four subspecies of elk in North America: Manitoban; *C.e.manitobensis* (Millais 1915), Rocky mountain; *C.e. nelsoni* (Bailey 1935), Roosevet elk *C.e. roosevelti* and Tule; *C.e. nannodes* (Merriam 1905), although genetic studies do not differentiate between the Manitoban and Rocky Mountain subspecies (Polziehn et al. 1998). Two subspecies, the Eastern Elk (*C. e canadensis* Erxelben 1777) and the Merriam elk (*C.e. merriami* Nelson 1902), are considered extinct (Bryant and Masser 1982). The current natural distribution of elk in North America ranges from the central to the western states and provinces. There have been many successful re-introduction programs in the United States and Canada, mainly due to the availability of large areas containing suitable habitat and low human densities (McClafferty 2000).

Elk were present during the 1700s between lakes Huron and Erie, and sub-fossil evidence shows early elk distribution from Ottawa, central Ontario to Sudbury (O’Gara and Dundas 2002). The cause of elk extirpation from Ontario is speculative; however they were gone by the early 1800s (Peterson 1957, Bosveld 1996). During the 1930s a number of translocations occurred, introducing about 200 Rocky Mountain elk from Alberta to southern Ontario (O’Gara and Dundas 2002). The population increased to approximately 300 animals by the 1940s, but the threat of giant liver fluke (*Fascioloides magna*) infestation brought the program under scrutiny and attempts were made to eliminate the herd; approximately 1000 elk were killed over the next decade (O’Gara and

Dundas 2002). A remnant population of approximately 50 animals persisted until the late 1990s in the Burwash-French River area (south of Sudbury). Recently, the province of Ontario undertook an elk restoration program, relocating a total of 443 western elk (*C.e. manitobensis*; Polziehn et al. 1998, Polziehn et al. 2000) from Elk Island National Park, Alberta, to four regions throughout the province.

Site assessment for the Ontario elk reintroduction program was completed at the scale of 1km. It was based on a weighted suitability of a combination of variables including the predicted historic range of elk, the mean maximum snow depth, the amount of agricultural and urban areas, human population density, white-tailed deer (*Odocoileus virginianus*) density and the amount of open foraging and cover areas. Open foraging and cover areas were determined using a classified vegetation cover from 1km advanced very high resolution radiometer (AVHRR) satellite imagery (Hutchinson et al. 2003). The classification of AVHRR data was based on 15 major global vegetation coverages such as evergreen needleleaf forest, evergreen broadleaf forest, deciduous needleleaf forest, deciduous broadleaf forests, wetland and cropland among others. (Loveland et al. 1999). The accuracy assessment for the classified AVHRR satellite data had a global average of 73.5% and varied from 63 to 83%, with an average North American accuracy of 63% (Loveland et al. 1999).

Based on the initial site assessments, a total of 172 elk were introduced to the Sudbury area in 1998-2001, 120 to Bancroft and 104 near Kenora in 2000-2001, and 47 to the Blind River area in 2001 (Rosatte et al. 2002a, Rosatte et al. 2002b). Since the introductions, the Bancroft and Blind River herds have shown a steady growth of approximately 40-67% and 28-38%, respectively (Young et al. 2004). The Sudbury herd has decreased overall by 24-36%, but during 2004-2005 the herd has shown a small increase. The Kenora herd decreased considerably (56-66%) to an estimated population of 35-45 animals in 2004.

Average calving success ranged from 16% over 5 years for the Sudbury herd, 42% over 4 years for the Bancroft herd, 21% over 4 years for the Kenora herd and 33% over 3 years for the Blind River herd (Young et al. 2004).

Lake of the Woods Elk Restoration Initiative

The Lake of the Woods (LOW) elk restoration initiative introduced a total of 104, including 70 radio-collared elk, south of Kenora, northwestern Ontario (Figure 1) in 2000 and 2001. Two years after the release, 70% of the collared elk remained within 20km of the initial release site (north site) while 30% (10 bulls and 12 cows) of the collared elk dispersed approximately 90km south of the release site (south site) (McIntosh 2003).

Non-random resource use patterns based on forest type, stand age and elevation were observed in the reintroduced elk (McIntosh 2003). Resource use patterns were based on a binary use versus available resource approach, where use was modeled on fine (50% adaptive kernel) and coarse (95% adaptive kernel) scales (McIntosh 2003). Forest stands used by elk from the north site in decreasing importance included red pine/ white pine and mixed conifer, cedar lowland, mixed hardwood and poplar (McIntosh 2003). Elk used stands ranging in age from 1 to 25 years, and use of older stands declined (McIntosh 2003). At the fine scale, elk used areas ranging in elevation from 340m to 400m above sea level (a.s.l.) in greater proportion than available, whereas at the coarse scale, elk used areas ranging from 400m-420m a.s.l. more often than other elevations (McIntosh 2003).

There were 23 recorded mortalities of radio-collared elk from January 2000 to June 2002 (McIntosh 2003). The causes of mortality were translocation injury (26%), unknown causes (22%), predation (17%), illegal shooting (17%), road kill (9%), trauma (4%) and drowning (4%) (McIntosh 2003).

A total of 69 of the original elk were estimated to be alive at the end of June 2002 (McIntosh 2003). An additional 8 calves in 2001 and 8 calves in 2002 were thought to have survived, resulting in a total of 85 elk present on the landscape at the end June 2002 (McIntosh 2003). Using McIntosh's (2003) dispersal data, where 30% of the elk dispersed to the south site, the estimated population in the south site was 25 animals while 60 elk remained in the north site with a total of 36 animals accounted for by radio-collars.

By the end of 2003 the number of radio-collared elk had decreased substantially to 16 because of dropped collars and elk mortality. The elk restoration program proposed re-collaring and newly collaring 25 to 40 additional elk residing in the northern portion of the study area at the beginning of my study. Unfortunately, only 6 additional mature uncollared elk were located by helicopter in January 2004, 4 of which were collared for the first time, and two of which were re-collared as they had previously shed their original collar. Helicopter flights in March 2005 and December 2005 sighted only 29 and 24 elk, respectively, furthering the possibility that elk survival and recruitment was poorer than originally estimated by McIntosh (2003).

The decline in the LOW elk population is a concern for those interested in the successful re-establishment of elk in Northwestern Ontario. At present, explanations for this decline are speculative in nature, but one concern is that the landscape does not contain the resources required to support a viable population, contrary to the original deductive model (Hutchinson et al. 2003).

Hypotheses and Objectives

To address the resource suitability concerns of the declining LOW reintroduced elk population, I hypothesized that the landscape suitability surrounding the north site was not as good as was originally estimated. Therefore, the first objective of this study was to investigate the general resource suitability of the landscape by creating and validating a summer elk HSI model for northwestern Ontario, specific to the north site where the majority of collared elk resided in 2004. I constructed the HSI solely for the summer season because I did not have enough data to validate a winter model. The deductive model is a compilation of elk-variable relationships outlined in previous models created for elk residing in Canada and the United States. As a second objective, I created a resource suitability model using an inductive approach, expecting to improve upon the deductive model. The aim of the inductive approach was to develop and validate a summer RUF model based on telemetry locations of radio-collared elk released in northwestern Ontario. I also hypothesized that the inductive approach would provide a more accurate model for predicting elk landscape suitability. Therefore, my third objective was to compare inductive and deductive resource selection modeling techniques for elk in northwestern Ontario, Canada.

To accomplish all objectives, I: (1) created separate resource selection models using inductive and deductive techniques, as above, using the same predictor variables for both; (2) validated both resource selection models; and (3) compared the ability of each approach to predict resource selection of reintroduced elk in northwestern Ontario.

Study Area

The spatial extent of the study area is defined by the furthest North, South, East and West locations of collared elk residing in the northern study site. This area spans approximately 1,300km^2 and is located 20km South-East of Sioux Narrows and 20km northeast of Nestor Falls in northwestern Ontario, Canada (49^{o}16’N, 93 ^{o} 42’W*;* Figure 1). The study area is underlain by Precambrian Shield bedrock and the canopy is dominated by pure or mixed stands of conifers: black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*) and tamarack (*Larix larcinia*) (Rowe 1972). Also present in the region are hardwoods, including white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*) and large tooth aspen (*Populus grandidentata*) (Rowe 1972, McIntosh 2003). Soil deposits are thin and very coarse in texture (Rowe 1972). The terrain is irregular in nature, ranging from lowland peat bogs to exposed elevated bedrock (McIntosh 2003) and is reflected by a large number of rock-rimmed lakes (Rowe 1972). The range in elevation varies from 100m above sea level (a.s.l.) to 490m a.s.l. on hills and ridges, with a mean elevation of 356±10m a.s.l. (McIntosh 2003). The region supports ongoing forestry activities (both harvesting and forest fire suppression), resulting in a patchwork of different aged stands. The regeneration initiatives are both artificial and natural, and consist of red pine (*Pinus resinosa*), white pine (*Pinus strobes*), spruce and aspen.

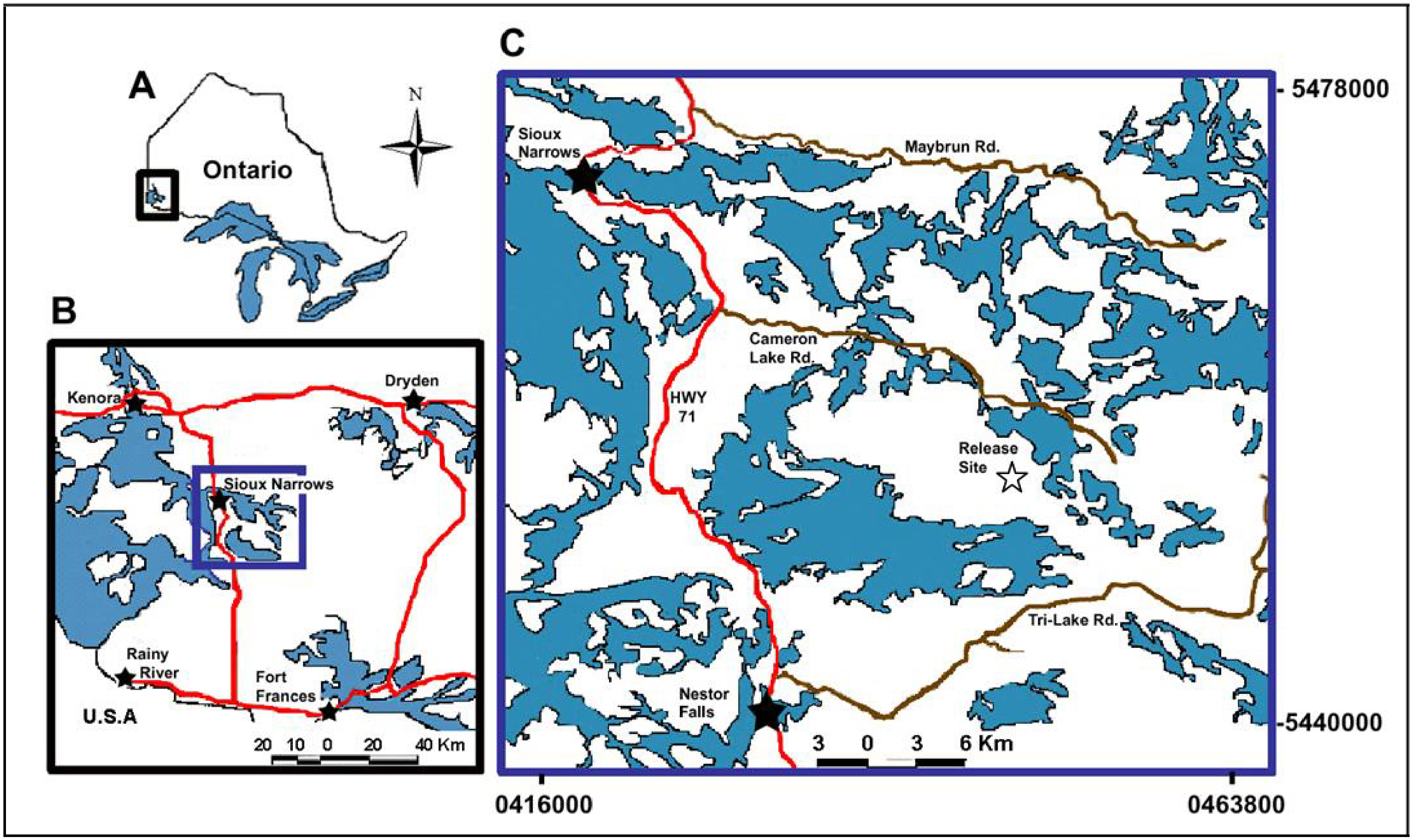

Figure 1. Map of the study area showing the province of Ontario, Canada (A), the greater study area (B) which encompasses the southern site between Rainy River and Fort Frances and extending north to the northern study site (C) in the Cameron Lake area. Filled stars represent towns and the open star in (C) marks the release site.

General Methods

Some data collection, preparation and model validation techniques follow the same methods for both types of models developed in this study. To avoid repetition, this ‘general methods’ section outlines methods used in the development and validation of both modeling approaches. This section does not need to be read from start to finish, but can be referred to as these techniques are applied in subsequent sections.

1. Telemetry data acquisition

Telemetry data were collected by McIntosh (2003) using vehicle, snowmobile and on foot from 2000-2002 on a weekly basis throughout the spring and summer months and biweekly throughout the fall. Tracking continued on a biweekly basis from the fall of 2002 until the spring of 2003, at which point weekly spring and summer tracking and biweekly fall and winter tracking resumed. Thirty elk were radio-collared and tracked beginning in the winter of 2000 and an additional 43 elk were radio-collared and subsequently tracked in the winter of 2001 (McIntosh 2003). In January 2004, an additional 4 animals were radio-collared, and 2 animals re-collared.

Elk locations were obtained by manual remote triangulation. A four-element directional antenna and portable receiver (Model TRX-2000S, Wildlife Materials Inc., Carbondale, Illinois and Model STR-1000, Lotek Engineering Inc., Newmarket, Ontario) were used to detect elk radio-signals. Bearings in the direction of elk radio-signals were taken using a compass. A hand-held Global Positioning System (GPS) was used to determine the location at which bearings were taken. Locations and bearings were plotted and triangulated on 1:50,000 national topographic maps and within the triangulation program Locate II (Nams 2001) to obtain animal location estimates and associated 95% error polygons. A minimum of 3 bearings were collected for each elk to complete triangulation and obtain an animal location estimate. Thirty-five test collars were thrown at random throughout the study area during the first study period from 2000-2002 (McIntosh 2003) and 58 test collars during the second study period from 2003-2005 to provide an accuracy assessment of triangulation. Average distance between triangulated locations and GPS-determined locations were 157m (±11m) for the first study period and 134m (±35m) for the second.

Within approximately 605m (±78m, n=251) of an animal, radio-signals are loud and can be heard on an “attenuation” level. Attenuated signals were used during the fall of 2002, when in close proximity to radio-collared elk, to estimate elk locations.

2. Light Intensity

I used a measure of canopy openness to delineate open forage and closed forage areas for both HSI and RUF models. Canopy openness was measured using a canopy-scope; a Plexiglass square marked by a 5 x 5 grid of dots situated 3cm apart with a 20cm string attached to one corner (Brown et al. 2000). The observer held the string of the canopy scope eye-level and extended the plexiglass grid in the direction of the largest canopy gap until the string became taught. The number of dots within the canopy gap was recorded.

I recorded canopy openness at 3 sites within 232 forest stands ranging in age from 0 to 120 years. Average canopy openness significantly decreased when stands reached 45 years of age (ANOVA; $P<0.05$, n=232).

3. GIS layers used in model building

The study area spans two administrative districts; Kenora and Fort Frances. Forestry sectors in each district compile a forest resource inventory (FRI) of their forest management units. These FRIs are based on ground truthing and aerial photography, where forested stands are delineated and classified based on age, height and species composition. Non-forested areas are categorized into different landforms such as lakes, wetlands, roads and private land. I used the 2004 FRI data for the Kenora district and the 1997 FRI for the Fort Frances district. I updated the stand ages of the Fort Frances FRI in ArcView 3.2 (ESRI 2000) to correspond with the 2004 FRI data from Kenora. I used the FRI as the major data layer to calculate and summarize vegetation and road cover variables used in both models.

4. Landscape Scripting Language

Landscape Scripting Language (LSL) is a proprietary geographic information system (GIS) developed by the Ontario Ministry of Natural Resources (OMNR) (Kushneriuk and Rempel 2004). The program uses multiple attribute data to specify spatially explicit wildlife-resource models. The basic unit of LSL is the hexagon. LSL overlays a landscape with a grid of hexagons within which spatial metrics are calculated and summarized.

LSL has a fundamental data type called the parcel. Parcels are portions of a GIS polygon that intersect a hexagon (Figure 2). Metrics are calculated at the parcel level and can be rolled up to the hexagon level using either: 1) a weighted average, where metrics for individual parcels are weighted by the area of the hexagon it occupies, then averaged across all parcels, or 2) a majority rule, where only the metrics for the parcel occupying the largest area of a hexagon (over 50% of the hexagon area) are rolled up.

I calculated landscape metrics within hexagonal units of 1/7th of a hectare. This particular hexagon size was recommended by Rob Kushneriuk at the OMNR and is currently being used within the OMNR Landscape Guide Science teams as the hexagon size for 16 HSI models for the Great-Lakes Saint Lawrence region (e.g. pileated woodpecker (*Dryocopus pileatus*), moose(*Alces alces*), white-tailed deer). This hexagon size is considered a good compromise between accuracy when calculating distance metrics and keeping computer files within a reasonable size.

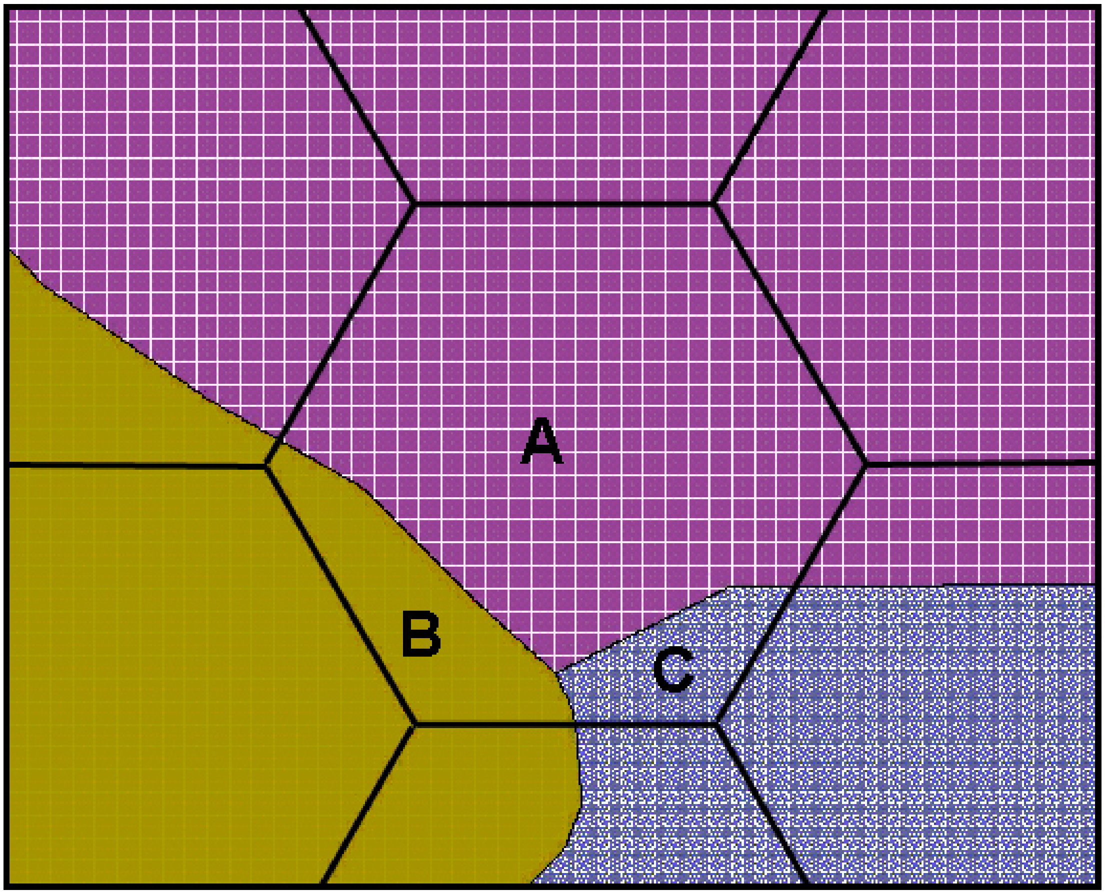

Figure 2. Centre hexagon contains three parcels; A, B and C. If using the majority rule where the three parcels represent different stand ages (A= 30 years, B=75 years and C=5 years) then the stand age for the hexagon would be 30 years. If using the weighted average rule where each parcel is weighted according to the proportion of the hexagon in occupies (A=0.8, B=0.15, C=0.5) then the stand age for the hexagon would be approximately 38 years.

I calculated stand age for each hexagon using the majority rule, and assigned stands that did not have an associated age (wetlands, bush-alder and rocky-outcrops) as 0. I defined "cover" as parcels with a stand age equal to or older than 15 years and "open forage" as parcels with stands younger than 45 years. Edge was defined on a per hexagon basis as the length of shared edge between forage and cover parcels. The distance to a forage-cover edge was calculated as the distance from the centre of a hexagon to the centre of the nearest hexagon containing edge. The proportion of deciduous trees in the canopy was calculated using the weighted average. Road density was summarized for each hexagon as the length of primary and secondary roads per circular km^2 surrounding the hexagon.

The width of cover was calculated using a multi-step process. All hexagons were first defined as cover or non-cover. Six lines were drawn through the centre of each cover hexagon, 3 through the paired edges and 3 through the paired corners (Figure 3). These lines project outwards until they hit a non-cover hexagon. Cover width was calculated using a weighted average of the 3 shortest lines;

$$\text{Cover width} = \frac{(2r + x_1 + x_2)/4}{1.077} \qquad \text{(Equation 1)}$$

Where, r represents the shortest distance to a non-cover hexagon and x_1 and x_2 represent the 2nd and 3rd shortest distances. The denominator of Equation 1 (1.077) is a correction factor that aims to offset the normally longer 2nd and 3rd shortest lines (Figure 4) using a weighted average. It is based on an ideal scenario where r is equal to 1 and the interface of the edge creates a hypotenuse triangle with lines x_1 and r or x_2 and r (Figure 4). When r is equal to 1, x_1 and x_2 are calculated by;

$$x_i = r / \cos 30^{\circ} = 1/0.866 = 1.1547 \qquad \text{(Equation 2)}$$

And all three lines are weighted accordingly;

$$\frac{2r + x_1 + x_2}{4} + \frac{2(1) + 1.1547 + 1.1547}{4} = \frac{4.3094}{4} = 1.077 \qquad \text{(Equation 3)}$$

Twenty-five smoothing passes throughout the landscape were then done to remove the effect of small edge irregularities that may result in a shorter calculated width than expected (Figure 5). Smoothing passes calculate average cover width for a hexagon using the centre hexagon and the surrounding 6 hexagons.

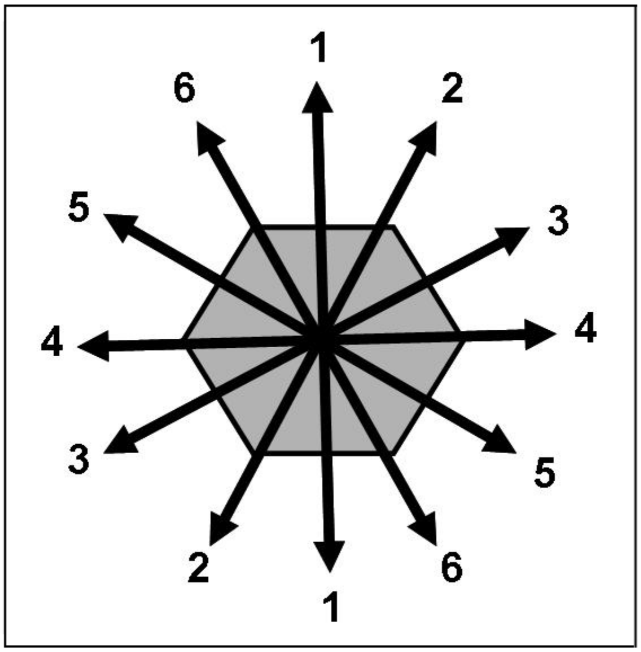

Figure 3. A hexagon with six paired lines projecting outward, where numbers represent pairs.

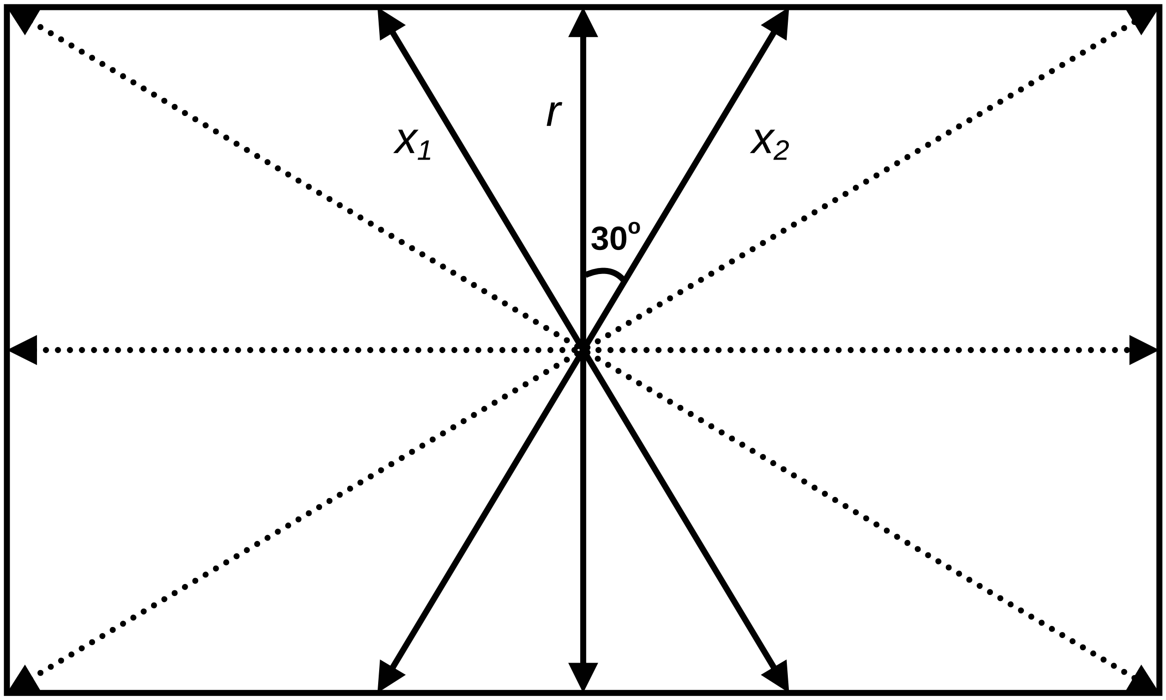

Figure 4. Using a weighted average of the shortest (*r*), 2nd and 3rd shortest lines (x_1 and x_2) to obtain the width of cover. The calculation is based on an ideal scenario where the interface of the edge creates a hypotenuse triangle with the lines *r* and x_1, as well as *r* and x_2. The length of line x_i is calculated using Equation 2, and the three lines are weighted using Equation 3.

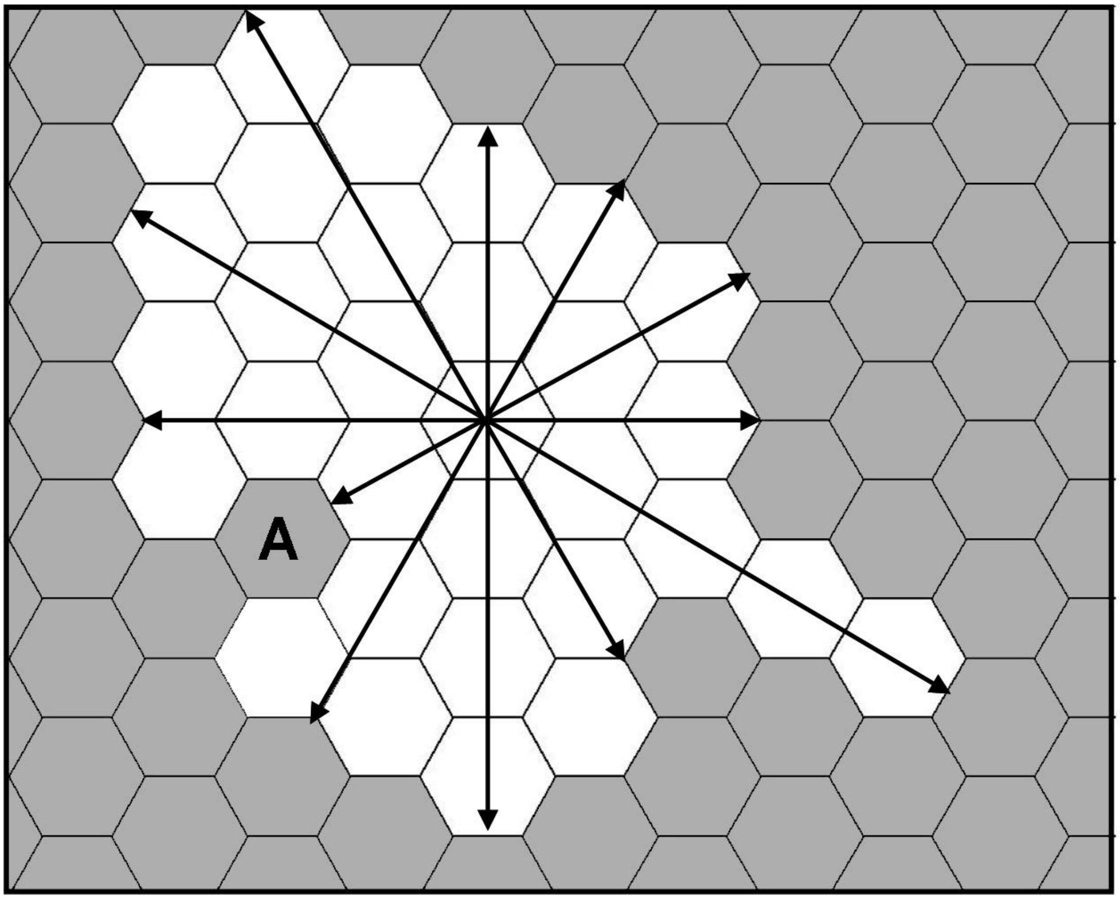

Figure 5. Grey hexagons represent open forage, and white hexagons represent cover. Arrowed lines extend outward until they reach a non-cover hexagon. Hexagon "A" represents a small edge irregularity that would result in an underestimated width.

5. Model validation technique

5.1 Estimating utilization distributions from kernel analysis

Model validation initially required the calculation of summer utilization distributions (UD) (Silverman 1986) for each elk using relocation data. I first defined summer and winter seasons explicitly using temperature and snow depth. Specifically, temperatures including and below -20^{o}C, as well as snowdepths greater or equal to 40cm normally induce elk to seek shelter for thermoregulation or change normal summer foraging habits, respectively (Skovlin et al. 2002, Sweeney and Sweeney 1984). Therefore, "winter" was defined as the period when elk temperature regulation begins at -20^{o}C or when snow depths exceed 40cm. I used the average daily minimum temperatures and "snow on the ground" from three weather stations (Kenora, Mine Centre and Dryden) surrounding the study site (Environment Canada) from 2000 to 2005 to delimit the seasons (Table 1).

Table 1. Summer season start and end dates from 2000 to 2005.

Summer Start Date	*Summer End Date*
March 17, 2000	November 21, 2000
March 26, 2001	December 27, 2001
March 26, 2002	December 17, 2002
March 11, 2003	December 1, 2002
April 5, 2004	December 1, 2004
April 4, 2005	October 31, 2005*

* End date is seasonally premature because data collection stopped.

I calculated the summer 99% UD for individual elk using the fixed kernel analysis function in the Home Range Extension (HRE) for ArcView GIS 3.2 (Rodgers and Carr 1998, ESRI 2000). I chose the fixed kernel analysis method because it is robust with respect to sample size, autocorrelation, centre of activity and outliers (Kernohan et al. 2001). The fixed kernel has a constant bandwidth that is applied to the whole area under evaluation and results in a more accurate representation of the outer contours of the home range (Kernohan et al. 2001). Because a kernel analysis estimates an animal's probability of occurrence in a particular area, it will never describe an animal's total (100%) use of an area. Therefore, I used the 99% probability of occurrence as a best estimate of total area use. I employed Least Squares Cross Validation (LSCV) (Kernohan et al. 2001) to estimate bandwidth for each set of animal locations. The kernel estimator of the UD is calculated as follows (Kernohan et al. 2001):

$$\hat{\int}(x) = \frac{1}{nh^2}\sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right) \qquad \text{(Equation 4)}$$

Where $\hat{\int}(x)$ is the utilization distribution (UD),

n is the number of locations

h is the smoothing parameter/bandwidth

X_i contains a matrix of *x* and *y* coordinates

x is the point at which the kernel is positioned

K is the kernel function (probability density function)

Although, fixed kernel estimation with sample sizes greater than 30-50 relocation points are reported to perform well, particularly at the outer boundaries (Seaman et al. 1999), I did not have that many relocations for most of the radio-collared elk in my study. So, I investigated the minimum sample size required to give the best estimates of the area of a 99% fixed kernel UD as denoted by the whole summer season radio-telemetry data set, to determine the point at which the effects of small sample size levelled off. To do so, I calculated the 99% UD and its respective area after each relocation point was added to an animal's data set. I calculated the proportion of each 99% UD area relative to an animal's final (containing all of an animal's relocation points) 99% UD. I plotted the proportions for each animal, beginning with 3 relocation points and up to a maximum of 83 relocation points (Figure 6). In doing so I determined that the proportion of the final 99% UD area levelled off at 18 radio-telemetry fixes. Therefore, I included all animals with a summer sample size greater than 18 telemetry fixes in the development or validation of models (Appendix 1).

The HRE kernel analysis output provides a set of embedded polygons where the outermost isopleth denotes the area within which an animal will be located 99% of the time, and the innermost isopleth represents the area within which an animal will be located 10% of the time (Figure 7). I calculated 99, 90, 80, 70, 60, 50, 40, 30, 20, and 10% isopleths for each UD. I transformed the embedded kernel polygons into a single grid using LSL. Within LSL, I clipped the 90% isopleth out from the 99% isopleth, and the 80% from the 90% (and so on) until all isopleths represented spatially independent "bands". Each band corresponded to a relative proportion of time that the animal spent within its respective boundaries. For example, the outermost band (99%) was used 1% of the time (where its relative space use density was 0.01), and the innermost band (10%)

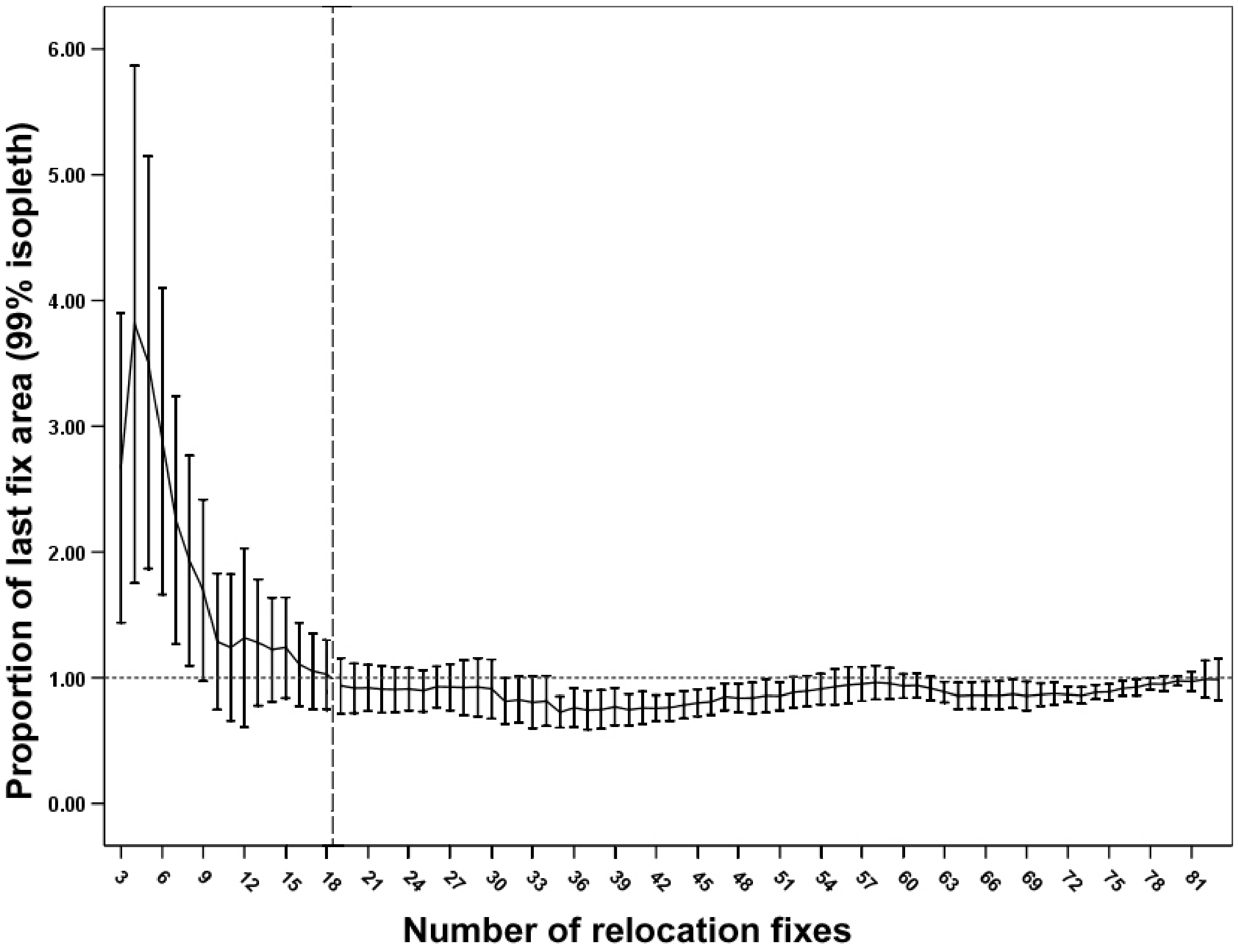

Figure 6. The effect of successive relocation fixes on the proportion of the last relocation fix area. The proportion of last fix area begins to level off when the average across all collars crossed 1.0 (dotted horizontal line) after 18 telemetry fixes (hatched vertical line). Bars represent 95% confidence intervals of the mean (solid line).

was used 90% of the time (where its relative space use density was 0.9). Each UD was then considered to be made up of ten density bands ranging from 0.01 for the outer polygon to 0.9 for the innermost polygon (Figure 7). In order to relate the density of space use to landscape suitability, I standardized the UD to range from 0 to 1.0, by dividing each space use density band by 0.9. Consequently, a standardized suitability of 0 represents relatively poor suitability and 1.0 represents relatively high suitability. This "suitability distribution" is represented in 3 dimensions by plotting the spatial location of the standardized bands (easting and northing coordinates) along the x and y axes, and the suitability (standardized relative space use density from the UD) along the z axis (Figure 8).

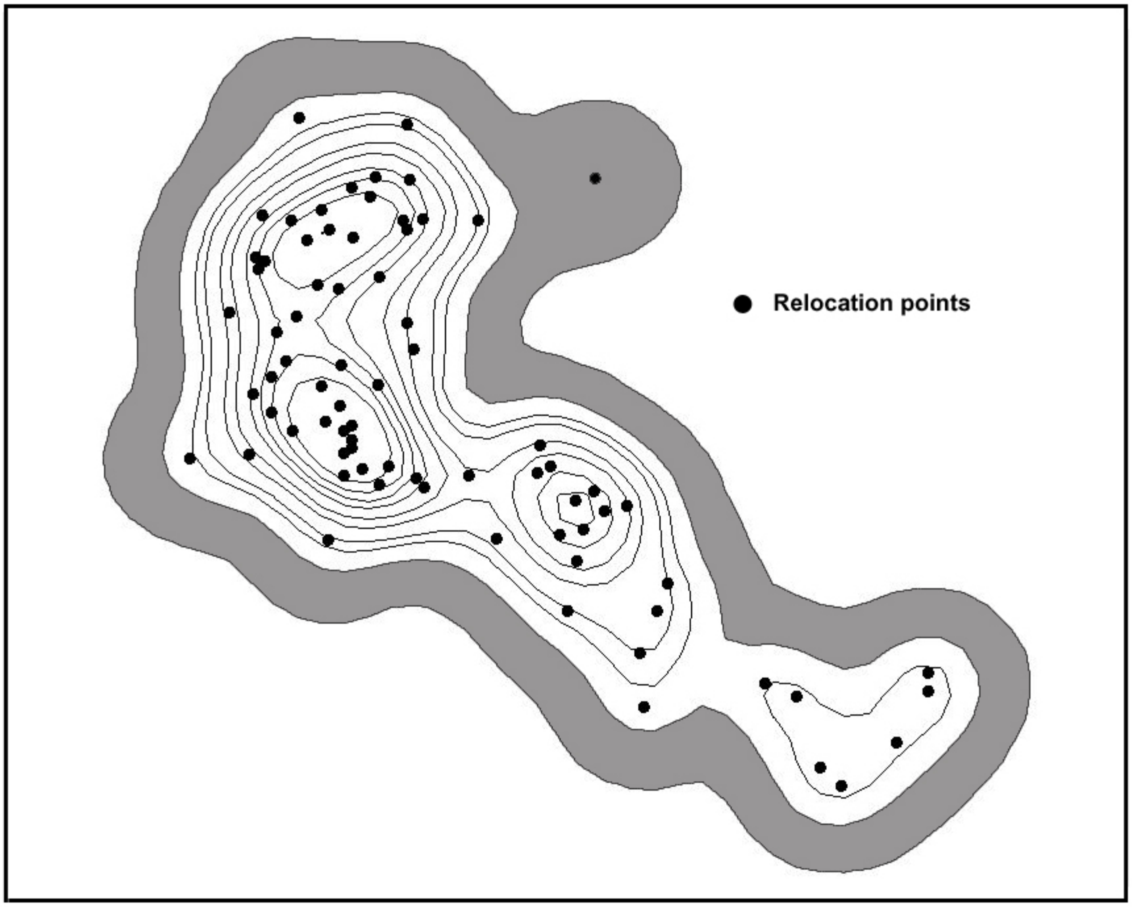

Figure 7. UD based on fixed kernel analysis. Outermost band (grey) represents the lowest probability of use (1%), where 99% of the animal's space use occurred within the outer isopleth of this band. The innermost band represents highest probability of use (90%).

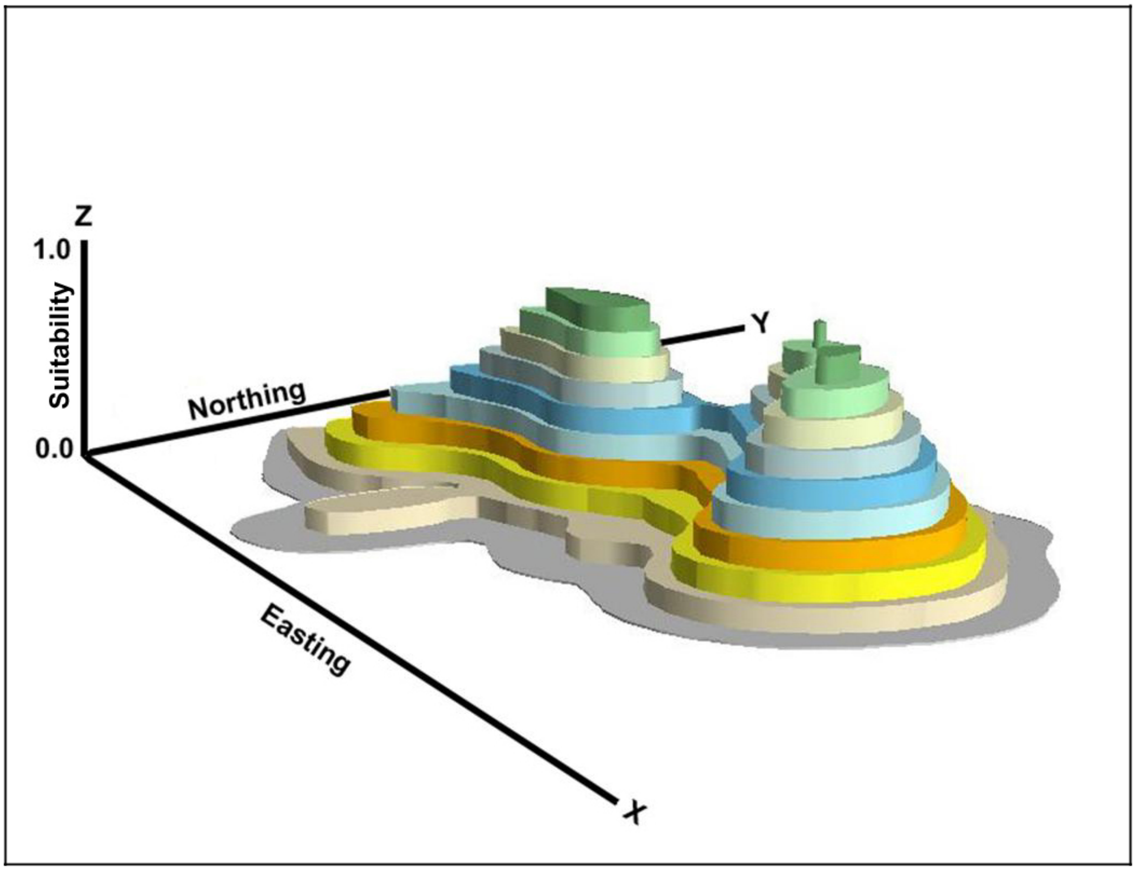

Figure 8. Suitability distribution constructed from a kernel analysis. X and Y axis represent the easting and northing coordinates, whereas the Z axis represents the suitability.

5.2 Volume of Intersection Index and the derivation of the DVI Index

I used the Volume of Intersection (VI) Index (Seidel 1992) to validate and compare the predictive ability of both the HSI and RUF models. This index assesses the degree to which the habitat model reflects an animal's perceived value of the landscape (i.e. from its relative space use or UD). For instance, does the suitability from the model increase as an animal's relative use of the same area increases? The VI Index does not assess whether a model is "good" or "bad" but whether it mimics animal use intensity. The VI Index provides a measure of the degree of overlap between two utilization distributions or, as used in this study, two suitability distributions (two volumes), and is computed by:

$$\text{VI Index} = \iint \min\left(\hat{f}1\,(x,y),\ \hat{f}2(x,y)\right)dxdy \qquad \text{(Equation 5)}$$

Where $\hat{f}1$ is the standardized suitability from the radio-telemetry locations (kernel analysis) at hexagon x, y and $\hat{f}2$ is the predicted suitability from a resource suitability (HSI or RUF) model at hexagon x, y. Each SD is first standardized to 1, so the suitability values of all hexagons within each SD sum to 1. The VI Index sums the minimum standardized suitability (either $\hat{f}1$ or $\hat{f}2$) for all hexagons where both SDs overlap. The VI Index ranges from 0 to 1, where 0 denotes no overlap between the two volumes and 1 denotes a total overlap between the two volumes (Millspaugh et al. 2000, Seidel 1992). I also directly compared the two suitability distributions from the RUF and HSI models (Chapter 3) using the VI Index (where $\hat{f}1$ is the predicted suitability distribution from the HSI and $\hat{f}2$ is the predicted suitability distribution from the RUF) to determine the similarity between models.

When using the VI Index to compare a suitability distribution derived from a UD (which always ranges from 0.01 to 1.0) to a resource map (does not necessarily range from 0.01 to 1.0), the VI Index does not represent the true overlap between volumes of two distributions because of standardization. The VI Index has a tendency to artificially inflate or deflate resource suitability when volumes are standardized to 1 (Figure 9). Therefore, VI Index scores from different models cannot be directly compared.

To eliminate this problem, instead of comparing absolute overlap (from VI Index scores) between a resource model and an animal's SD, I compared the deviation of the VI Index (calculated between the resource model and an animal's SD) from a pattern of 'no selection', or a completely flat resource model (Figure 10), henceforth referred to as the deviation from the volume of intersection (DVI) index:

DVI Index= (True VI Index) – (VI Index 'no selection')   (Equation 6)

The VI Index of 'no selection' is calculated using equation 5, where $\hat{f}1$ is the standardized suitability from the radio-telemetry locations (kernel analysis) at hexagon x, y, as before. The suitability values for all hexagons in a model SD representing 'no selection' are identical and can be assigned any arbitrary value greater than 0 before being standardized. Regardless of the value chosen, following standardization, the suitability value of each hexagon is equal to 1 divided by the total number of hexagons. Subsequently, $\hat{f}2$ is the standardized suitability from a 'no selection' pattern (see Appendix 2 for sample calculations).

The resulting DVI Index compares the relative shape of the resource model to the animal's SD and provides an assessment of whether the model shows a similar pattern of suitability to animal space use. When the DVI Index is positive, the model shows a similar trend in animal space use (approaching Figure 10c). When the DVI Index is negative, the model does not follow a similar pattern of animal space use (approaching Figure 10b). As the DVI Index approaches zero, it becomes closer to a scenario of 'no selection' (Figure 10a). The magnitude of difference between DVI Index scores can be compared between models. To provide a benchmark of how well the model mimics animal use intensity, I compared the DVI scores against a null model. If the DVI score of the resource model is greater than the DVI score of a null model, the resource model is better at predicting animal use intensity than by random chance.

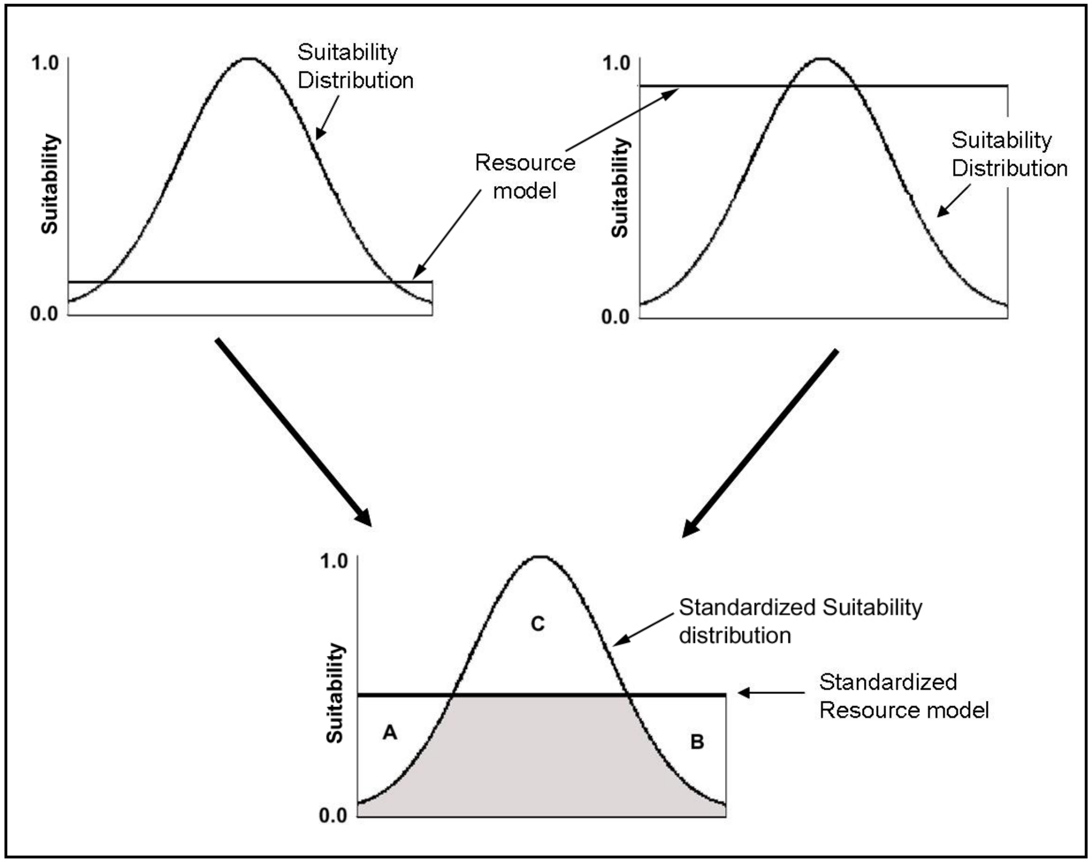

Figure 9. Each suitability distribution must be standardized to 1 to calculate the volume of intersection index. By standardizing a resource model and suitability distribution, the non-overlapping portions of the resource model (portions A and B of the bottom figure) become equal to the non-overlapping portion of the suitability distribution (portion C of the bottom figure). This process can artificially inflate the importance of a poor resource model (top left figure) or deflate the importance of a good resource model (top right) so that both situations, when standardized, result in the same VI Index, or overlap (grey portion of bottom figure). *Y* axis represents resource suitability on a scale of 0 to 1.

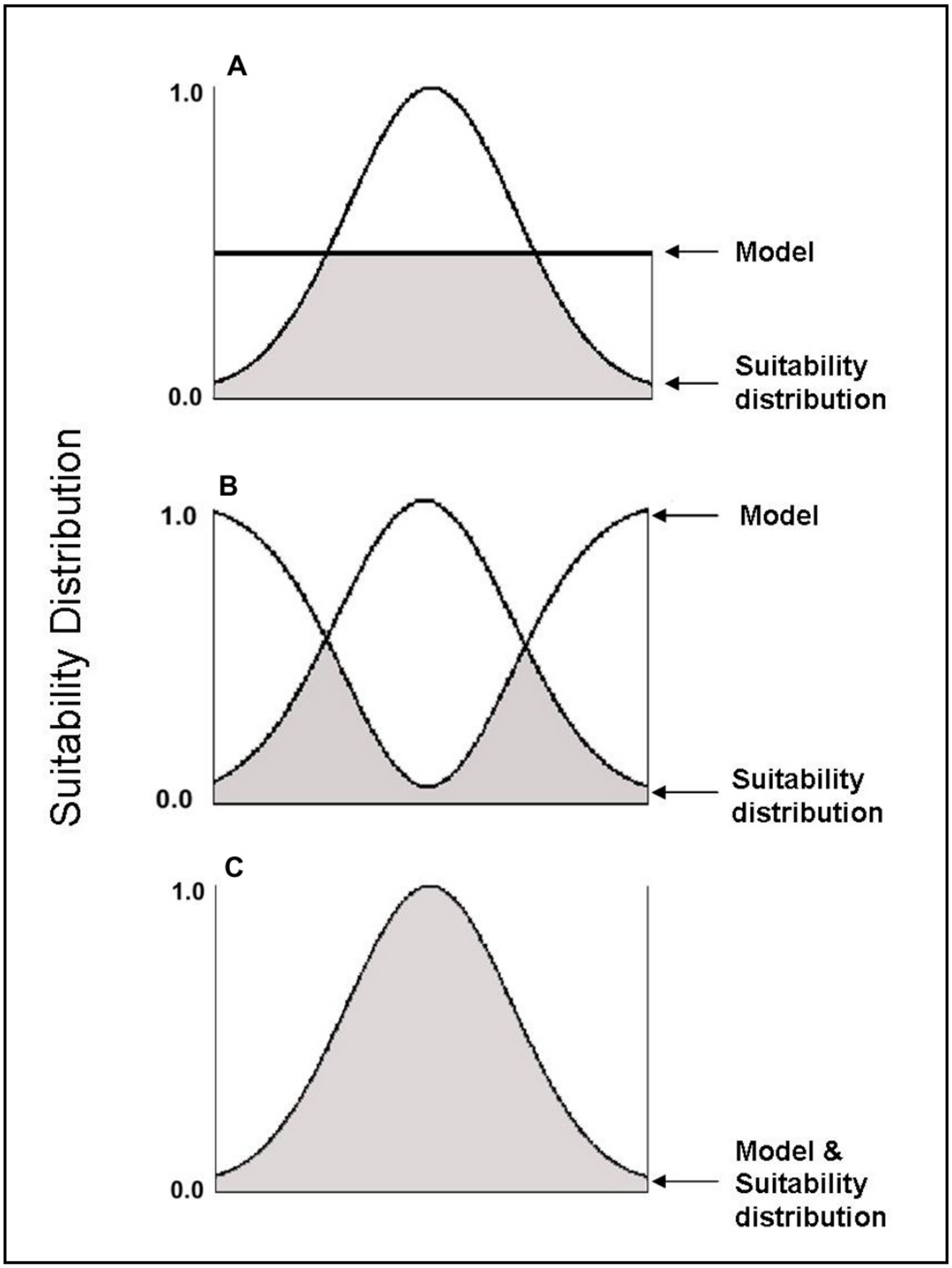

Figure 10. Selection patterns relative to no selection. The top figure (A) represents a resource model with no selection pattern, meaning that it is a flat suitability distribution. The middle figure (B) shows an opposite selection pattern to that of an animal's home range use intensity (suitability distribution) whereas the bottom figure (C) represents a resource model that is in complete agreement with animal use intensity. The grey area represents a relative estimate of the VI Index between the resource model and suitability distribution.

5.3 Average overlap index and Weighted overlap index

I used an Average Overlap (AO) Index between the HSI or RUF model and the UD to assess the quality of resources (as predicted by the HSI or RUF models) within the spatial extent of an animal's 99% UD. The AO Index is calculated by:

$$\text{AO Index} = \frac{\sum_{i=1}^{n} HSI_i}{n} \quad \text{or} \quad \frac{\sum_{i=1}^{n} RUF_i}{n} \qquad \text{(Equation 7)}$$

where n is the number of hexagons within the 99% UD and HSI_i or RUF_i refers to the value of the resource model for that individual hexagon.

The weighted overlap (WO) Index is similar to the AO Index as it is also a measure of the quality of resources (as predicted by the HSI or RUF models) within the spatial extent of the 99% UD, but it weights the importance of each hexagon according to its relative use by an animal. This results in an index that weights areas of high use intensity more than areas at the outer boundaries (lower use intensity) of an animal's 99% UD. The WO Index is calculated as follows:

$$\text{SSD} = \sum_{i=1}^{n} SD \qquad \text{(Equation 8)}$$

where SD is the suitability value within a hexagon of the suitability distribution derived from a 99% UD and SSD represents the sum of all suitability values within the suitability distribution;

$$\text{WO Index} = \sum_{i=1}^{n} \left[\left(SD_i \div SSD \right) \times HSI_i \right] \text{ or } \sum \left[\left(SD_i \div SSD \right) \times RUF_i \right] \qquad \text{(Equation 9)}$$

where HSI_i and RUF_i represent the resource suitability values in each hexagon.

CHAPTER 1.

Development and validation of a Habitat Suitability Index model for elk (*Cervus elaphus*) reintroduced to the Lake of the Woods region, Ontario.

Introduction

Habitat suitability index models are popular deductive models used extensively by the USDA Fish and Wildlife Service (Morrison et al. 1998) to make predictions from cause-effect relationships (Guisan and Zimmermann 2000). A HSI model is defined as a numerical index that represents the ability of a suite of resources to support a particular wildlife species (USFWS 1981). Such models describe and quantify the major environmental factors using resource structure, composition and spatial arrangements (USFWS 1981, Buckmaster et al. 1999) that have an effect on the occurrence and abundance of individual species (Morisson et al. 1992).

HSI models are based on the assumption that a species or population will select areas upon a landscape that are most able to satisfy its life requisites. Thus, areas of better resource quality and quantity should result in greater use by the species (Van Horne 1983, Schamberger and O'Neil 1986). HSI models assume there is a direct linear relationship between carrying capacity and specific HSI values (USFWS 1981), that represent the final response of a species to overall environmental conditions of a suite of resources (Morrison et al. 1998). HSI models are not capable of providing information pertaining to population sizes or trends and cannot portray an individual's behavioural response to a change in resources (Morrison et al. 1998). Essentially, HSIs are hypotheses of species-resource relationships that can be tested and improved (Schamberger et al. 1982). HSI models are applied appropriately when used to compare the effects of alternative management plans on individual species (Morrison et al. 1998).

HSI models are not directly derived using statistical techniques. They are based on wildlife-resource relationships that have been previously tested in an area or within a separate system. Where species-resource relationships are unknown or cannot be determined, hypothesized resource-species relationships, developed by expert opinion, can also be used.

Habitat suitability is traditionally expressed as the geometric mean of n environmental variables (V) that are known or thought to be an important component of one or more life requisites (Morrison et al. 1998). Thus, the general formula for a HSI model is:

$$HSI = (V_1 \text{ x } V_2 \text{ x } V_3 \ldots . V_n)^{1/n} \qquad \text{(Equation 10)}$$

where $V_1 \ldots Vn$ are the environmental variables or resources. However, various weighting and averaging methods may be applied to a HSI model to best describe the overall relationship of a suite of environmental variables to the quality of a landscape patch (Cole and Smith 1983, Laymon and Barrett 1986). For example, different life requisites may require calculation of more than one environmental variable and overall resource suitability may be best described when life requisites are weighted differently;

$$Forage = (V_1 + V_2)/2 \qquad \text{(Equation 11)}$$

$$Cover = (V_3 \text{ x } V_4 \text{ x } V_5)^{1/3} \qquad \text{(Equation 12)}$$

$$HSI = ((4 \text{ x } Forage) + Cover)/5 \qquad \text{(Equation 13)}$$

HSI values are expressed on a scale of 0.0 to 1.0, from low to high resource suitability, respectively.

It is important to note problems associated with developing deductive models such as:

1) deductive models can be biased because they often apply causal relationships developed from site-specific population and resource data to a different system (Schamberger et al. 1982, Dettki et al. 2003), 2) expert knowledge is used to develop the hypothesized wildlife-resource relationships and/or the mathematical relationship between model components. Models that are based on expert knowledge are, by definition, biased, 3) HSI models that use hypothesized wildlife-resource relationships can be sensitive to variation in expert opinion (Johnson and Gillingham 2004), 4) mathematical models may lead to a greater understanding of the behaviour behind the mathematics than the true biological behaviour behind the system (Morisson et al. 1992), especially when models are not validated.

On the other hand, deductive models such as HSIs provide benefits:
1) They model general resource-species relationships and although they are not precise, they model a theoretical predicted response (Pickett et al. 1994 as cited in Guissan and Zimmermann 2000). As a result, when precision is not necessary, these models may be applied over a wider environmental and spatial range. They can also form the basis of a more specific model when model evaluation and subsequent adjustments to improve the model are made, 2) they are based on general relationships, so it is not necessary to study site-specific species-resource relationships, and therefore are relatively cheap to construct.

I compiled elk-resource relationships based on previously published material into a summer HSI model. The variables deemed important to elk in previous studies are forage, cover, roads and the spatial interactions between forage and cover (Wisdom et al. 1986, Thomas et al. 1988, Roloff et al. 1998, Benkobi et al. 2004).

Methods

Forage

Elk occupy many diverse ecosystems throughout North America and, as a result, their food habits vary greatly from region to region (Skovlin et al. 2002). Elk are adapted to both forested and open plain habitats but their feeding strategies are primarily geared towards graminoids (Geist 1982). Elk prefer to graze, and will feed in open areas including clear-cut areas, natural forest openings and burned areas (Nelson and Leege 1982, Unsworth et al. 1998): these are early successional communities that provide high volumes of suitable forage biomass (Parker 1990, Skovlin et al. 2002).

During the spring, Rocky Mountain elk typically graze on plant species that have an early green up, such as grasses. They will then switch their feeding to mainly shrubs and forbs for the summer (Marcum 1979, Parker 1990, Unsworth et al. 1998), and switch to browse (woody vegetation) during the fall (Marcum 1979). Historical evidence of elk in Ontario suggests that elk preferred open grassy habitats, such as the prairie ecosystems of southern Ontario, and grassy marshlands and wetlands (Bellhouse and Broadfoot 1998, Jost et al. 1999). They were also associated with deciduous and mixed-wood forests but avoided dense conifer stands (Bellhouse and Broadfoot 1998).

Manitoban Elk residing within the boundaries of Riding Mountain National Park would likely serve as the best example for predictions of diet selection in the northwestern portion of Ontario. These elk select woody browse as their annual mainstay diet (53%), whereas grasses make up an annual diet of 22-54% and are of major importance during the spring and early winter (Blood 1966). The dominant browse species is *Rosa* sp., but aspen and saskatoon (*Amelanchier alnifolia*) are also of importance (Blood 1966).

Forage potential, the interaction of forage quantity and quality (quantity meaning the amount of forage and quality meaning the relative nutritional value of forage), is recognized as an important factor that influences elk reproductive performance and resource selection (Irwin and Peek 1983b, Cook et al. 1996, Roloff 1998, Cook 2002). Higher sunlight intensities may provide the most palatable and nutritious browse leaves (Blair et al. 1983), greater opportunity for grass growth (Beall 1976) and the production of leaf biomass increases with increasing light intensity (Blair 1969). As a result, plants grown in open areas are expected to be of a higher quantity and quality than those grown in the shade. Northwestern Ontario is composed primarily of a forested landscape that is continuously disturbed by fire and timber harvesting. Early successional stages likely provide the best foraging opportunities for elk in the region (Irwin and Peek 1983a).

Light intensity analysis (General Methods 2) suggests that the early successional stage in the Cameron Lake region lasts until a stand is approximately 45 years of age, at which point canopy openness (light intensity) decreases significantly. Therefore, I defined a stand as being “forested” when it reaches 45 years of age. Figure 1.1a shows the relationship between stand age and predicted forage suitability. Forage suitability is the highest in early successional stages but declines after a stand reaches 45 years. Suitability increases slightly after a stand becomes overmature at the approximate age of

120 years. Forage located in forested stands is of better quantity and quality when there is a higher proportion of deciduous trees in the canopy (Figure 1.1b) relative to primarily coniferous stands (Buckmaster et al. 1999).

Cover

Hiding cover is of primary concern to elk during the non-winter months. It is used to evade predators and human disturbances (Lyon and Christensen 1992) and usually takes the form of vegetation or a topographic feature (Skovlin et al. 2002). Disturbance activities (logging, hunting) and associated features (such as roads and outpost camps) can negatively affect use of an area by elk. For example, logging activities may displace elk within 500-1000m of the disturbance (Edge and Marcum 1985), where elk resource use is affected more when the availability of appropriate hiding cover is unavailable (Lyon 1979).

Thomas et al. (1979) defined hiding cover as vegetation capable of hiding 90% of a standing adult elk from view of a human at a distance equal to or less than 61m. Coniferous trees will provide adequate hiding cover when they are at heights between 2-6m (Canfield et al. 1986), as will understory shrubs and trees with 1-2m high branches (Abbot 1991 as cited in Buckmaster et al. 1999). In the Cameron Lake region, coniferous stands above 2m in height or 15 years in age provide these characteristics of hiding cover and I considered these areas optimal (Figure 1.1c).

Forage and cover interactions

Ecotones, areas where there is a high juxtaposition of different vegetation types or stand ages, are an important habitat requirement for elk because they support a high diversity of forage (Sklovin et al. 2002) and provide security cover within close proximity. The key to elk use of forested habitats is the spatial interaction between forage areas and security cover (Thomas et al. 1979, Thomas et al. 1988), and is not solely a function of forage quantity and quality (Roloff 1998).

Elk are an "edge-loving" species and will select forested habitats within 274m of open foraging areas and open habitats within 90m of forest cover (Irwin and Peek 1983a, Witmer et al. 1985). As a forage area becomes larger than 90m in diameter or a cover area larger than 274m in diameter, elk will use less of the total area (Wisdom et al. 1986). A recent validation by Benkobi et al. (2004) of an HE model for elk in Custer State Park recommended a modification to these previous forage-cover interactions. They suggest using the same measure of elk use for distance to forage edge and distance to cover edge where optimal use is within 100m of a forage-cover edge, moderate use between 100-200m, low use between 200-500m and little or no use beyond 500m (Figure 1.1d*;* Benkobi et al. 2004). When the total width of cover associated with a forage-cover edge is less than 230m, it is not considered wide enough to provide optimal cover (Witmer et al. 1985) and will receive a suitability of less than 1 according to its width from the cover-forage edge (Figure 1.1e).

Roads

The presence, density, spatial distribution and human use of roads affect elk habitat use (Thomas et al. 1979, Lyon 1983, Cooper and Millspaugh 1999, Rowland et al. 2000, Benkobi et al. 2004). Roads remove land for forage and add a disturbance factor, reducing the landscape suitability of areas adjacent to roads. Rowland et al. (2000) found that female elk selected habitats away from roads consistently throughout the spring and summer months. Elk are known to minimize the effects of disturbance by using areas closer to roads disproportionately at night when traffic is minimal (Millspaugh 1999). Because we do not know the effects of roads on landscape suitability for elk in northwestern Ontario, I included the predicted effects of open road (primary and secondary) density as a precaution. Suitability rapidly declines as road density increases up to 1km of open primary and secondary road per km^2, after which suitability decreases moderately with increasing road density (Figure 1.1f). I defined primary roads in the study area as year-round gravel or paved roads open to the public for recreation (hunting, fishing, camping, etc.), or used extensively for forestry activities, mining, trapping, elk tracking, and by local residents. Secondary roads are not open year round, are maintained to a lesser degree than primary roads and have a lower volume of traffic use.

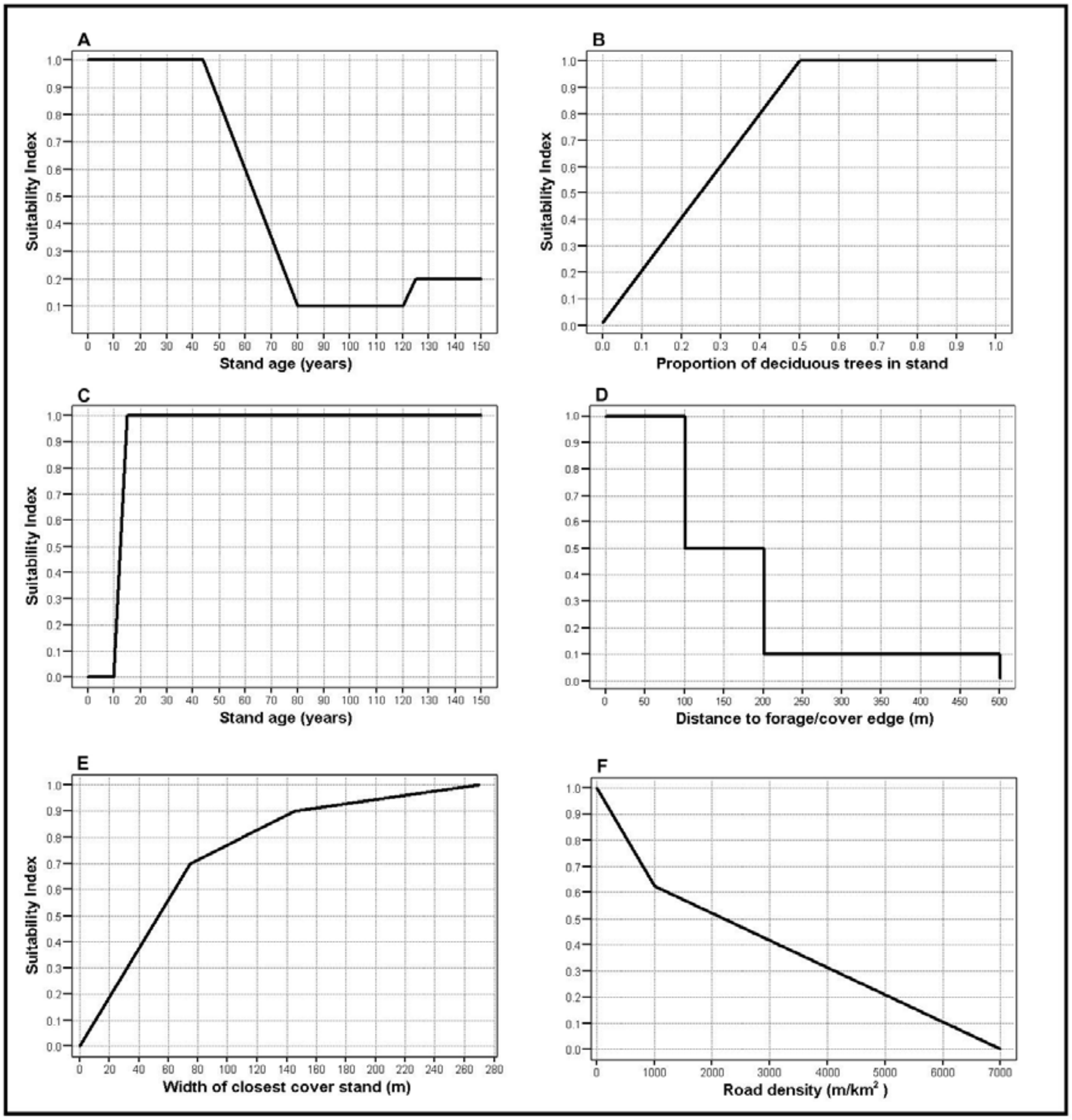

Figure 1.1. (a) Summer forage suitability based on stand age; (b) effects of the proportion of deciduous trees on the suitability of forested stands; (c) effects of stand age on suitability of hiding cover; (d) effects of distance from forage-cover edge on suitability; (e) the effect of hiding cover width on suitability; (f) the effects of road density on suitability.

Model Compilation

I compiled individual elk-resource relationships into their effects on forage, cover, forage-cover association (FCA) and roads, henceforth referred to as the model components (Equations 14-17). I used an additive function when variables were mutually exclusive (i.e., Forage, equation 14) and the geometric mean of n variables when variables were not mutually exclusive (i.e., FCA, equation 16).

$$Forage = (SFOSFC + SF) \quad \text{(Equation 14)}$$

$$Cover = SCSFC \quad \text{(Equation 15)}$$

$$FCA = (CW \text{ x } Prox)^{1/2} \quad \text{(Equation 16)}$$

$$Roads = SR \quad \text{(Equation 17)}$$

Where; *SFOSFC* is the suitability of forage in non-forested area (stands under 45 years; Figure 1.1a); *SF* was calculated in stands equal to and over 45 years and is the suitability of forage based on stand age from Figure 1.1a multiplied by the suitability of deciduous trees in the canopy (Figure 1.1b); *SCSFC* is the suitability of cover (Figure 1.1c); *CW* is the suitability of the width of cover associated with the closest forage-cover edge (Figure 1.1d); *Prox* is the suitability based on the distance to the closest forage-cover edge (Figure 1.1e) and *SR* represents the suitability of road density per km^2 (Figure 1.1f).

I used digital vegetation data layers compiled by two provincial government administrative districts as my primary source of vegetation coverage for subsequent analysis (General Methods 3). I used Landscape Scripting Language (LSL) (Kushneriuk and Rempel 2004) as a geographic information system wherein I quantified variables (General Methods 4) and calculated HSI values.

I calculated an overall *HSI* value using an additive mean of all model components;

$$HSI_A = (Forage + FCA + Cover + Roads) / 4 \qquad \text{(Equation 18)}$$

An overall geometric mean was not used because the cover and forage components could be mutually exclusive but still very beneficial to elk; i.e. these areas would be given an *HSI* value of zero, which is counterintuitive to predicted elk use.

Elk are known to use foraging areas more heavily than cover areas (Benkobi et al. 2004), so I investigated the effects of weighting forage more heavily than cover. Benkobi et al. (2004) suggested weighting the forage component 3 times greater than the cover component. But the degree of weighting likely varies with a landscape's distribution of forage and cover, as well as the amount of disturbance in the area. So, I also tested higher and lower forage component weightings and evaluated which weighting best predicted elk use;

$$HSI_B = ((2 \text{ x } Forage) + FCA + Cover + Roads) / 5 \qquad \text{(Equation 19)}$$

$$HSI_C = ((3 \text{ x } Forage) + FCA + Cover + Roads) / 6 \qquad \text{(Equation 20)}$$

$$HSI_D = ((4 \text{ x } Forage) + FCA + Cover + Roads) / 7 \qquad \text{(Equation 21)}$$

I hypothesized that the *FCA* component is more important than the Forage component for elk in northwestern Ontario, so I conducted a similar analysis of different weighting schemes, this time manipulating the weighting of the FCA component;

$$HSI_E = (Forage + (2 \text{ x } FCA) + Cover + Roads) / 5 \qquad \text{(Equation 22)}$$

$$HSI_F = (Forage + (3 \text{ x } FCA) + Cover + Roads) / 6 \qquad \text{(Equation 23)}$$

$$HSI_G = (Forage) + (4 \text{ x } FCA) + Cover + Roads) / 7 \qquad \text{(Equation 24)}$$

The overall HSI value was calculated for each hexagon throughout the study area in LSL. The deductive model output is a map of the landscape with corresponding suitability values, where the abscissa and ordinate represent the landscape coordinates and the resource suitability is denoted by the colour (Figure 1.2).

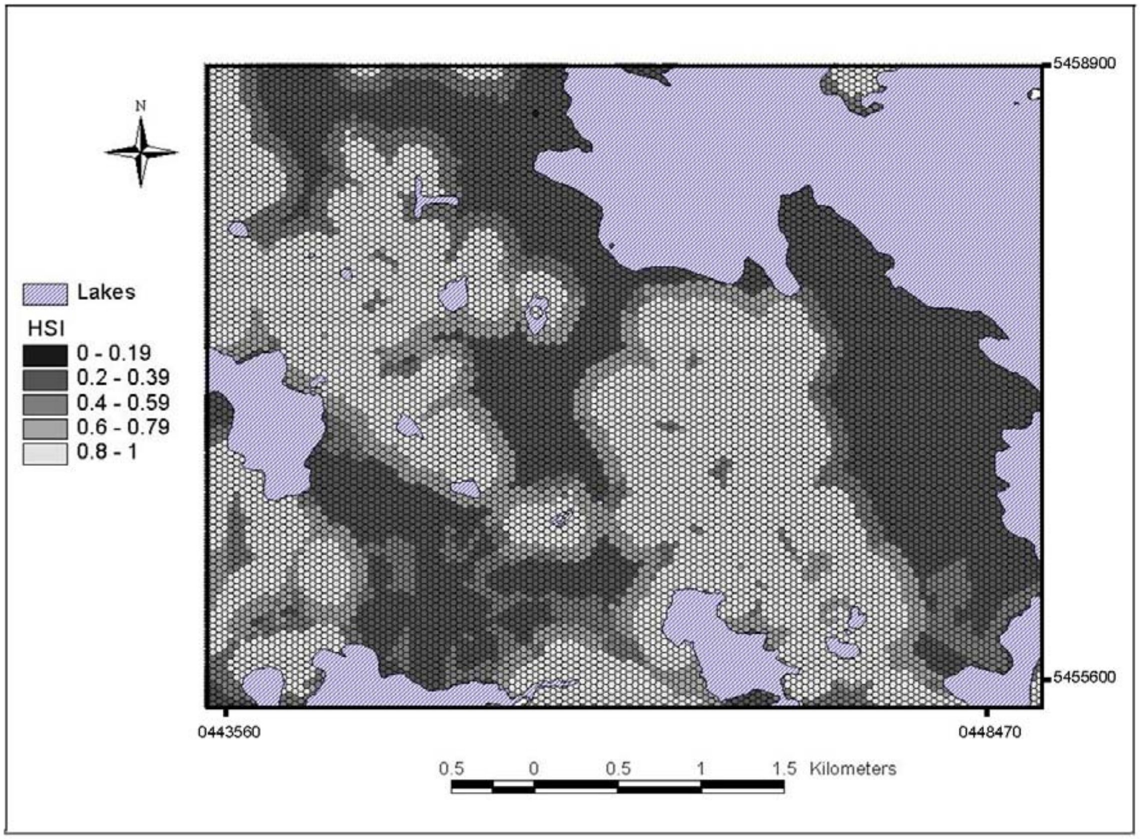

Figure 1.2. Example of a HSI model of part of the Cameron Lake area in northwestern Ontario showing resource suitability for elk within hexagons. Lighter shaded hexagons indicate better quality resources than darker shades.

Model Validation

I used a data set consisting of 19 elk suitability distributions (SD) based on radio-telemetry locations (General Methods 1) to validate the HSI models. SDs are based on utilization distributions, which are estimated from kernel analysis (General Methods 5.1). I measured how good each model was by using both an average (AO Index) and a weighted average (WO Index) of all hexagons within each animal’s SD (General Methods 5.3). I also used the deviation from ‘no selection’ as calculated using the VI Index (referred to as the DVI Index) to compare the relative ability of each model to predict animal space use (General Methods 5.2). I calculated these indices between the HSI map and each of the 19 individual elk SDs, as well as the associated mean and confidence intervals. I further compared index means using one-way analysis of variance (ANOVA) to test for significant differences among model indices.

To help benchmark model performance, I compared WO, AO and DVI Indices against a null model. The null model was created by taking individual validation SDs and randomly rotating them, then randomly distributing them throughout the study area. To ensure that the placement of each “random” SD mimicked an actual animal’s use of the landscape, I ensured that the SD peak was not covered by a lake. For each of the 19 true elk SDs used for validation, I created five “random” SDs for a total of 95 randomly placed SDs. I compared elk and random SDs for each model using a 2-tailed t-test. I calculated the difference between elk and random DVI Indices for each model and compared the magnitude of the differences using a one-way ANOVA.

In addition to WO and AO Indices, I graphed the mean of each variable in relation to elk use (each suitability band) and visually compared the regression line of actual resource use to hypothesized resource use. Relationships were not expected to be identical to those postulated for the HSI (Figure 1.1a-f) because use expressed in the form of a SD represents an animal’s response to the overall suite of variables, as opposed to the relationships of independent variables as modeled in the HSI. Despite this, the graphs can help identify any general relationships that warrant further site-specific investigation.

Results

All HSI models predicted landscape suitability slightly better than by random chance. The poorest predictive ability was noted for HSI_A which had only a 1.3% higher WO Index than by random chance and the best predictive ability for model HSI_G which had an 8% higher WO Index than by random chance. Model HSI_G also showed the highest increase in space use predictive ability over the random SDs.

Average suitability of the study area ranged from 0.565 (±0.194, n=404,889) for $\mathrm{HSI_D}$ to 0.694 (±0.123, n=404,889) for $\mathrm{HSI_A}$ (Figure 1.3a-g, Table 1.1). Average suitability and weighted average suitability of elk SDs was lowest for HSI_D (mean AO Index=0.592, SE=0.005; WO Index = 0.614, SE=.008; n=19) and highest for HSI_G (AO Index =0.720, SE=0.006; WO Index=0 .749, SE=0.009; n=19; Table 1.2). Model HSI_D demonstrated the lowest average suitability of random SDs (mean AO Index=0.558, SE=0.006; mean WO Index= 0.568, SE=0.007; n=95) whereas model HSI_A had the largest average suitability of random SDs (mean AO Index = 0.695, SE=0.004; WO Index=0.694, SE=0.005; n=95; Table 1.3).

Mean WO Index scores and AO Index scores were significantly different among models (ANOVA: $P<0.01$, df =6;126; Table 1.2 and Figure 1.4). The AO Index did not differ among models HSI_A, HSI_E, HSI_F and HSI_G and was significantly greater than the AO Index for models HSI_B, HSI_C *and* HSI_D. The WO Index did not differ between models HSI_E, HSI_F and HSI_G and was significantly greater than the WO Index for models HSI_A,

HSI_B, HSI_C *and* HSI_D. Only model HSI_A did not have significantly higher AO and WO Indices as compared to random SDs (HSI_A 2 tailed t-test; P=0.169 and P=0.173, respectively; Figure 1.5, Table 1.4).

There was no difference among elk DVI Index scores of different models (ANOVA: P=0.224, df =6; 126; Figure 1.6). Models HSI_C, HSI_E, HSI_F and HSI_G predicted animal space use patterns significantly better than by random chance (Figure 1.6, Table 1.5) whereas the magnitude of difference between actual elk and random use patterns was significantly greater than HSI_A (ANOVA: $P<0.001$, df = 6; 658) for models HSI_D, HSI_F and HSI_G (Figure 1.7).

Elk use decreased substantially at distances greater than 100m from a forage-cover edge (ANOVA: $P<0.001$, df = 2; 176; Figure 1.8) and the distance to a forage-cover edge was negatively correlated with elk use (r=-0.68, R^2 = 0.46, n=190; Figure 1.9a). Road density was positively correlated with elk use (r=0.45, R^2=0.21, n=190; Figure 1.9b) and stand age was negatively correlated with elk use (r= -0.56, R^2 =0.31, n=190; Figure 1.9c). Cover width and the proportion of deciduous trees in the canopy showed non-linear relationships (r= 0.37, R^2 = 0.13, n=190 and r=0.48, R^2= 0.23, n=190, respectively; Figure 1.9d-e). All correlation and regression relationships were significant (Pearson Correlation (2-tailed): $P<0.001$ and ANOVA: $P<0.001$, df = 1;188, respectively).

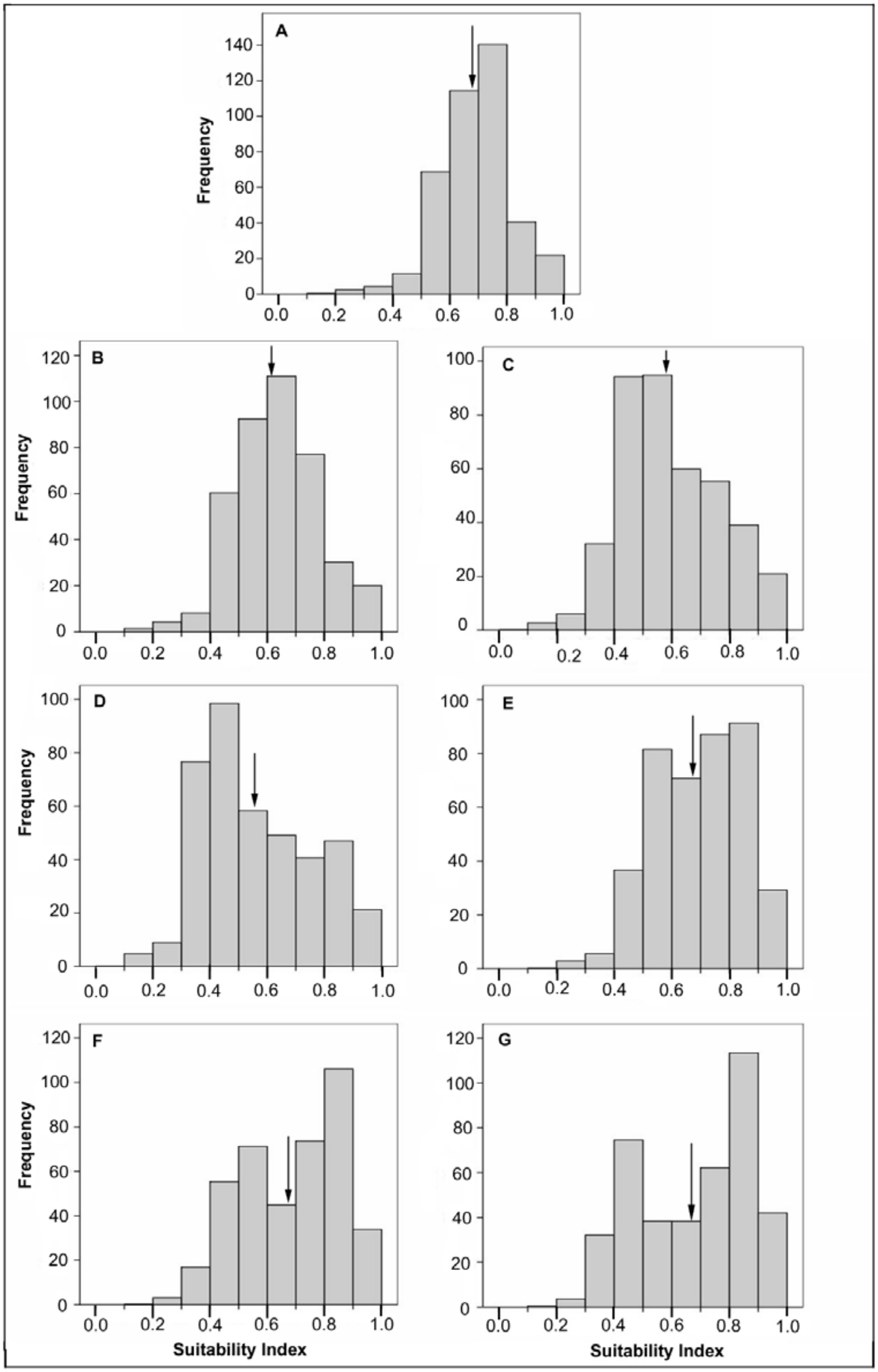

Figure 1.3. Frequency (in thousands) of suitability index scores for each hexagon within the study area, for HSI models A to G. Mean is approximated by arrow.

Table 1.1. Mean HSI values across the study area for each of the seven models. Number of hexagons in the landscape is 404,889.

Model	*Mean HSI*	*Standard Deviation*
HSI_A	0.694	0.123
HSI_B	0.634	0.145
HSI_C	0.594	0.172
HSI_D	0.565	0.194
HSI_E	0.688	0.151
HSI_F	0.684	0.176
HSI_G	0.682	0.195

Table 1.2. Average WO Index and AO Index calculated between each HSI model and 19 elk suitability distributions.

Model	*WO Index*	*Standard Error for WO Index*	*AO Index*	*Standard Error for AO Index*
HSI_A	0.705^{c}	0.006	0.703^{d}	0.004
HSI_B	0.662^{b}	0.007	0.651^{c}	0.005
HSI_C	0.634^{a}	0.007	0.617^{b}	0.005
HSI_D	0.614^{a}	0.008	0.592^{a}	0.005
HSI_E	0.725^{cd}	0.007	0.711^{d}	0.005
HSI_F	0.739^{d}	0.008	0.716^{d}	0.005
HSI_G	0.749^{d}	0.009	0.720^{d}	0.006

*Different superscripted letters represent significantly different means at $P<0.05$ (Tukey HSD and Games-Howell).

Table 1.3. Average WO Index and AO Index calculated between each HSI model and 95 random suitability distributions.

Model	*WO Index*	*Standard Error for WO Index*	*AO Index*	*Standard Error for AO Index*
HSI_A	0.694	0.005	0.695	0.004
HSI_B	0.633	0.006	0.636	0.004
HSI_C	0.596	0.006	0.596	0.005
HSI_D	0.568	0.007	0.558	0.006
HSI_E	0.692	0.006	0.691	0.005
HSI_F	0.692	0.007	0.691	0.005
HSI_G	0.692	0.007	0.692	0.006

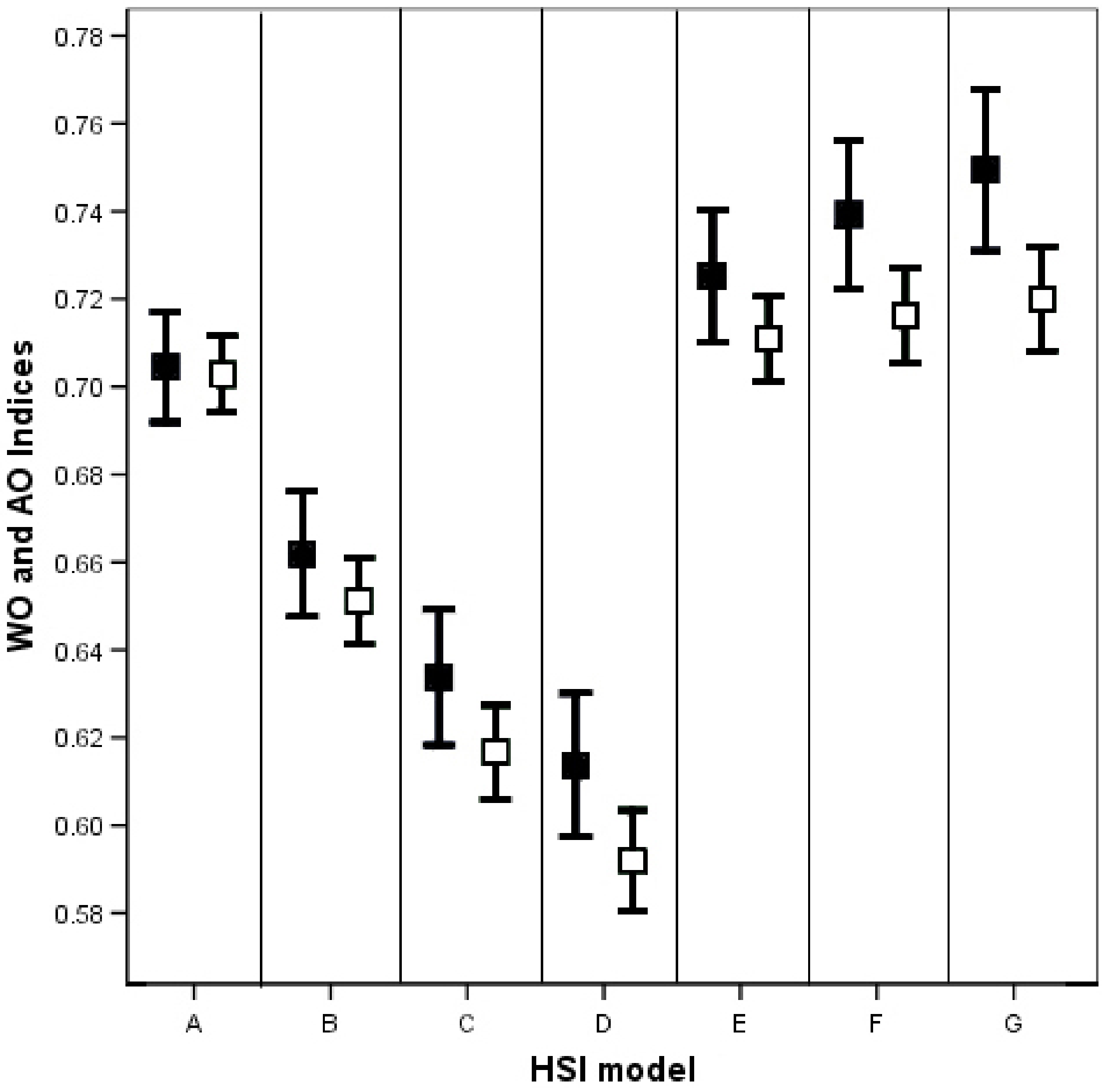

Figure 1.4. Weighted overlap (filled squares) and average overlap (open squares) indices between each HSI model and 19 elk utilization distributions. Open squares represent mean, bars represent 95% confidence intervals of the mean.

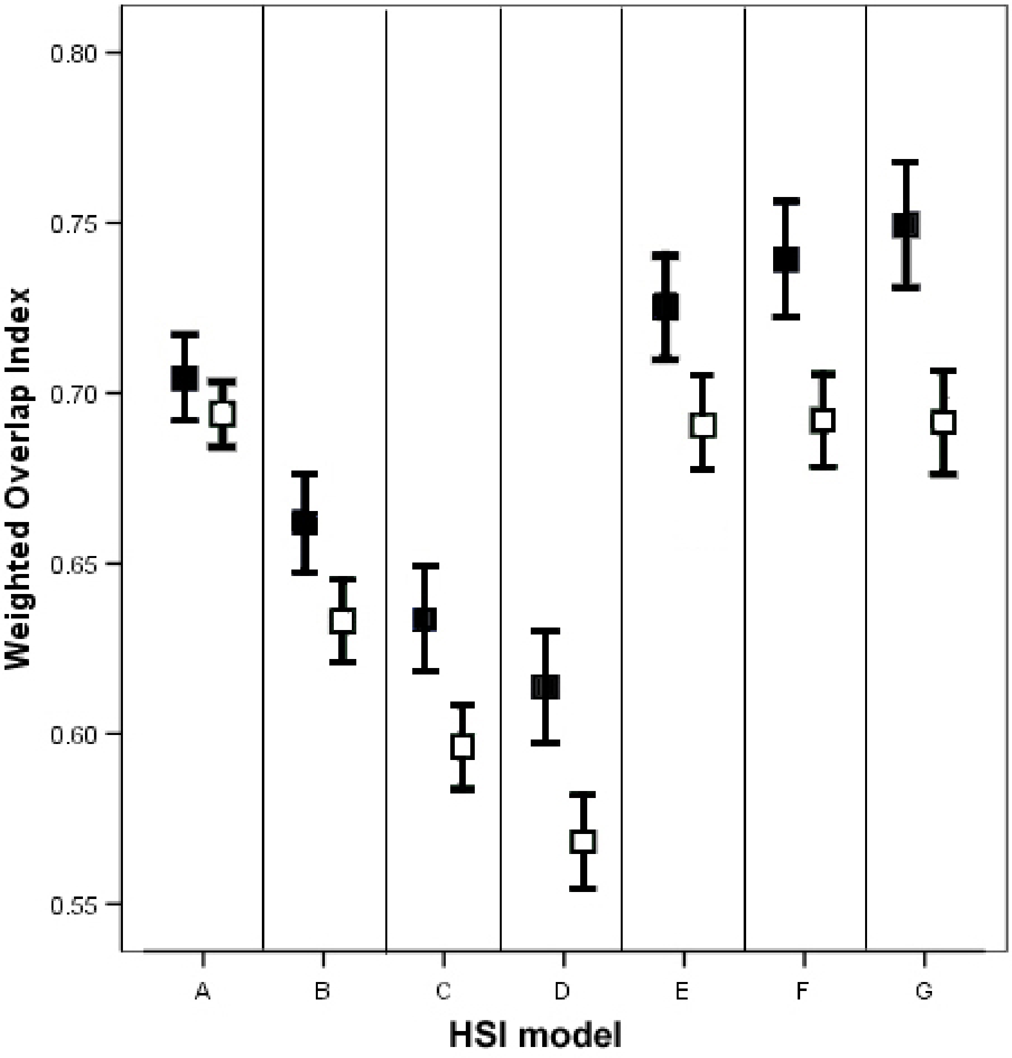

Figure 1.5. Weighted overlap index between 19 elk suitability distributions and each HSI model (filled squares) as well as 95 random utilization distributions and each HSI model (open squares). Squares represent mean, bars represent 95% confidence intervals of the mean.

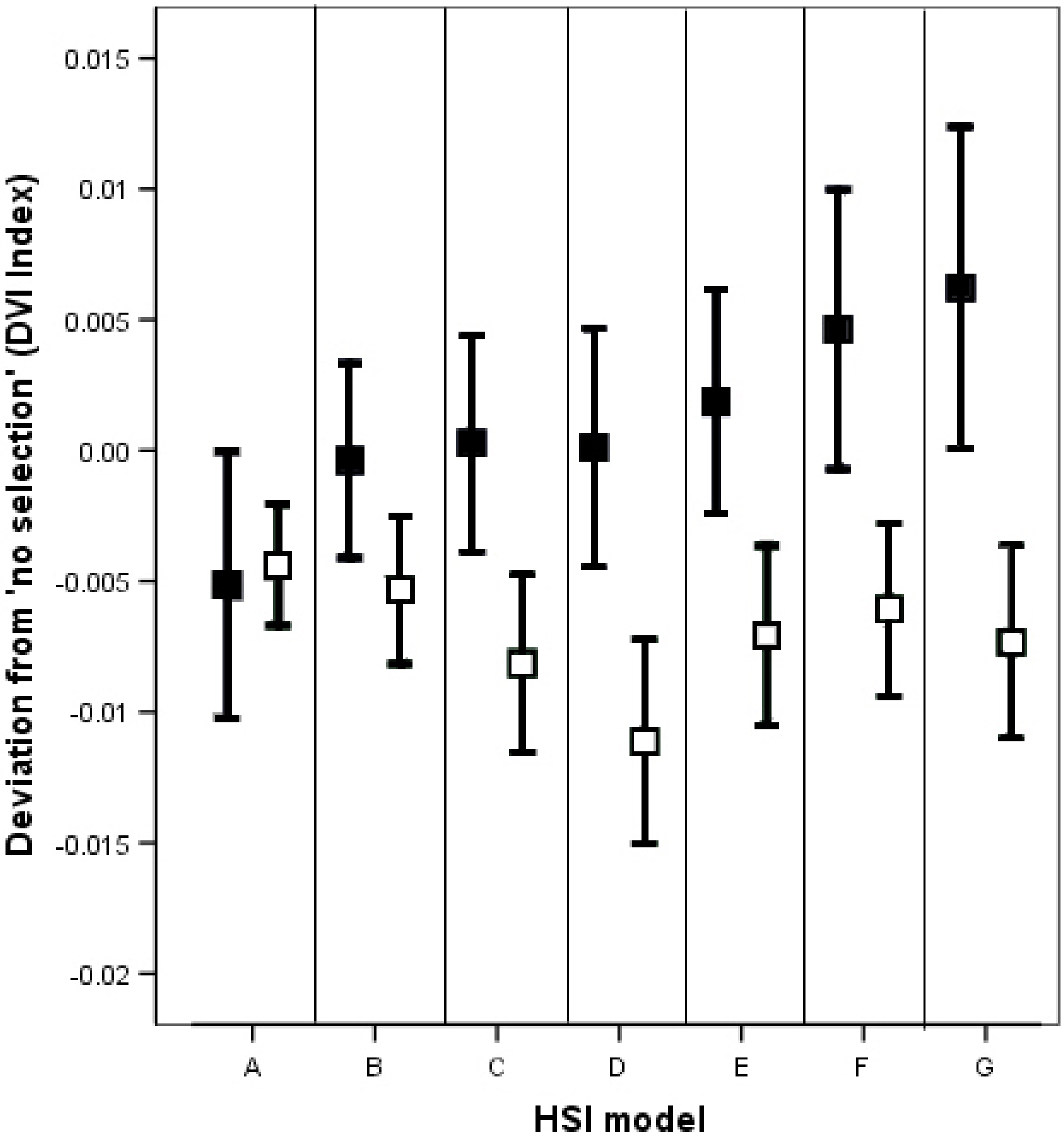

Figure 1.6. DVI Indices calculated for 19 true elk SDs (filled squares) and 95 random SDs (open squares) for all seven HSI models. Squares represent mean, bars represent 95% confidence intervals of the mean.

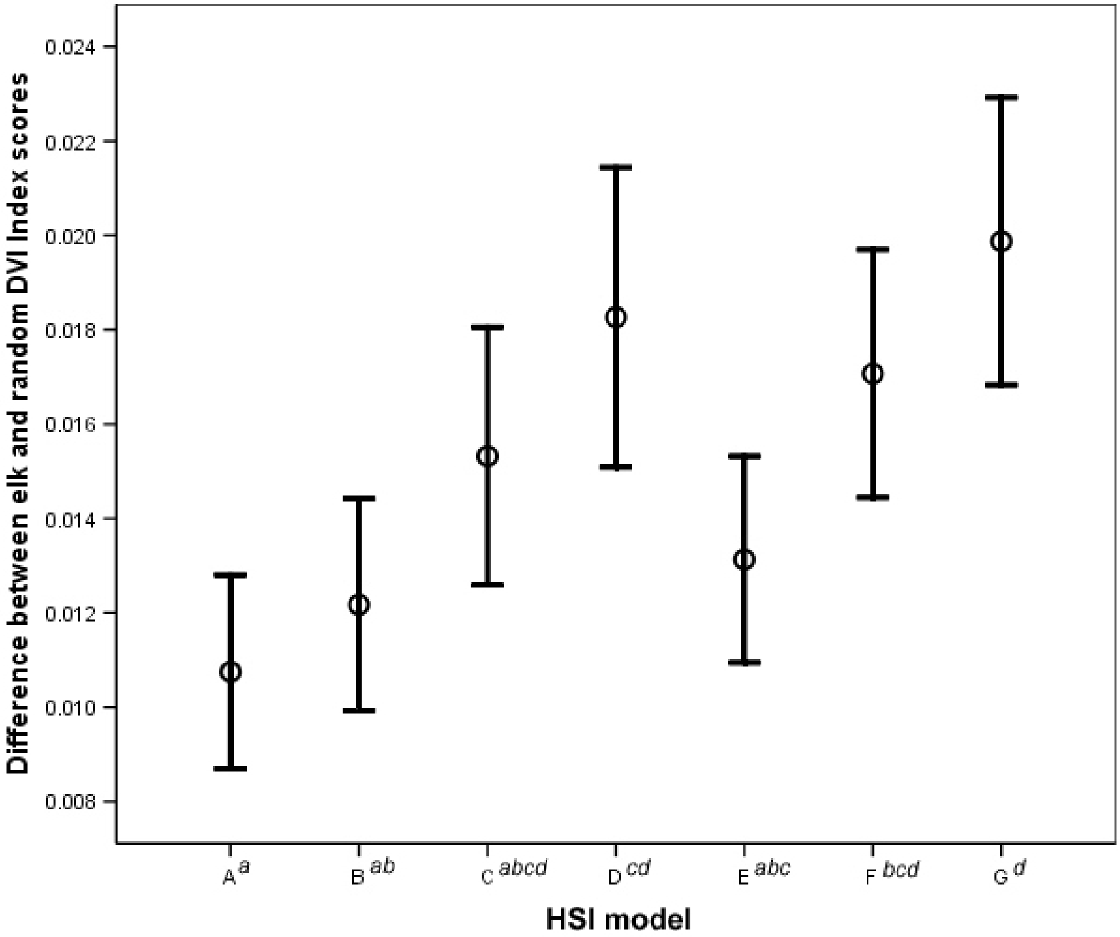

Figure 1.7. Mean absolute difference between elk and random DVI Index scores. Open circles represent mean, bars represent 95% confidence intervals of the mean. Italicized letters represent membership to significantly different means (Tukey HSD and Games-Howell).

Table 1.4. Comparison between elk SDs and random SDs for WO and AO Indices.

Model	*Weighted Overlap Index*			*Average Overlap Index*		
	t	d.f.	2-tailed Sig.	t	d.f.	2-tailed Sig.
HSI_A	1.385	45.327	0.173	1.395	52.908	0.169
HSI_B	3.167	51.180	0.003	2.417	56.346	0.019
HSI_C	3.885	48.801	0.000	2.892	59.461	0.005
HSI_D	4.387	50.673	0.000	4.116	74.024	0.000
HSI_E	3.607	46.719	0.001	2.899	64.687	0.005
HSI_F	4.475	47.868	0.000	3.432	62.811	0.001
HSI_G	5.009	49.310	0.000	3.476	63.586	0.001

Table 1.5. Comparison of DVI Index for elk SDs and random SDs.

Model	*D.VI Index*		
	t	d.f.	2-tailed Sig.
HSI_A	-0.269	112	0.788
HSI_B	1.503	112	0.136
HSI_C	3.227	50.05	0.002
HSI_D	3.834	52.65	0.000
HSI_E	3.346	48.08	0.002
HSI_F	2.753	112	0.007
HSI_G	3.105	112	0.002

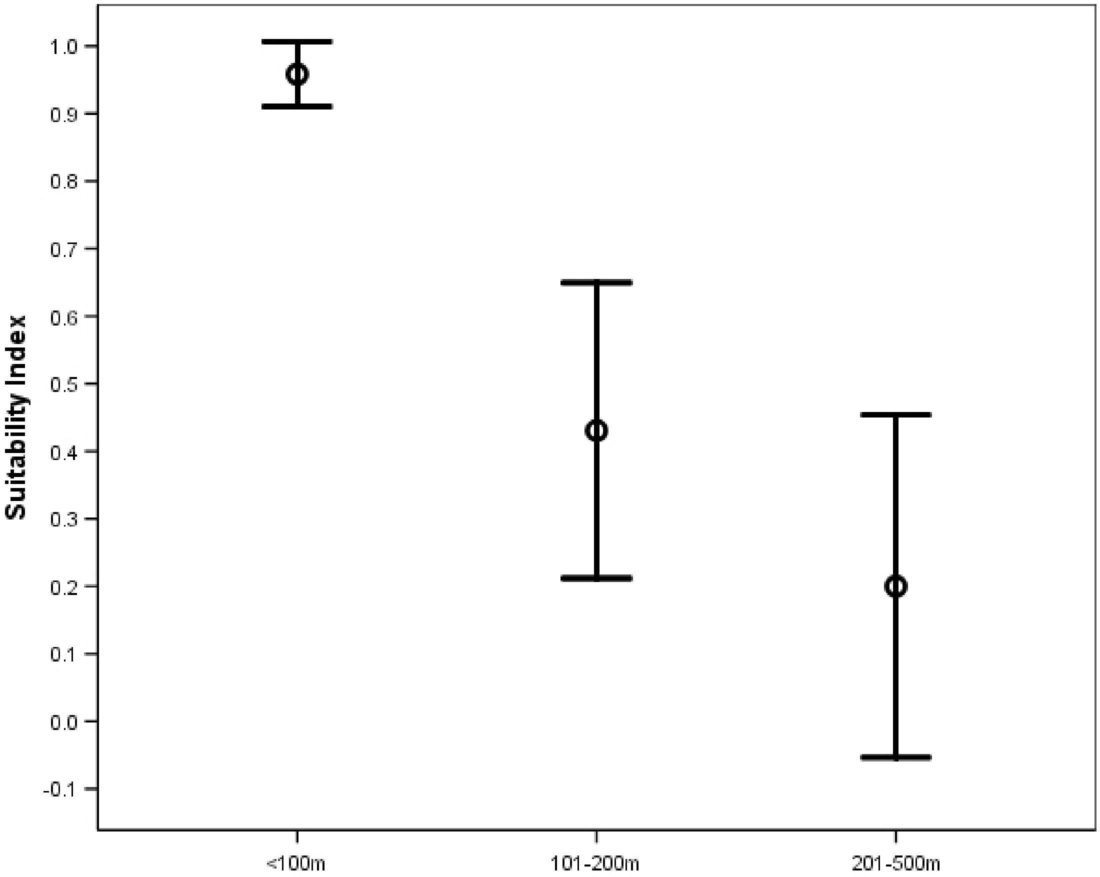

Figure 1.8. Suitability associated with three categories of average distance to nearest edge (Prox). Open circles represent mean, bars represent 95% confidence intervals of the mean.

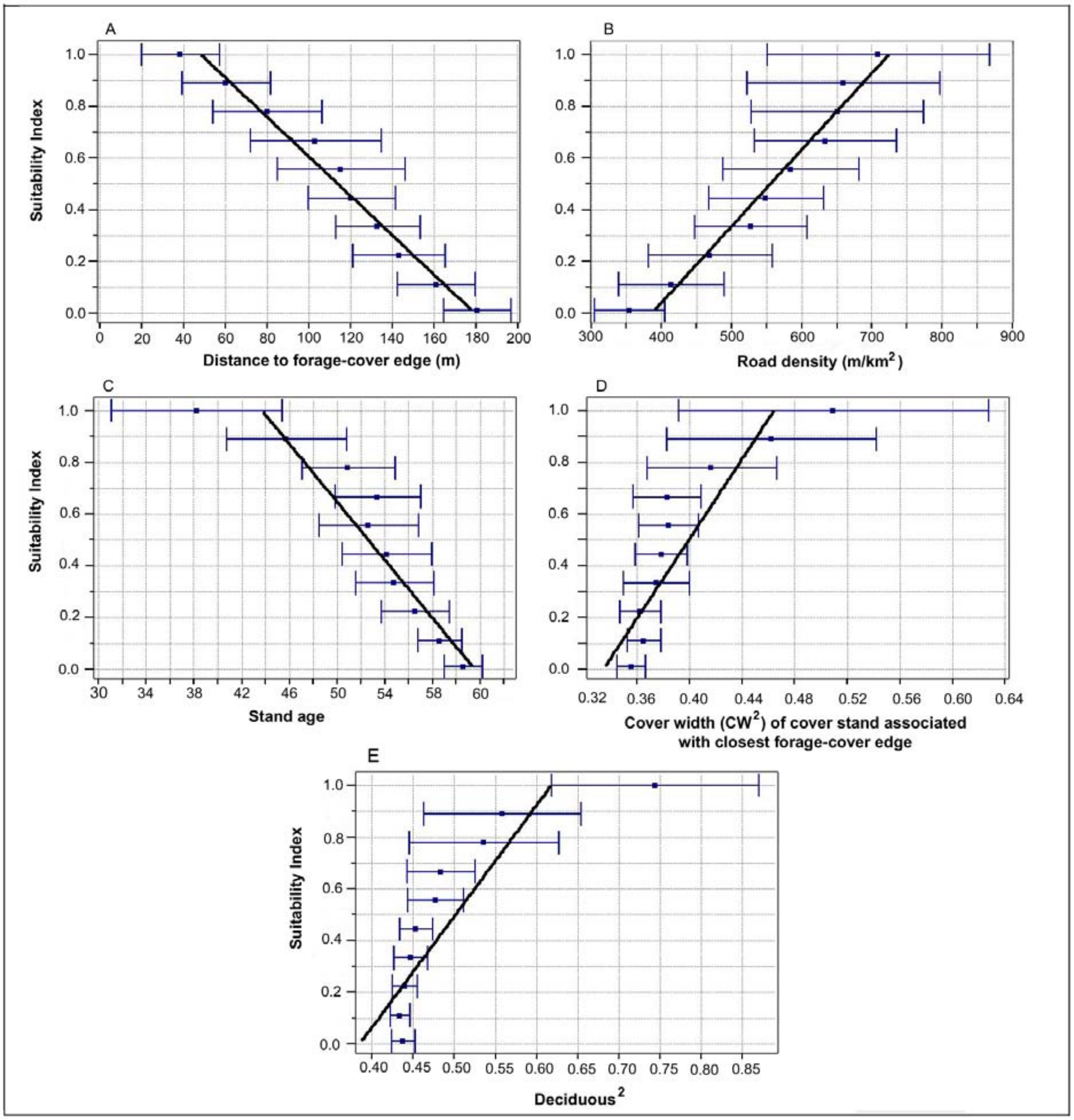

Figure 1.9. Relationship between elk use and A) distance to nearest forage-cover edge (Prox), B) road density (Roads), C) stand age (Age), D) cover width associated with the nearest forage-cover edge (CW^2) and E) proportion of deciduous trees in the canopy ($Deciduous^2$). Bars represent the 95% confidence intervals of the mean (squares) and regression line is denoted by the solid line.

Discussion

A simple modification of the mathematical formula of an HSI can often ameliorate its predictive ability. This was found in the elk habitat effectiveness model validated by Benkobi et al. (2004) for elk residing in Custer State Park, South Dakota. They modified the original geometric mean formula to an arithmetic mean, and weighted the forage component 3 times heavier than other model components. Similar changes in the weighting of forage actually decreased model performance in northwestern Ontario HSI models, suggesting that higher resource value here is not placed on forage alone. Most HSI relationships are based upon relationships within the western states and provinces of North America where there are many open grassy meadows. The foraging opportunities are quite different in the Cameron Lake region as there are no such meadows. The most similar natural landscape feature to grassy meadows are wetlands, which elk do not select as habitat in northwestern Ontario (McIntosh 2003). Elk seem to be influenced to a greater extent by forage-cover interactions rather than forage alone. An increase in the weighting of the forage-cover interaction component improved the weighted average model performance (WO Index) as compared to no weighting, but the average model (AO Index) performance was not significantly improved.

Models that weighted FCA interactions (HSI_E, HSI_F, and HSI_G) predicted the highest resource suitability and performed better than random resource suitability assessments. These models also portrayed actual resource use intensity better than random. There was no significant difference among these three models with respect to WO, AO and DVI Indices and as a result, I considered all three as being equal and the most powerful out of the suite of HSI models that I tested. Although a trend towards increased suitability was evident as weighting of the *FCA* component increased, I believe these models showed no statistical difference because the weighting of the forage-cover interaction component was not large enough to see significant improvement.

Although these models performed significantly better than my random models, the range in predictive ability of the models was not great, predicting model suitability at best 8% better than random and congruence with actual animal use intensity up to 2% better than by random chance. The poor predictive ability of the model may have resulted because the landscape within the greater study area is similar to the areas elk selected, or the variables modeled are not greatly influencing elk selection.

Another possibility that might cause poor model predictability is the discrepancy in modeled variable relationships and actual variable relationships. For example, the actual relationship between road density and elk use is markedly different from that predicted by the HSI. It appears as though elk are using areas with higher road densities. In fact, elk have demonstrated an attraction to roads at small scales (Anderson et al. 2005). At small scales, roadsides can provide an abundance of forage biomass and are often considered edges when this high biomass of forage is in close proximity to cover (Tufto et al. 1996, McCorquodale 2003, Wolff and Van Horn 2003). Furthermore, the major foraging areas for elk in the Cameron Lake region are highly associated with roads because they consist of recent clear cuts and reforested stands. As a result, forestry activities in the Cameron Lake region provide a patchwork of forage and cover areas, which ultimately results in increased amounts of edge. It is therefore difficult to tease out whether elk are selecting for roads or if the perceived selection of greater road density is secondary to the selection for better foraging opportunities and greater amounts of edge.

Cover width is another variable that shows a different relationship than modeled by the HSI. This variable is modeled as linear but shows a non-linear relationship with animal space use. The non-linear selection pattern may be a product of the study design and not reflect actual selection patterns by elk. For instance, in northwestern Ontario, buffer strips are often left between clear cuts and lakes. These buffers range in width from 50 to100m from a clear-cut to the water's edge. The inclusion of buffer strips into the highly suitable portion of the SD likely occurs because the buffer strips are within very close proximity to good forage, and included in the UD only because of small sampling intensities.

Some relationships were similar to those modeled in the HSI. For example, elk in northwestern Ontario exhibited highest use within 100m from a cover-forage edge (Figure 1.10). This is comparable to the relationship predicted by Benkobi et al. (2004) for elk in Custer State Park, but in my study area there was no difference in actual elk resource use when average distance per band was greater than 200m from a forage-cover edge, suggesting that elk greatly value areas in very close proximity to edges. This relationship is illustrated when assessing the correlation between distance to a forage-cover edge and elk space use. This correlation showed a marked negative linear trend and explained almost half of the variation in elk use intensity. The high correlation between distance to a forage-cover edge and elk space use provides further evidence for weighting the FCA component rather than the forage component.

HSI models constructed using *a priori* relationships can be helpful tools to assess if there is an adequate resource base within an area to support a reintroduced animal population. The initial site assessment model to determine suitable sites to reintroduce elk was performed at a coarse scale with respect to quantity of forage, quantity of cover and road density and did not include important interactions between forage and cover (Hutchinson et al. 2003). It is not surprising that when the reintroduced elk population decreased dramatically, the resource quantity and quality of the landscape came under scrutiny. Fortunately, the relatively good average HSI value (for each of the models) throughout the study area is evidence that there is a reasonable resource base for elk present within the Cameron Lake region. Despite this, the large discrepancies between the individual variables used to construct the model and the actual relationships expressed by elk use suggests that some of the modeled general elk-resource relationships may in fact be more site-specific to northwestern Ontario. To investigate this, I also created a resource selection model using an inductive approach in an effort to improve upon the accuracy of modeled resource use for elk in the Cameron Lake region.

CHAPTER 2.

Development of a Resource Utilization Function model; an inductive approach.

Introduction

The development of predictive resource suitability models has recently increased within the field of ecology (Guissan and Zimmermann 2000). These inductive models are both probabilistic and static, as they aim to relate the geographical distribution of a species, community or population to their current environment using statistical analyses (Guissan and Zimmermann 2000). Resource utilization function (RUF) models are one of the most recent inductive techniques proposed to relate the probability of occurrence of an animal or a population to environmental characteristics (Marzluff et al. 2004).

The basis for a RUF model is the utilization distribution (UD). A UD is a probability density function (Silverman 1986) that quantifies an individual's relative use of space (Kernohan et al. 2001, Marzluff et al. 2004). It is based on relocation point data, and often calculated using a kernel analysis. A UD describes the probability of an animal occurring at any given point within its home range as a function of the number and spatial arrangement of relocation points (White and Garrott 1990), and is best understood when visualized as a three dimensional unit (Figure 2.1). Peaks occur in areas with greater clustering of relocations as compared to areas with smaller amounts or no clustering, and the probability of an animal occurring on the landscape (density of animal use) is proportional to the height of the UD at a given point.

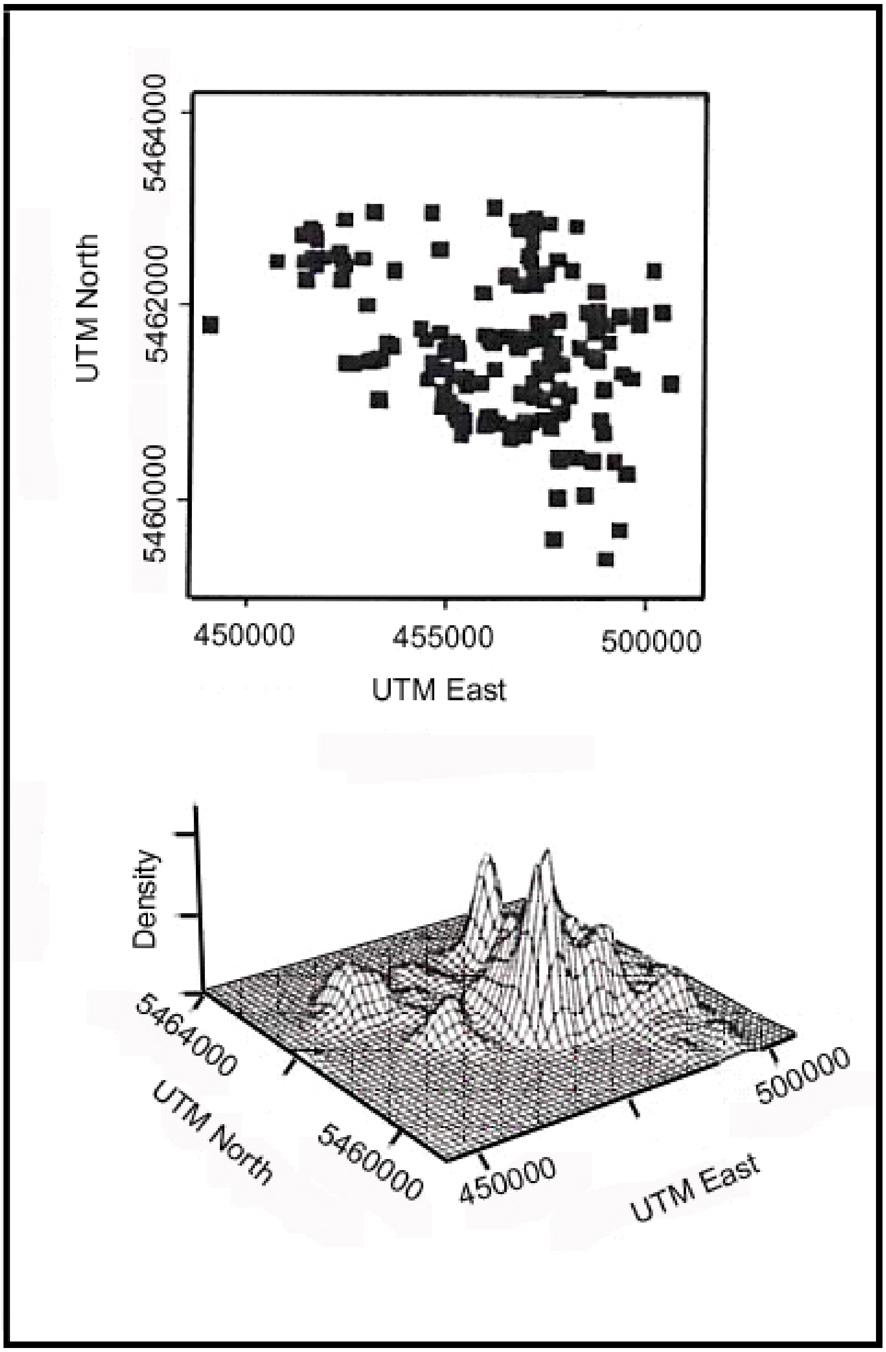

Figure 2.1. The bottom figure is a three dimensional representation of relocation points (top) known as a utilization distribution. The probability of an animal occurring on the landscape (density of animal use) is proportional to the height of the utilization distribution. Figure adapted from Roloff et al. (2001).

To relate space use to resources we assume that a higher probability of animal use is directly related to the quantity or type of resources in an area (Marzluff et al. 2004). Probability distributions rarely reach 100% (or 1.0), but when relating space use to resources we assume that the optimal resources occur at the spatial location under the highest peak in density. Consequently, I transformed each elk UD into a suitability distribution (SD), by standardizing it on a scale from 0 to 1 (General Methods 5.1). SDs are related to resources using multiple regression, where the variation in the height of a SD is attributed to variation in a set of environmental predictor variables or resources (Marzluff et al. 2004).

Using a UD (or SD) to relate space use to resource use has advantages such as: 1) it reduces the impact of telemetry error because resource use is estimated along a gradient rather than at a series of relocation points (Marzluff et al. 2004), 2) autocorrelation (Swihart and Slade 1997) is not an issue because decreased time intervals between relocation points result in a more accurate UD estimation (Marzluff et al. 2004), 3) the animal or population is the study unit rather than the relocation point (Marzluff et al. 2004), 4) the entire distribution of the animal is considered rather than just the relocation points (Marzluff et al. 2004), 5) the sensitivity of resource use modeling is increased because it is executed on a continuous (or discrete) probability metric (as opposed to a binary logistic regression composed of used vs. unused categories), therefore resource use of varying intensities can be captured (Marzluff et al. 2004), 6) the spatial extent of available resources is limited to an animal's UD, thus resource use is modeled as a probability of use, and never estimates non-use (Marzluff et al. 2004), 7) studies that do not incorporate a 24hour sampling design run the risk of underestimating resource use because animals may be inactive during specific periods of the day, but the UD can reduce these concerns because resources used during these periods are likely to be captured within the UD (as opposed to using point data); however, this does not hold true for animals that move large distances between foraging and resting sites.

Although the general HSI model estimated a relatively good resource base for elk in the Cameron Lake area, there was some discrepancy between modeled and actual elk-variable relationships (Chapter 1). As a result, I hypothesized that a more site-specific inductive approach would provide further insight into elk-variable relationships and elk space use within the Cameron Lake region. My objective for this chapter was to construct a RUF model for the Cameron Lake region based on telemetry locations of radio-collared elk released in the area, to assess the predictive performance of the model and provide insight into how important each variable is in influencing elk space use.

Methods

I quantified the stand age (*Age*), distance to nearest cover-forage edge (*Prox*), the width of the cover area associated with the closest forage-cover edge (*CW*), the proportion of deciduous trees in the stand (*Deciduous*) and road density (*Roads*) using Landscaping Scripting Language (LSL) (General Methods 4). I did not group variables into model components as in the HSI model.

I calculated individual summer SDs from relocation point data for 18 elk (General Methods 5.1) used for model construction (Appendix 1). I overlaid each SD across the study area and erased all lakes because kernels often incorporate obvious barriers such as bays or water surrounding a peninsula. I then clipped the SD and all landscape metrics calculated therein (Figure 2.2) to obtain a SD complete with all data layers. I summarized an animal's probability of resource use by calculating the mean of each variable over the suite of hexagons within each SD band (General Methods 5.1). I pooled the means in each band for all 18 animals, checked assumptions of normality and assessed if the relationships between animal use and each variable were linear or non-linear. I graphed the mean of each variable in relation to elk use (each suitability band) to visually compare resource relationships between the model building cohort and the model validation cohort.

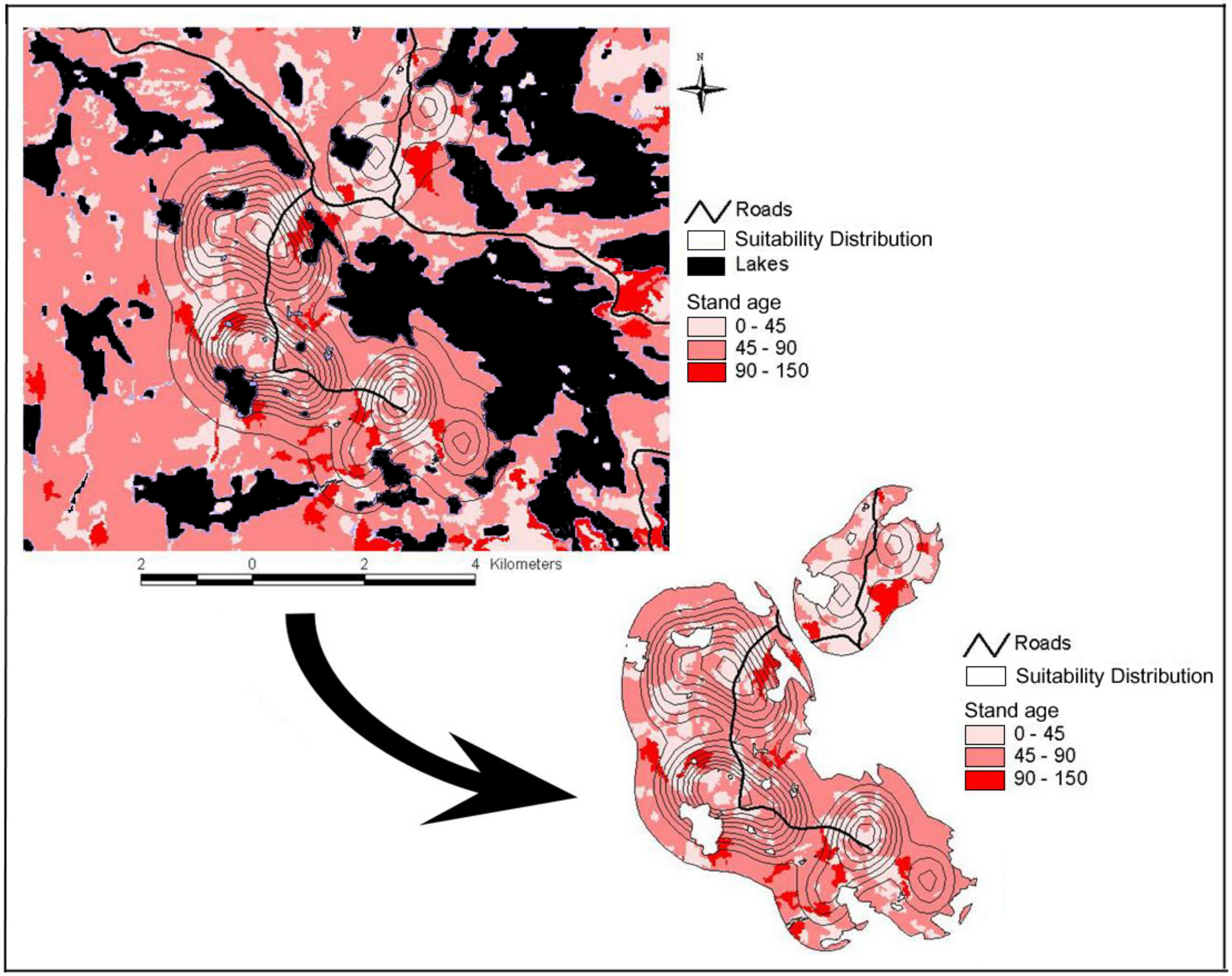

Figure 2.2. Example of a clipped SD with calculated landscape metrics and without lakes.

I used multiple linear regression to relate resource attributes to the probability of use (height of the SD) by elk (Equation 2.1). I regressed the mean calculated resource metric (independent variable) for each band of the SD (dependent variable) to get an overall RUF model;

$$\text{RUF} = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \ldots.. \beta_n X_n + e \qquad \text{(Equation 2.1)}$$

where;

β_o = intercept

β_n = Regression coefficients of n environmental variables

X_n = Independent variables

RUF = Predicted elk space use as a function of n environmental variables.

I entered all the linear relationships into the multiple linear regression model, but only obvious non-linear relationships were included. I used backwards stepwise multiple regression to identify significant variables and obtain the final beta coefficients and constant. I applied the RUF model back to the landscape by calculating suitability for each hexagon using the regression model and created a suitability map of the study area.

The model was evaluated using an independent data set of 19 elk (Appendix 1). I visually compared individual elk-variable relationships between the model building and validation cohorts. I assessed the mean landscape suitability as predicted by the RUF model as well as compared the individual elk SDs to the RUF model using the WO, the AO and the DVI Indices (General Methods 5.2-5.3). I also compared random SDs to the RUF model (as in Chapter 1) using WO, AO and DVI Indices. I evaluated if the model predicted each of these indices better than by random chance using a 2-tailed independent samples t-test. I calculated the mean and 95% confidence intervals of the mean of all indices for both elk and random comparisons. I deemed the model as having predictive ability if it performed better than random chance with respect to all three indices.

Results

Backwards stepwise multiple regression identified *Prox, CW,* CW^2*, Deciduous*^{2} and *Roads* as significantly influencing elk space use and together explained 61.3% of the total variation in elk space use (ANOVA; $P<0.001$, df = 5; 173; Table 2.1). Stand age was highly correlated with Prox (Pearson Correlation (2-tailed) $r=0.82$; $P<0.001$) and subsequently eliminated from the multiple linear regression model. Roads, Deciduous^2 and CW^2 showed positive linear relationships between suitability and elk use ($r=0.585$, $R^2= 0.342$; $r= 0.432$, $R^2=0.187$, and $r= 0.288$, $R^2= 0.083$; respectively). *Age*, *CW* and *Prox* showed negative relationships with elk use ($r= -0.692$, $R^2= 0.479$, $r= -0.020$, $R^2= 0.000$, and $r= -0.714$, $R^2= 0.510$, respectively), all correlation and regression relationships were significant (Pearson Correlation (2-tailed): $P<0.001$ and ANOVA: $P<0.001$, respectively) except for *CW* (Pearson Correlation (2-tailed): $P=0.788$ and ANOVA: $P=0.788$; Table 2.2). Relationships were similar to the validation cohort (Table 2.3; Figures 2.3 and 2.4).

Average suitability of the landscape was 0.692 (Std.dev = 0.38; n= 404,899; Figure 2.5) whereas average suitability of individual elk SDs (AO Index) was 0.767 (SE= 0.008; n=19) and weighted average suitability of individual elk SDs (WO Index) was 0.862 (SE= 0.015; n=19; Figure 2.6). Average suitability and weighted average suitability of random SDs (AO Index =0.727, SE= 0.011; WO Index=0.726 SE= 0.014, n=95, respectively) were significantly lower than for elk SDs (2-tailed t-test $P=0.013$ and $P<0.01$, respectively; Figure 2.6). Mean difference between elk and random DVI Indices was 0.0491 (95% C.I. lower: 0.0392, upper: 0.0598). The RUF model performed 16%

better than by random chance alone and predicted elk space use significantly better than by random chance (2-tailed t-test $P<0.01$; Figure 2.7).

Table 2.1. Estimates of RUF coefficients (β) and standardized coefficients (β_1)

	Predictor	β	*Std. Error of* β	*Standardized coefficients;* β_1
Enter	Constant	0.306*	0.150	
	Prox	-0.003***	0.000	-0.529
	CW^2	0.607***	0.148	+0.229
	Roads	0.000***	0.000	+0.220
	CW	0.000***	0.000	-0.185
	$Deciduous^2$	0.255*	0.125	+0.110

Note: Relative importance of variables is indicated by the magnitude of β_1.
R^2=0 .613 ($P<0.001$). * $P<0.05$, ***$P<0.001$.

Table 2.2. Correlation and regression analyses between each variable and the suitability band for the model development cohort of 18 elk utilization distributions.

Variable	*r*	*Pearson Correlation*	R^2	*ANOVA*
Roads	0.585	0.000	0.342	0.000
$Deciduous^2$	0.432	0.000	0.187	0.000
CW	-0.020	0.788	0.000	0.788
CW^2	0.288	0.000	0.083	0.000
Age	-0.692	0.000	0.479	0.000
Prox	-0.714	0.000	0.510	0.000

Table 2.3. Correlation and regression analyses between each variable and the suitability band for the validation cohort of 19 elk utilization distributions.

Variable	*r*	*Pearson Correlation*	R^2	*ANOVA*
Roads	0.454	0.000	0.210	0.000
$Deciduous^2$	0.483	0.000	0.230	0.000
CW	-0.139	0.057	0.014	0.057
CW^2	0.367	0.000	0.130	0.000
Age	-0.556	0.000	0.310	0.000
Prox	-0.676	0.000	0.460	0.000

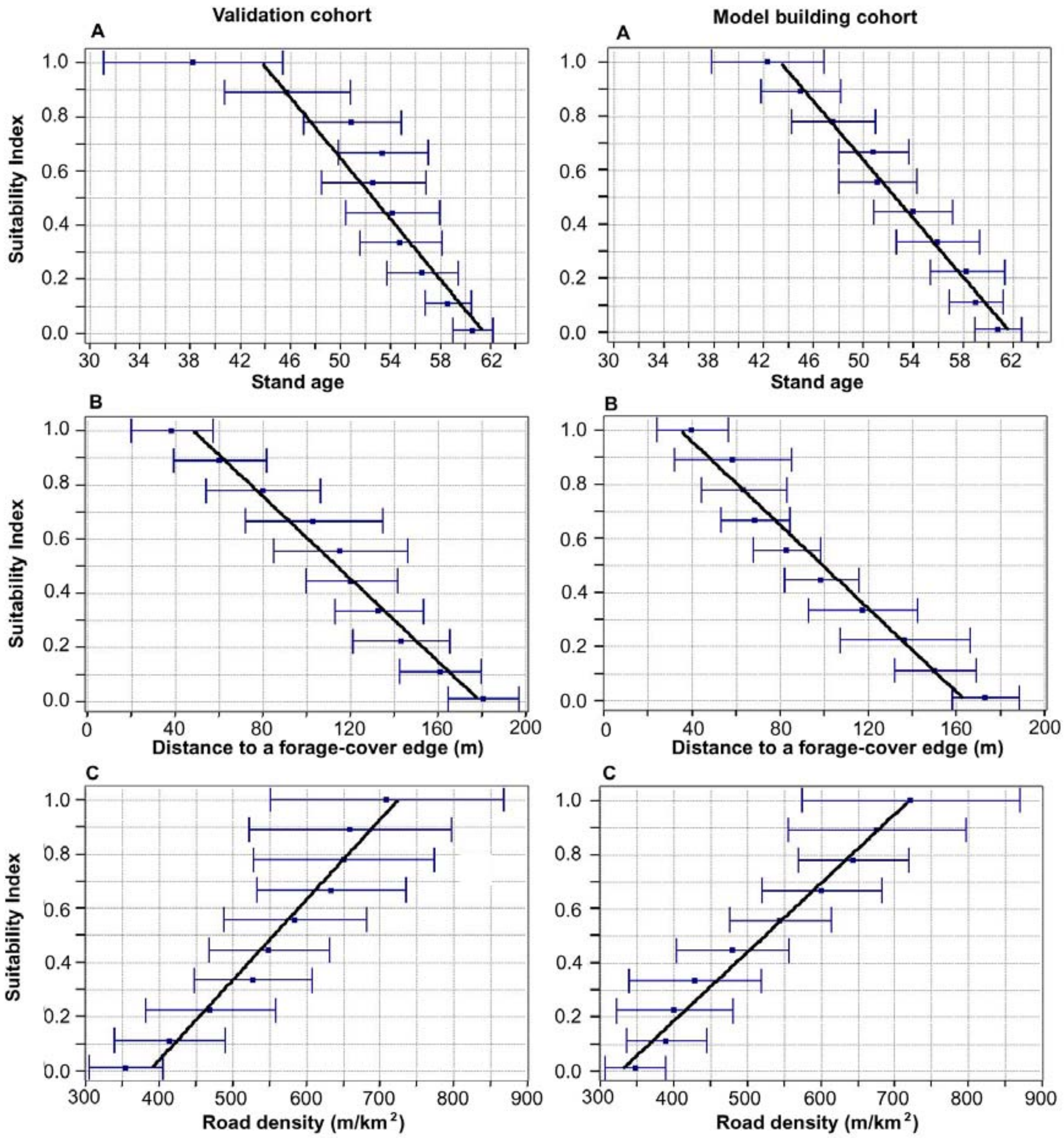

Figure 2.3. Elk-variable relationships for both cohorts of elk data in the Cameron Lake region. Left column represents validation cohort of 19 elk and right column represents model development cohort of 18 elk.

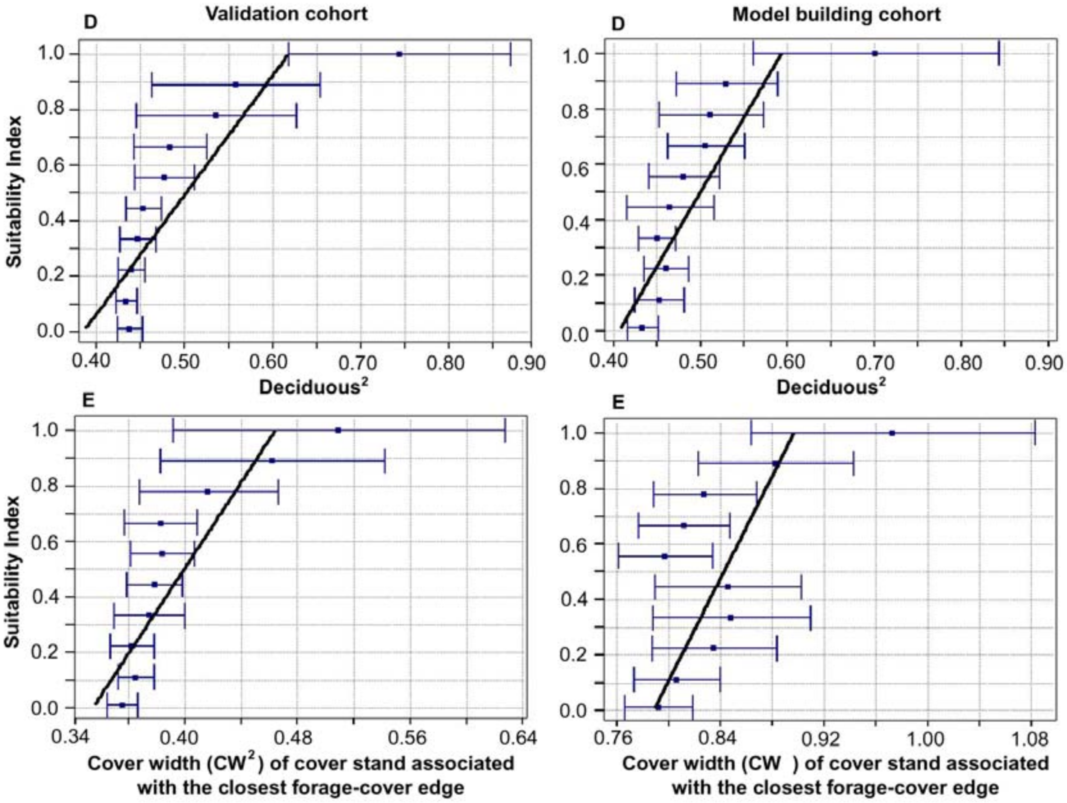

Figure 2.4. Elk-variable relationships for both cohorts of elk data in the Cameron Lake region. Left column represents validation cohort of 19 elk and right column represents model development cohort of 18 elk.

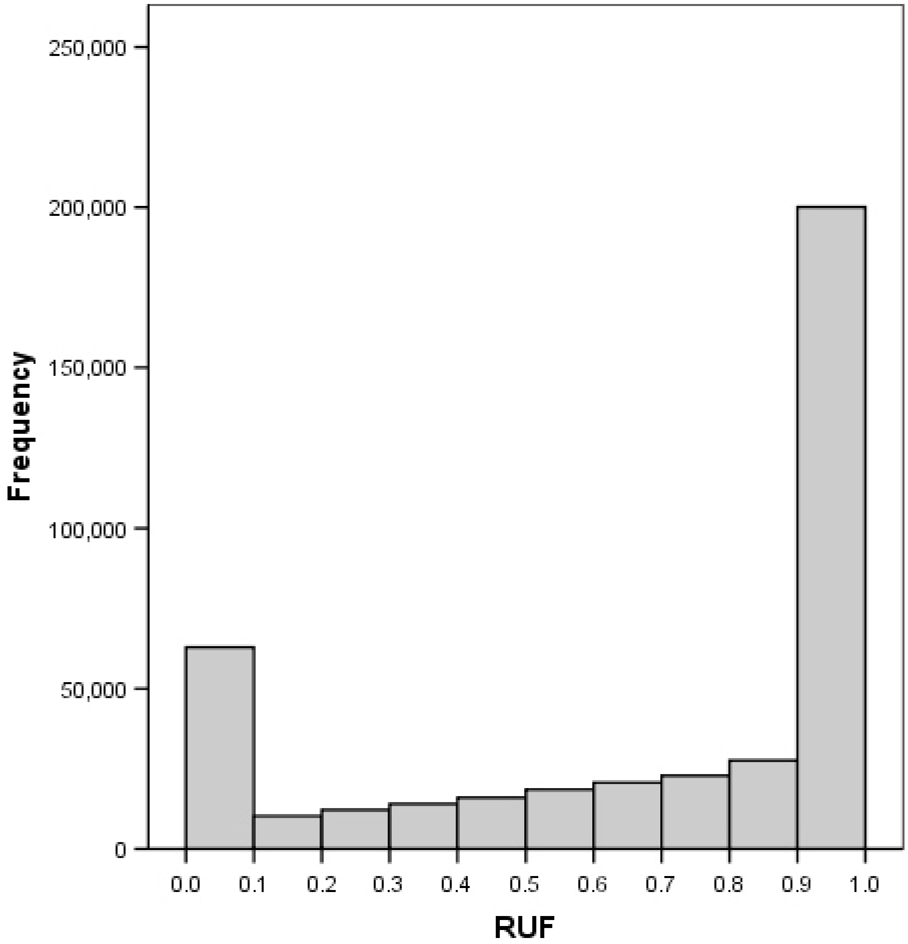

Figure 2.5. Frequency of RUF suitability for all hexagons in the study area (n=404,899).

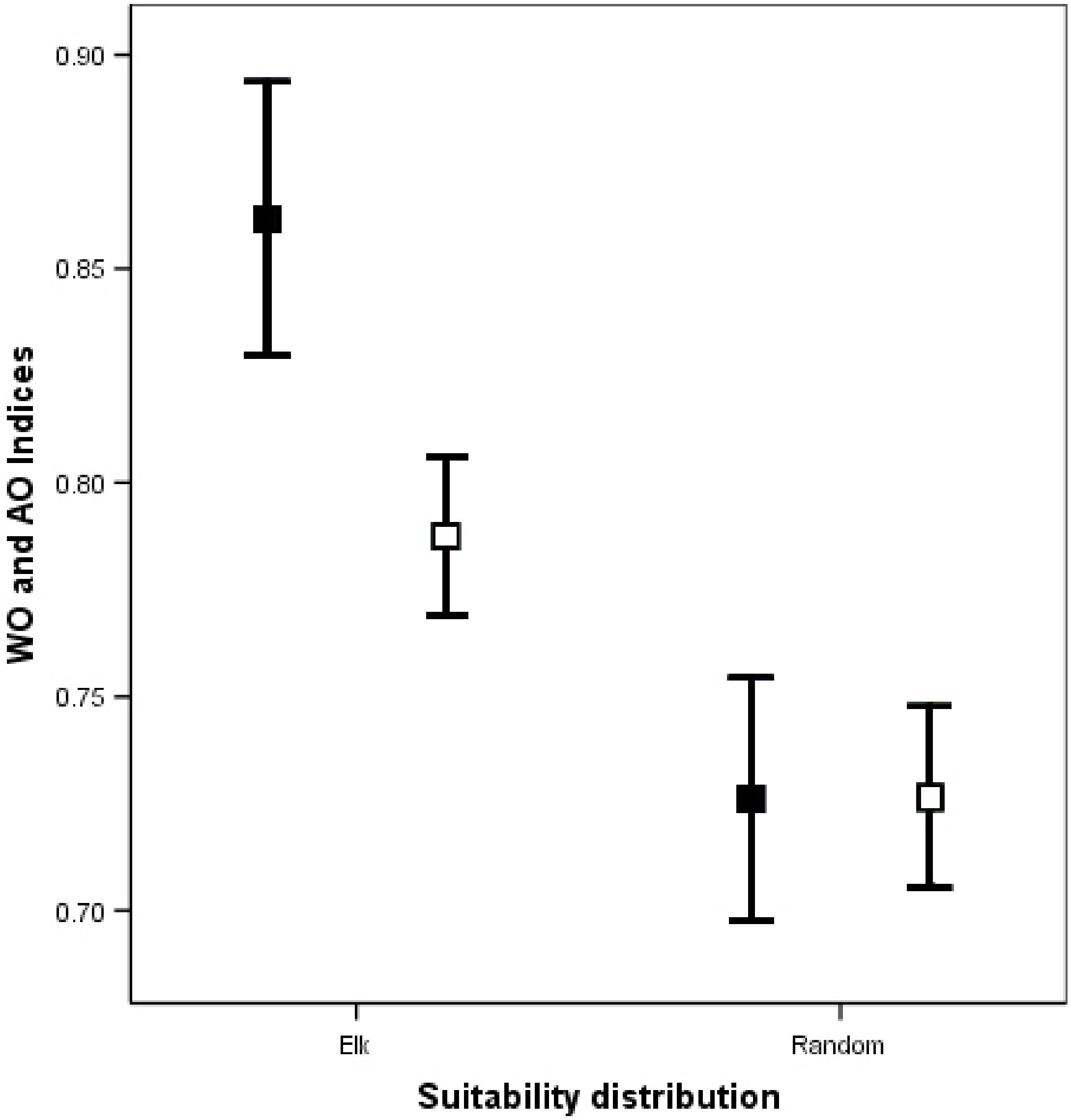

Figure 2.6. Weighted overlap (filled squares) and average overlap (open squares) index scores between the RUF model and 19 individual elk SDs and between RUF model and 95 random elk SDs. Mean is represented by squares; bars represent 95% confidence intervals.

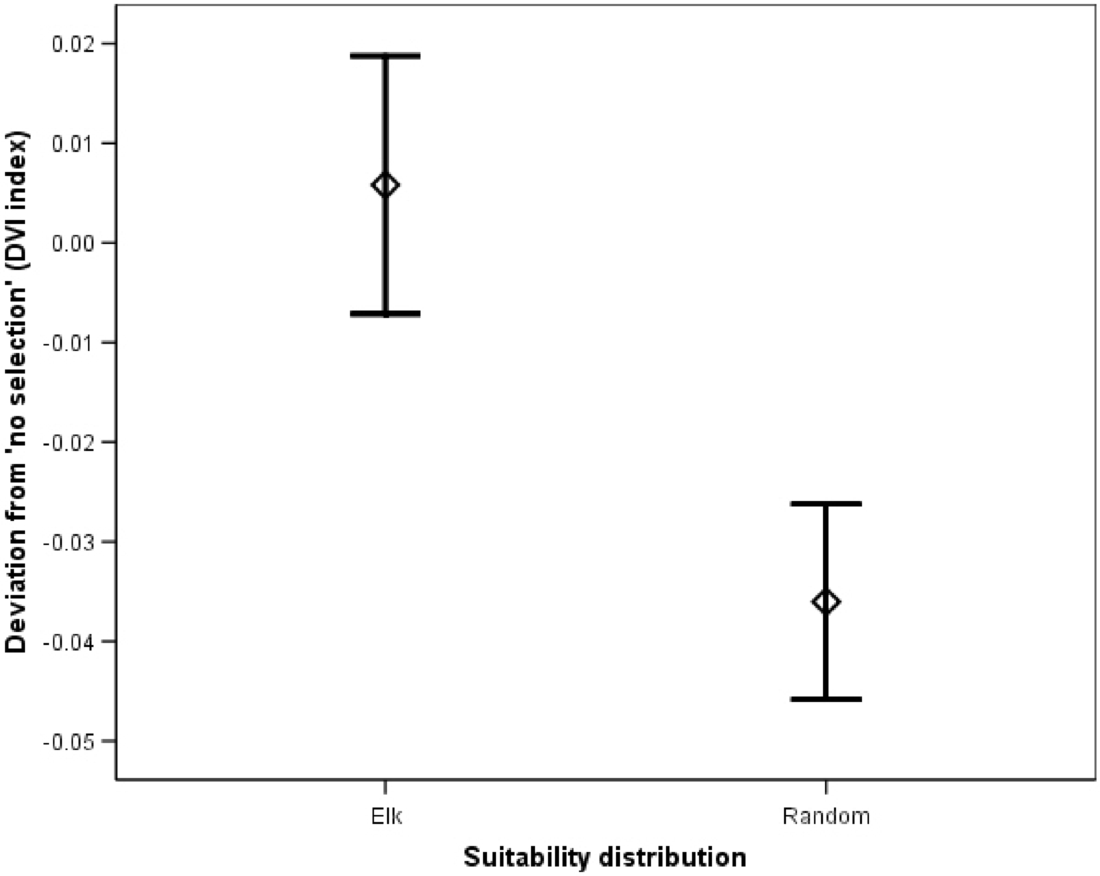

Figure 2.7. Deviation from 'no selection' pattern between the RUF model and 19 individual elk SDs and between the RUF model and 95 random elk SDs. Means are represented by diamonds; bars represent 95% confidence intervals.

Discussion

Inductive models do not provide the underlying ecology behind the observed resource selection, therefore they are less informative than deductive models. They simply help to identify significant variables that can account for the observed variation in animal distribution or space use (Morrison et al. 1992) and do not consider the effects of site familiarity or fidelity. But, inductive models are very helpful when used for exploratory purposes as they can sift through many variable relationships and identify those which might warrant further investigation.

In this case, the variable relationships used in the RUF model reflected elk resource use patterns, which was a notable improvement upon the HSI model (Chapter 1). The RUF model identified the proximity to a forage-cover edge as having greatest relative influence on elk space use, explaining approximately 50% of the variation. The relationships outlined by the regression model suggest that we can expect to see elk using edge or adjacent habitat. Younger forest stands that provide both forage and cover are also highly favourable as are areas along roadsides in close proximity to recent logging and reforestation operations. The elk-variable relationships depicted in this model suggest a dependence on recent forest harvesting activities; these relationships, especially roads, should be individually investigated before accepting these correlations as causal evidence. Nevertheless, if management for increased elk density becomes a primary goal within the Cameron Lake area and possibly within the greater Kenora region, decisions will be tied to harvesting and silvicultural practices that enhance the amount and quality of edge.

The RUF model predicted a good overall landscape suitability, but the distribution was very skewed towards the extremes, with the majority of the landscape having very high (0.9 to 1.0) suitability and a smaller proportion having very poor suitability (0.0 to 0.1). The highly skewed distribution resulted in a poor reflection of animal use intensity as measured by the DVI Indicex. Without a strong variability in RUF values (especially intermediate RUF values) within the spatial extent of an animal’s home range, these indices have difficulty detecting a selection pattern, even when selection is obvious at the landscape level. I found it surprising that the RUF model did not depict a gradual change in suitability between areas of high and low use intensity, considering the model is based on varying degrees of use intensity rather than a binary used and available design. I am curious to know if this is a result of including animals that are unsuccessful or who do not belong to the same life history cohort (sex or age groups) or low sampling intensities, as all of these actions may bring extra variation into the system and act to dilute (or average) the relationship between use intensity and resources.

RUF models will always show an extreme variation in resource suitability (0 to 1) even in circumstances when actual resource suitability is not optimal. When unsuccessful animals, living in sink environments, are included in a RUF model, they add poor resource-use intensity relationships to the model, which act to moderate the true successful relationships. Therefore to reduce variability in these resource-suitability relationships, RUF models should be based only on successfully reproducing animals. Grouping animals of similar age or sex categories or creating RUF models based on a particular behaviour (Marzluff et al. 2001) may also help to alleviate some of the variation and facilitate a better understanding of the ecological relationships behind the space use pattern. Unfortunately, my sample size was not large enough to create separate RUF models for different elk cohorts or behaviours.

A greater number of fixes used to create the UD will characterize an animal's space use with greater accuracy, showing detailed peaks and valleys within a home range (Burt 1943) or even core areas (Samuel et al. 1985). New technologies such as Global Positioning System (GPS) and satellite collars make it possible to achieve extremely high fix intensities, attaining good depiction of animal space use by reducing the inclusion of obvious barriers (lakes) or unused resources. The application of brownian bridges to kernel estimators is the next step in furthering the accurate portrayal of animal space use, since they aim to connect disjointed regions based on the time and distance of successive relocation points (Powell 2000). For this study, I did not have a large enough sample size to exclude animals with lower sampling intensities so I may have increased the possibility of inaccurately depicting elk resource use in the Cameron Lake area.

Although I was not able to meet the above requirements to minimize variation, the validity of the model should not be too highly scrutinized because it did explain over 60% of the variation in elk space use, improved upon the null model by 16% and performed significantly better than the null model with respect to space use. The more important question is; did constructing the RUF model, based on actual animal radio-locations with the possibility of including sources of variation, significantly improve upon the more general HSI approach? This question is addressed in chapter 3.

CHAPTER 3.

A comparison of deductive and inductive modeling approaches.

Introduction

Inductive modeling techniques require a tremendous amount of data collected on specific wildlife populations to accurately portray and predict resource use. They require one data set for the construction of the model as well as a separate data set (independent animals) to properly assess the predictive ability of the model. When much of a species' ecology is well known, deductive models are less expensive to construct as they require only one data set for validation and any subsequent model adjustments. At present, we do not know if there is a scientific benefit of using one technique over the other, so when much of today's ecological research is limited by strict financial budgets it seems only logical to use the most economical study design for a research project. In light of this, the current trend toward expensive inductive wildlife-resource modeling techniques (Corsi et al. 1986, Boyce and McDonald 1999, Marzluff et al. 2001, Boyce et al. 2002, , Manly et al. 2002, Marzluff et al. 2004) is unfounded since a direct comparison between the two approaches has yet to be accomplished.

A recent attempt was made by Dettki et al. (2003) to compare inductive and deductive resource modeling techniques, but a direct comparison turned out to be impossible because differences were attributed to variation in model variables. To accurately compare these two modeling approaches, the models must be built using the same variables so any difference in predictive ability is attributed to the method of model construction, and not to differences in variables.

My goal for this chapter was to determine which modeling technique, inductive or deductive, demonstrated the best predictive ability when using the same variables. I hypothesized that the inductive approach would produce the better predictive model because it is based on how animals are actually using the resources, rather than a perceived notion of how they should be using them.

Methods

I tested two competing methods of model development in order to determine which method better described resource use of reintroduced elk in northwestern Ontario. Both methods used identical variables; distance to the nearest forage-cover edge (*Prox*), density of primary and secondary roads per km^2 (*Roads*), stand age (*Age*), the width of cover associated with an edge (*CW*), and the amount of deciduous trees in a stand (*Deciduous*). Where the deductive model assigned a predicted suitability to the value of each variable and grouped them into model components (Chapter 1), the inductive model did not group variables into model components and related the value of each variable to the degree of animal space use using multiple regression (Chapter 2).

Because I could not detect a significant difference between HSI models *E*, *F* and *G* (Chapter 1), I compared the RUF model to all three of these HSI models. To do so, I compared the AO and WO Indices (General Methods 5.3) between the resource models and elk SDs to determine which model predicted the highest resource suitability (General Methods 5.3). I then compared AO and WO Indices between elk and random SDs (as in Chapter 1) to evaluate if the model predicted each of these indices better than by random chance using a 2-tailed independent samples t-test. I calculated the difference between elk and random index scores and assessed which model outperformed random index scores the most using a one-way ANOVA.

I compared each model’s ability to predict elk space use in northwestern Ontario using the DVI Index (General Methods 5.2) and further assessed the difference between actual elk suitability distributions and random suitability distributions. I calculated the difference between elk and random DVI Index scores and assessed which model best outperformed random index scores using a one-way ANOVA. I also assessed the similarity (or overlap) of the resulting suitability maps between the two types of models (HSI_G and *RUF*) using the VI Index.

The model that predicted the highest weighted overlap and DVI Index score between the model and actual elk suitability distributions, as well as showed the greatest difference between actual and random indices, was deemed 'the best'.

Results

The overall landscape suitability was similar for all models but the average RUF suitability of elk SDs was higher than those of the HSI models (ANOVA for WO and AO Indices: $P<0.001$, df =3; 376; Figure 3.1). All models predicted suitability better than by random chance (all WO and AO Index 2-tailed t-tests: $P<0.01$; Table 3.1) but the difference between elk and random suitability was greatest for the RUF model (ANOVA for WO Index: $P<0.001$, df =3;376; Figure 3.2). Mean DVI Index scores among the RUF and HSI models were the same (ANOVA: p=0.847; df=3; 72) but the RUF showed the greatest difference between elk and random DVI Indices (ANOVA: $P<0.01$, df = 3; 72; Figure 3.3). Figures 3.4 and 3.5 show maps of the study area derived using the HSI model and RUF model, respectively. Note that model HSI_G was used as a visual representation of all three HSI models as they were not significantly different from one another. The predicted suitability of models HSI_G and RUF were similar (VI Index =0.883; upper 95% CI=0.891; lower 95% CI =0.875) throughout areas used by elk.

Table 3.1. Comparison between elk and random SDs for WO and AO Indices.

Model	*Weighted Overlap Index*			*Average Overlap Index*		
	t	d.f.	2-tailed Sig.	t	d.f.	2-tailed Sig.
HSI_E	3.607	46.719	0.001	2.899	64.687	0.005
HSI_F	4.475	47.868	0.000	3.432	62.811	0.001
HSI_G	5.009	49.310	0.000	3.476	63.586	0.001
RUF	6.513	55.416	0.000	4.404	77.330	0.000

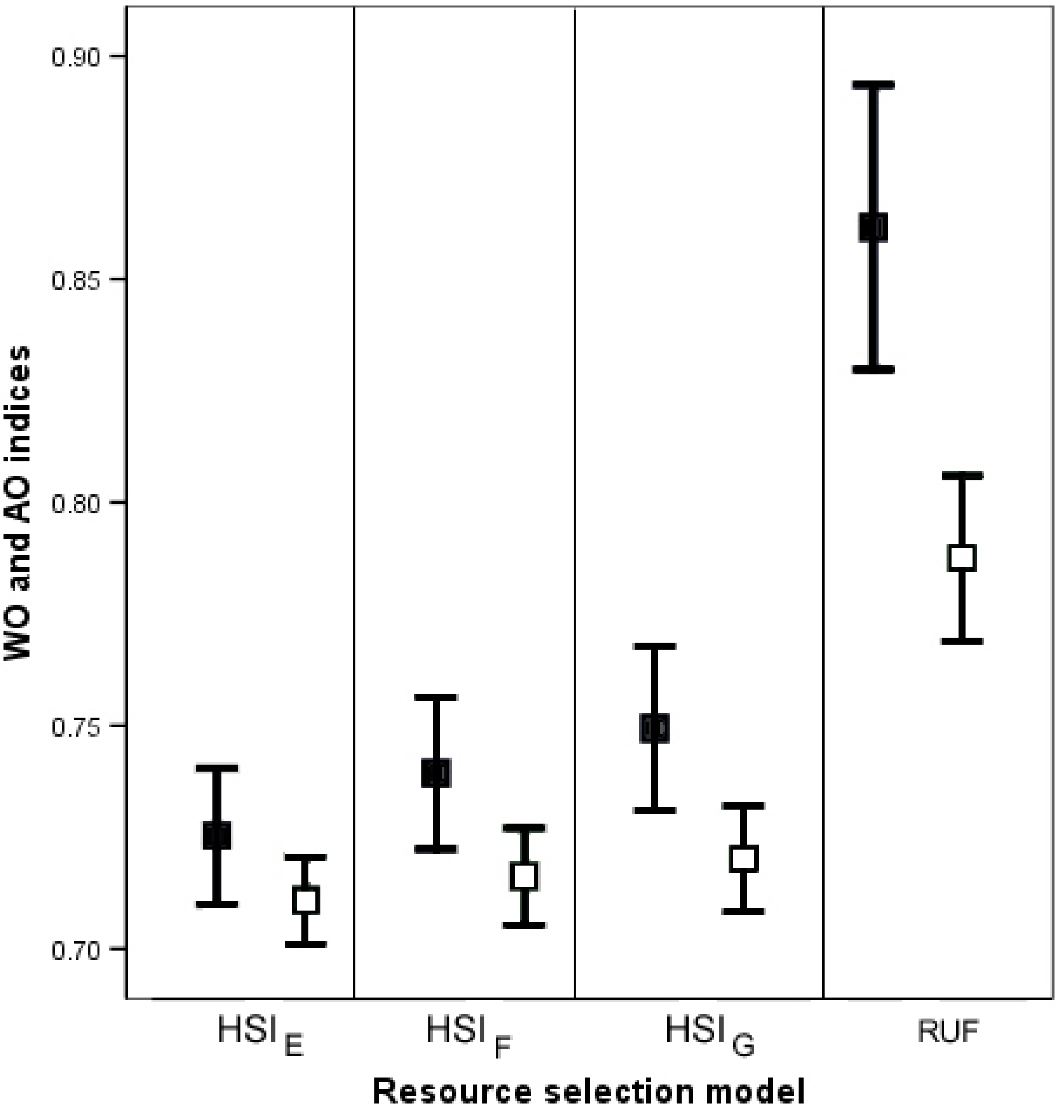

Figure 3.1. Weighted overlap (filled squares) and average overlap (open squares) index scores between models and 19 elk SDs. Squares represent mean, bars represent 95% confidence intervals of the mean.

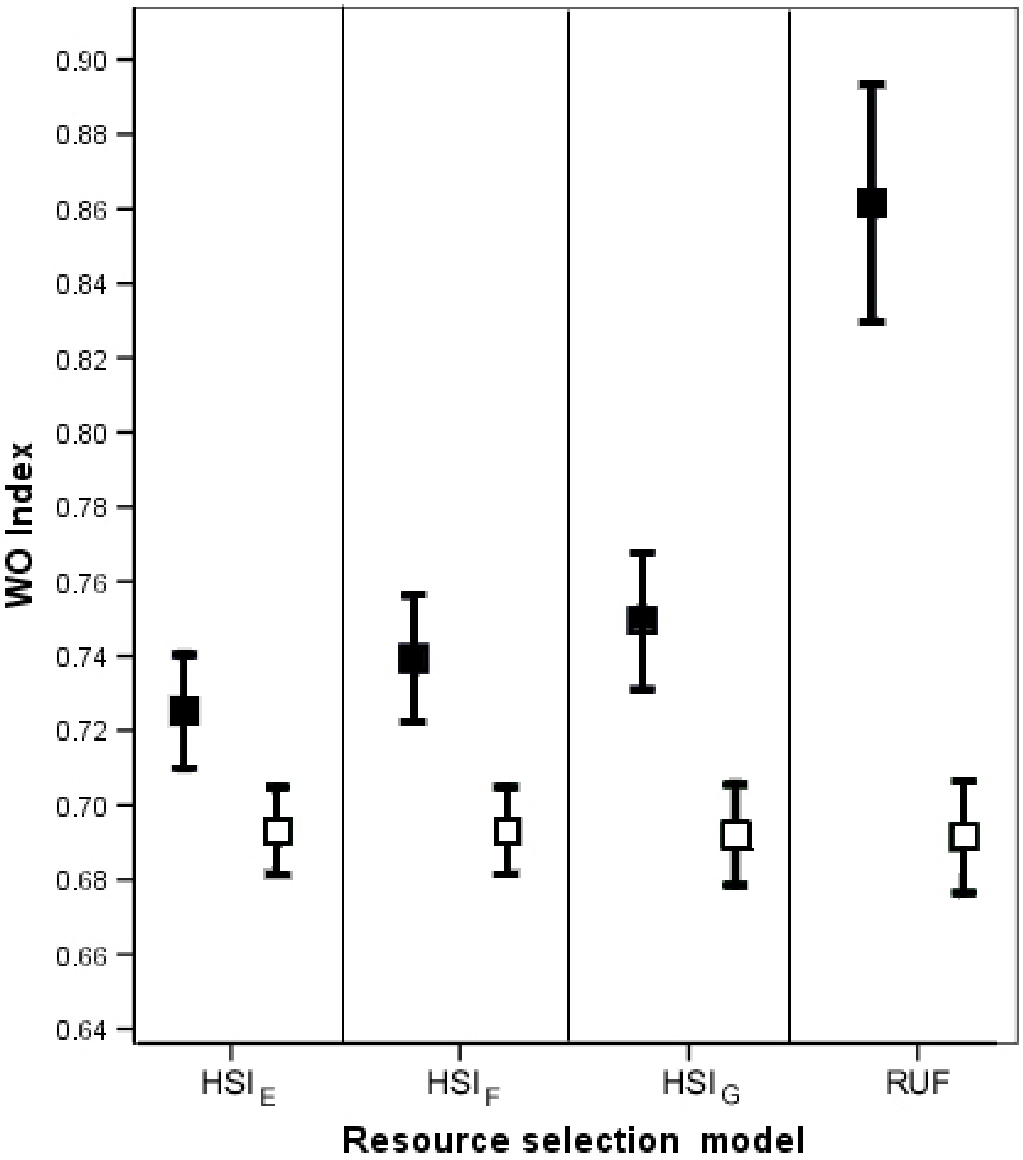

Figure 3.2. Difference between elk (filled squares) and random (open squares) SDs Squares represent mean, bars represent 95% confidence intervals of the mean.

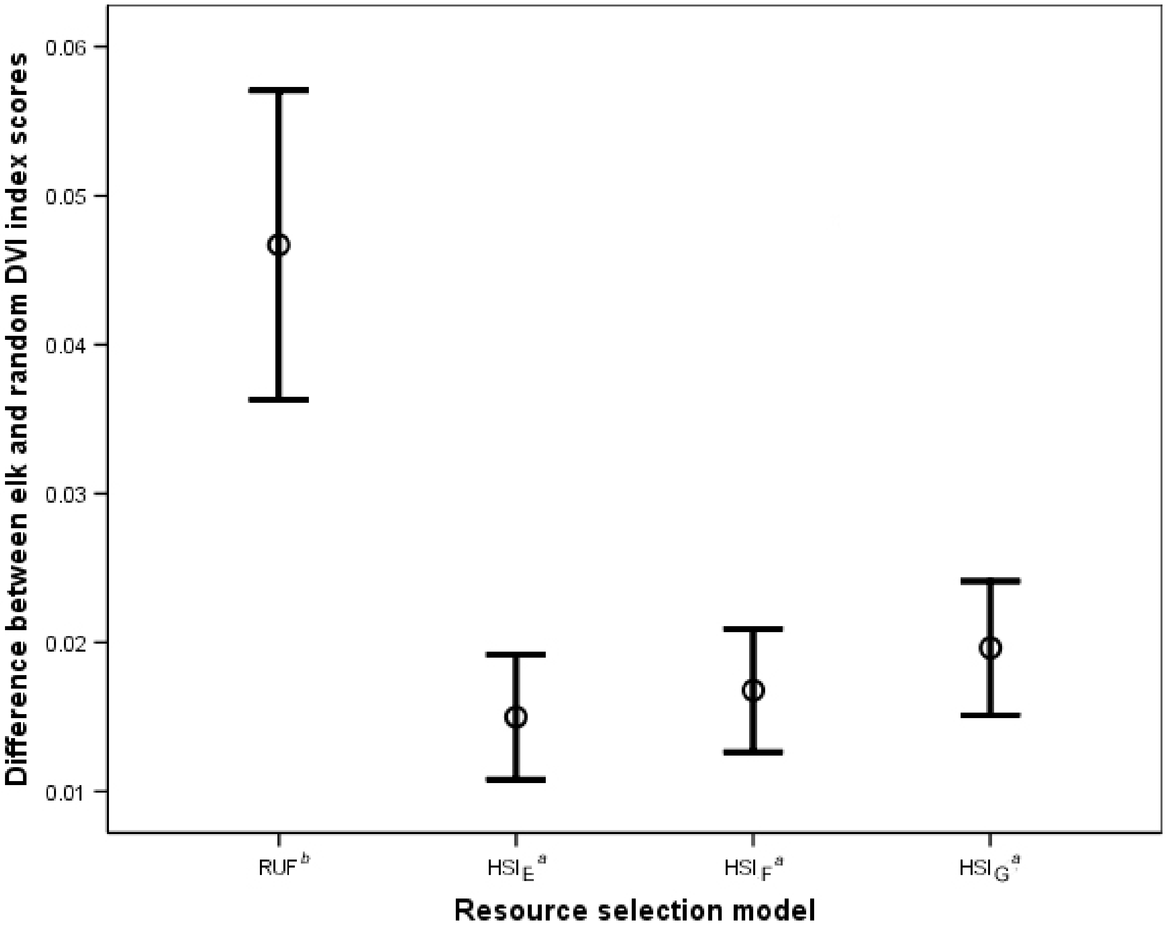

Figure 3.3. Mean absolute difference between elk and random DVI Index scores. Open circles represent mean, bars represent 95% confidence intervals of the mean. Italicized letters represent membership to significantly different means (Tukey HSD and Games-Howell).

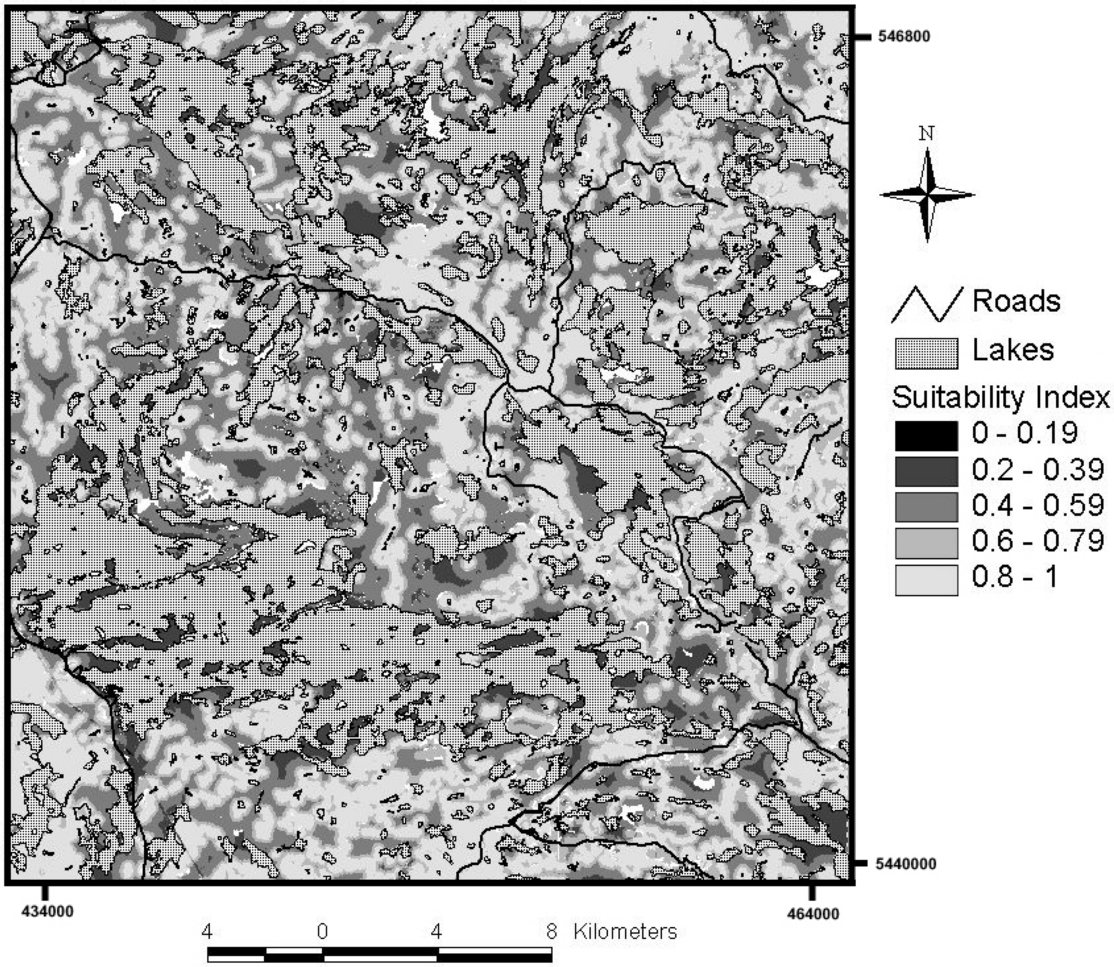

Figure 3.4. Resource suitability map of HSI_G in the Cameron Lake area. Darker shades represent lower elk resource suitability.

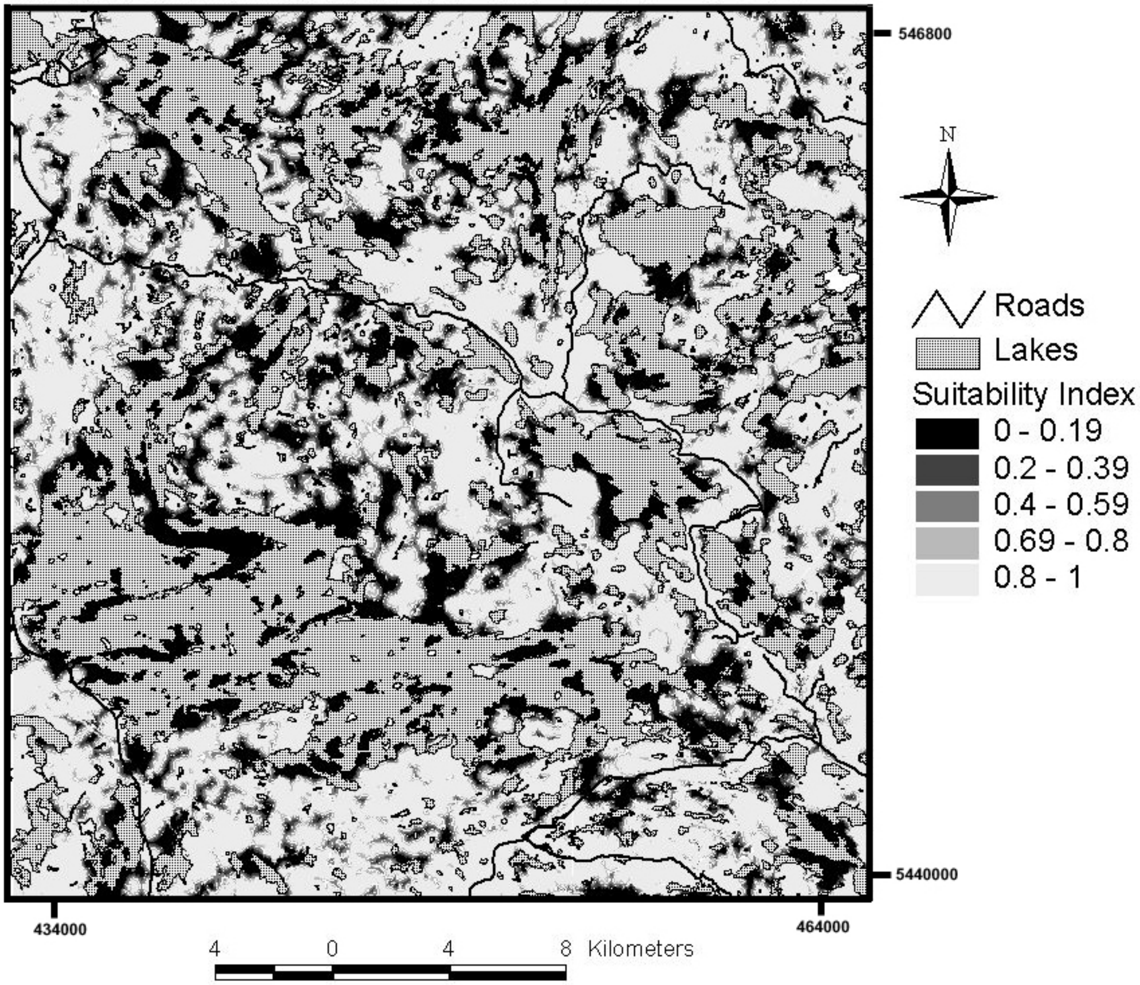

Figure 3.5. RUF suitability map of the Cameron Lake area. Darker shades represent lower elk resource suitability.

Discussion

The RUF model appeared to show a better predictive ability than the HSI models since 1) the RUF model showed the highest suitability of elk SDs (WO and AO Indices), even though mean landscape suitability for the HSI and RUF models were similar, and 2) the RUF showed a greater difference between random and elk indices (WO and DVI) as compared to the HSI model. It seems reasonable that the RUF would perform better than the HSI because it is based on how the elk are actually using the resources. However, all models showed similar DVI Index scores, which sheds some concern on the apparent success of the RUF.

Although the landscape suitability did not differ among models, the RUF model predicted a more drastic change in resource suitability throughout the landscape (Figure 3.5), ranging from 0 to 1.0, as compared to the range in HSI suitability, which was more moderate and never reached 0 (Figure 3.4). The drastic change in resource use predicted by the RUF model can be attributed to the underlying assumption of RUF models. They always assume that there are relatively poorer and higher quality resources in an area (in the outer and inner bands of the SD, respectively) and that the degree of space use is directly related to resource quality. When this assumed change in resource suitability is used to construct a regression model, it should result in a resource suitability that spans the scale of the suitability distribution (as long as the model is applied to the same spatial location from which it is derived). On the contrary, variable components within HSI models do not necessarily have suitability ratings that range the extent of a SD, or from 0 to 1 (Figure 1.1a), nor are the combined effects of all variables forced to range from 0 to

1. As a result, it is unlikely that a HSI model will have the same variation in suitability as predicted by a RUF model. It is this difference that probably accounts for the perceived better performance of the RUF as compared to the HSI model.

When visually comparing the HSI and RUF models (Figures 3.4 and 3.5) it appears as though the models predict similar areas as highly suitable (although some variation is noticeable). As such, when comparing the relative shape, or pattern of space use (DVI Index) of actual elk SDs, the models do not differ because elk are located primarily within the areas of the highest suitability. The models were also very similar when the predicted suitability of areas known to have elk occupancy were directly compared (from the VI Index). This provides evidence that both models predict good elk habitat similarly. It is not surprising that the RUF model predicts space use better than random chance as compared to the HSI as the degree of space use is highly dependent on the magnitude of difference between the highest and lowest suitability values. A model that has very poor suitability located at the peak of a random SD will show a greater difference between elk and random DVI Indices (assuming the elk SD has a high suitability at its peak) as compared to a model with a moderate suitability at the peak of a random SD.

The RUF would follow the space use pattern of elk SDs more closely than the HSI model if the RUF model had fewer sources of variation (i.e. Chapter 2) because it would show differences of within-home range suitability. The inclusion of many sources of variation in the RUF model may have brought it closer to depicting general elk-resource relationships, (which is the ultimate goal of an HSI model) and thus showed a similar space use pattern to the HSI model. An alternative approach that may eliminate some sources of variation would be to create separate RUF models for individual animals (as in Marzluff et al. 2004) but this technique would require validation to occur on a temporal scale (e.g. individual models built from data collected in years 1 and 2 but compared to SDs created with data collected in years 3 and 4) as opposed to using a separate cohort of animals.

General Summary

Landscape suitability and the decline of the LOW population

A reasonable resource base within the Cameron Lake area was demonstrated by the HSI models. The RUF model also identified edge, a prominent feature within the region, as the major driving force behind elk resource selection. As a result, I conclude that a lack of proper resources did not cause the decline in the Cameron Lake elk population. Instead, the decline may be a reflection of an adjustment period; where animals explore the landscape for appropriate forage, learn methods to minimize interspecific competition, how to evade predators and encounter new diseases or parasites.

One known threat to the LOW elk herd is Meningeal worm (*Parelaphostrongylus tenuis*), a parasitic nematode normally found in white-tailed deer within the eastern states and provinces. The nematode rarely causes disease in white-tailed deer (Lankester 2001) but can cause serious pathology in elk (Anderson et al. 1966). Infection has been implicated in the failure of some eastern elk reintroductions (Carpenter et al. 1973, Raskevits et al. 1991), was thought to limit population growth in Pennsylvania (Eveland et al. 1979) and was diagnosed within the reintroduced elk herd in Bancroft, Ontario (Rick Rosatte, pers. comm.). Meningeal worm is widespread within the white-tailed deer population in the Cameron Lake area, where infection rates are known to reach 85% (McIntosh 2003). Consequently, transmission from deer to elk is very possible and requires further investigation as meningeal worm may be a limiting factor to the success of the Cameron Lake elk herd.

Deductive models

HSI models describe causal relationships between individual variables and animal use, but may improperly model the overall relationship of the combined variables. For example, most general HSI models created for elk, suggest weighting the forage component more heavily than other model components. This weighting scheme was not the most appropriate for elk in northwestern Ontario. As such, deductive models may lack precision and should be fine tuned when applied to a specific area, especially when the general wildlife relationships were derived in a very different location. But because HSI models describe causal relationships, they can be extremely useful for evaluating landscape suitability for reintroduction programs. This aspect is increasingly important as national and international biodiversity strategies aim to monitor, remediate and even expand habitats for the purpose of protecting species.

Inductive models

Although inductive modeling techniques can fine tune relationships to a specific area, their major downfall is not the technique, rather it is their improper use. For instance, sample sizes are often very small as it is expensive to collect data for the construction of inductive models (e.g. GPS locations to create a Resource Selection Function model). As a result, researchers may be reluctant to group animals by specific cohorts (e.g. sex, condition or age) or behaviours (as in Marzluff et al. 2001) or to eliminate unsuccessful animals. However, without controlling for these factors, inductive techniques may be modeling an inappropriate representation of important resources. When inductive models are used appropriately, they are powerful tools to assess the relative influence that a suite of variables or an individual variable has on resource selection.

Researchers should be aware of the limitations and benefits of different inductive modeling techniques as the choice of technique will depend upon the question or nature of each study. RUF models always model within home-range suitability, either at the individual level or at the herd or population level. As a result they provide a finer resolution to general used vs. available study designs. However, they always assume that differences in use intensity are linearly related to perceived resource quality. This aspect of RUF models should be further investigated as this assumption may not hold true. For example, resource use may be based on perceived thresholds rather than a gradual linear function. In addition, RUF models do not take into account site familiarity or fidelity, as these may play a larger role in determining selection than the quality or quantity of resources alone.

Suggested method for applying inductive and deductive models

The most important part of developing a wildlife-resource model is the validation process. Models lacking this evaluation should never be used to make management decisions. It is therefore mandatory to collect at least one data set to complete the validation process regardless of which modeling technique is used. With this in mind, I suggest a partnership between deductive and inductive techniques as they are both helpful in developing the best possible model to describe wildlife-resource use. When budgets are tight or the specific wildlife-resource relationships are well known for a particular region, a model should be built using a deductive approach. The required data set put aside for model validation can also be employed to construct an inductive model and subsequently used to help fine tune the deductive model by providing insight into the appropriate mathematical combination or weighting scheme of HSI variables. This helps provide a repeatable and empirical method for determining appropriate weighting of model components.

When budgets are not tight or the underlying ecological relationships are not well understood, and information on individual reproductive success is available, an inductive approach can be used. I suggest collecting two independent data sets; one for model building and one for validation, as the integrity of this model needs to be well established since the underlying ecological relationships are typically unknown or not modeled independently.

If recruitment data are unavailable, deductive techniques should be employed to provide information on the spread of resource quality on the landscape. This will give baseline information to help choose appropriate animals to fine tune the deductive model or to create an inductive model (i.e. not including animals occupying unsuitable or possible sink areas). There is no point in creating or fine tuning a resource model that is based on inferior resources!

Reintroductions

Reintroduction programs are challenging to model since the general wildlife-relationships of a deductive model, or traditional weightings of model components, may not hold true in the new landscape. This was very apparent within the Cameron Lake region as the important factor driving elk selection was forage-cover edge and not strictly forage. On the contrary, inductive methods should not be applied as a stand-alone procedure because they do not show cause and effect relationships. Therefore, resource evaluation for introduction programs should be conducted as a two step process, ideally before animals are introduced into a landscape.

A deductive model should be completed and based on general wildlife-resource relationships, at an appropriate scale relevant to the animal or population, to assess the quality and quantity of resources within an area. If resources are deemed adequate and there are no other known factors that may be problematic (e.g. known parasites or predator densities that may hinder reintroduction success) then the reintroduction program can go ahead. Once animals have had an appropriate amount of time to disperse and adjust to the landscape, I propose that an inductive model should be completed to evaluate if general wildlife-resource relationships hold true within the new system or whether they require adjustment. Creating the inductive model will help researchers to fine tune their understanding of the population in its new environment and may bring forth new information that will help with future management decisions. If the population does not flourish within its new environment, the inductive model may help to identify possible factors causing the decline. This information may be helpful to remediate problems within the area or can be used to further the knowledge base of factors inhibiting reintroduction success for the species under study.

Model validation

Assessing the predictive performance of a model is extremely important. I believe that the VI Index, in its present state, does not provide the best method for validating resource models by comparing them to animal space use. The problem arises because a resource model typically does not have the same range of within home-range suitability as does a SD based on animal relocations. As a consequence, any comparison between the SD and resource model using the VI Index is strictly relative (J.J. Millspaugh, pers. comm.) and empirical assessment of ‘how good the model is’ is not possible. This can be problematic when the goal is to compare more than one model. In this case, I developed the DVI Index to facilitate the direct comparison of multiple models, but I am not convinced that this is the answer to the validation dilemma. In the future, I would like to see a resource map transformed into a utilization distribution (and adjusted to a SD). This would ensure that both the resource model and the SD have the same range in suitability (i.e. 0 to 1) and would facilitate a direct comparison using the VI Index. Comparison would be done at an appropriate scale (i.e. individual, herd or population) and would occur within the same spatial location. I suggest creating a UD from the model by placing random points within the resource suitability categories (i.e. categories of 0.1 suitability increments as in this study), where the number of points placed in a category is proportional to the category’s resource suitability and the amount of area within the SD that the category occupies.

Resource modeling

Resource selection studies assume that the selection of higher quality resources will result in higher fitness (Rosenzweig and Abramsky 1986, Garshelis 2000) but higher quality resources are rarely pre-determined using fitness data. Therefore resource selection modeling techniques may incorporate poor relationships into a model. To address this problem, the direction of resource modeling should steer towards using fitness to identify optimal choices of resource selection (Marzluff et al. 2004). This will likely require the synthesis of traditional habitat selection studies (Rosenzweig 1981, Morris 2003) with new resource selection techniques (Boyce et al. 2002, Marzluff et al. 2004). Such a synthesis would be beneficial as management decisions that manipulate resources that are closely tied to animal fitness should result in a more powerful response to treatments.

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Appendix 1.

Table 1. Summer sample sizes of elk used for model building and model validation.

Model Building		Model Validation	
Tag	Number of relocation points	Tag	Number of relocation points
73	30	88	31
85	25	90	32
89	28	91	32
111	76	98	36
112	21	113	26
118	25	115	21
119	75	122	75
120	48	398	26
316	70	400	27
402	20	401	81
403	78	405	49
404	82	407	27
406	30	408	23
409	26	410	80
411	68	412	29
415	20	416	24
427	83	417	21
441	27	420	72
		552	26

Appendix 2. Sample calculations of the DVI Index.

Table 2. Suitability values for each hexagon within three distributions, HSI, SD and ‘no selection’, their respective standardized suitability at each hexagon and the minimum standardized suitability between the SD and HSI, and between the SD and ‘no selection’. The suitability of the HSI model deviates in shape from the animal’s SD.

	Suitability			**Standardized suitability**			**Minimum standardized suitability**	
Hexagon label	**HSI**	**SD**	**No selection**[1]	**HSI**	**SD**	**No Selection**[2]	**SD & HSI**	**SD & ‘no selection’**
1	0.5	0.01	0.7	0.037594	0.000988	0.045455	0.000988	0.000988
2	0.3	0.1	0.7	0.022556	0.009881	0.045455	0.009881	0.009881
3	0.5	0.2	0.7	0.037594	0.019763	0.045455	0.019763	0.019763
4	0.8	0.3	0.7	0.06015	0.029644	0.045455	0.029644	0.029644
5	0.6	0.4	0.7	0.045113	0.039526	0.045455	0.039526	0.039526
6	0.6	0.5	0.7	0.045113	0.049407	0.045455	0.045113	0.045455
7	0.4	0.6	0.7	0.030075	0.059289	0.045455	0.030075	0.045455
8	0.4	0.7	0.7	0.030075	0.06917	0.045455	0.030075	0.045455
9	0.6	0.8	0.7	0.045113	0.079051	0.045455	0.045113	0.045455
10	0.8	0.9	0.7	0.06015	0.088933	0.045455	0.06015	0.045455
11	0.9	1.0	0.7	0.067669	0.098814	0.045455	0.067669	0.045455
12	0.2	0.9	0.7	0.015038	0.088933	0.045455	0.015038	0.045455
13	0.6	0.8	0.7	0.045113	0.079051	0.045455	0.045113	0.045455
14	0.6	0.7	0.7	0.045113	0.06917	0.045455	0.045113	0.045455
15	0.4	0.6	0.7	0.030075	0.059289	0.045455	0.030075	0.045455
16	0.8	0.5	0.7	0.06015	0.049407	0.045455	0.049407	0.045455
17	0.9	0.4	0.7	0.067669	0.039526	0.045455	0.039526	0.039526
18	0.9	0.3	0.7	0.067669	0.029644	0.045455	0.029644	0.029644
19	0.7	0.2	0.7	0.052632	0.019763	0.045455	0.019763	0.019763
20	0.7	0.1	0.7	0.052632	0.009881	0.045455	0.009881	0.009881
21	0.6	0.1	0.7	0.045113	0.009881	0.045455	0.009881	0.009881
22	0.5	0.01	0.7	0.037594	0.000988	0.045455	0.000988	0.000988
Sum	**13.3**	**10.12**	**15.4**	**1**	**1**	**1**	**0.672427**	**0.709486**

[1] Note: the suitability value of each hexagon in the ‘no selection’ model can be any arbitrary value greater than 0.

[2] Note: following standardization, the suitability value of each hexagon in the ‘no selection’ model is equal to 1 divided by the total number of hexagons.

Table 3. Suitability values for each hexagon within three distributions, HSI, SD and ‘no selection’, their respective standardized suitability at each hexagon and the minimum standardized suitability between the SD and HSI, and between the SD and ‘no selection’. The suitability of the HSI model is similar in shape to the animal’s SD.

	Suitability			**Standardized suitability**			**Minimum standardized suitability**	
Hexagon label	**HSI**	**SD**	**No selection**[1]	**HSI**	**SD**	**No Selection**[2]	**SD & HSI**	**SD & ‘no selection’**
1	0.01	0.01	0.7	0.000987167	0.000988	0.045455	0.000987	0.000988
2	0.01	0.1	0.7	0.000987167	0.009881	0.045455	0.000987	0.009881
3	0.2	0.2	0.7	0.019743337	0.019763	0.045455	0.019743	0.019763
4	0.2	0.3	0.7	0.019743337	0.029644	0.045455	0.019743	0.029644
5	0.5	0.4	0.7	0.049358342	0.039526	0.045455	0.039526	0.039526
6	0.5	0.5	0.7	0.049358342	0.049407	0.045455	0.049358	0.045455
7	0.7	0.6	0.7	0.069101678	0.059289	0.045455	0.059289	0.045455
8	0.7	0.7	0.7	0.069101678	0.06917	0.045455	0.069102	0.045455
9	0.8	0.8	0.7	0.078973346	0.079051	0.045455	0.078973	0.045455
10	0.8	0.9	0.7	0.078973346	0.088933	0.045455	0.078973	0.045455
11	1	1	0.7	0.098716683	0.098814	0.045455	0.098717	0.045455
12	1	0.9	0.7	0.098716683	0.088933	0.045455	0.088933	0.045455
13	0.7	0.8	0.7	0.069101678	0.079051	0.045455	0.069102	0.045455
14	0.6	0.7	0.7	0.05923001	0.06917	0.045455	0.05923	0.045455
15	0.6	0.6	0.7	0.05923001	0.059289	0.045455	0.05923	0.045455
16	0.6	0.5	0.7	0.05923001	0.049407	0.045455	0.049407	0.045455
17	0.3	0.4	0.7	0.029615005	0.039526	0.045455	0.029615	0.039526
18	0.4	0.3	0.7	0.039486673	0.029644	0.045455	0.029644	0.029644
19	0.2	0.2	0.7	0.019743337	0.019763	0.045455	0.019743	0.019763
20	0.2	0.1	0.7	0.019743337	0.009881	0.045455	0.009881	0.009881
21	0.1	0.1	0.7	0.009871668	0.009881	0.045455	0.009872	0.009881
22	0.01	0.01	0.7	0.000987167	0.000988	0.045455	0.000987	0.000988
Sum	**10.13**	**10.12**	**15.4**	**1**	**1**	**1**	**0.941043**	**0.709486**

[1] Note: the suitability value of each hexagon in the ‘no selection’ model can be any arbitrary value greater than 0.

[2] Note: following standardization, the suitability value of each hexagon in the ‘no selection’ model is equal to 1 divided by the total number of hexagons.

The general formula to calculate the standardized suitability for HSI_i (or SD_i or '*no selection*$_i$') is as follows:

$$Std.HSI_i = \frac{HSI_i}{\sum_{i=1}^{n} HSI_i}$$

where $Std.HSI_i$ represents the standardized suitability of *HSI* (or SD_i or '*no selection*$_i$') at hexagon *i*. Appendix Figures 1a and 1b show a two-dimensional representation of the unstandardized, and standardized HSI and SD, respectively, as shown in Appendix Table 2. Appendix Figures 1c and 1d show a two-dimensional representation of the unstandardized and standardized 'no selection' and SD, respectively, as shown in Appendix Table 2. Appendix Figures 2a-d provide a visual representation of a similar example using data from Appendix Table 3. In both examples, the VI Index of 'no selection' is the same, but the resource model in Appendix Figures 2a and b resembles animal space use to a greater degree than the resource model depicted in Figures 1a and b.

The VI Index between the SD and HSI is calculated using equation 5 (General Methods 5.2), or by summing the minimum standardized suitability (column "SD & HSI"). The resulting VI Index using data in Appendix Table 2 is 0.672427. The VI Index of no selection is calculated using the same method, by summing the minimum standardized suitability (column "SD & no selection"). The resulting VI Index of no selection using data in Appendix Table 2 is 0.709486.

Using equation 6 (General Methods 5.2), the DVI Index is calculated as follows;

$$\text{DVI Index} = 0.672427 - 0.709486 = -0.037059$$

Similarly, the DVI Index using data in Appendix Table 3 is 0.231557

When the DVI Index is negative, the resource model does not reflect actual resource suitability as predicted by animal space use (Appendix Table 2, Figure 1). When the DVI Index is positive, the model shows a similar pattern of resource suitability as compared to animal space use (Appendix Table 3, Figure 2).

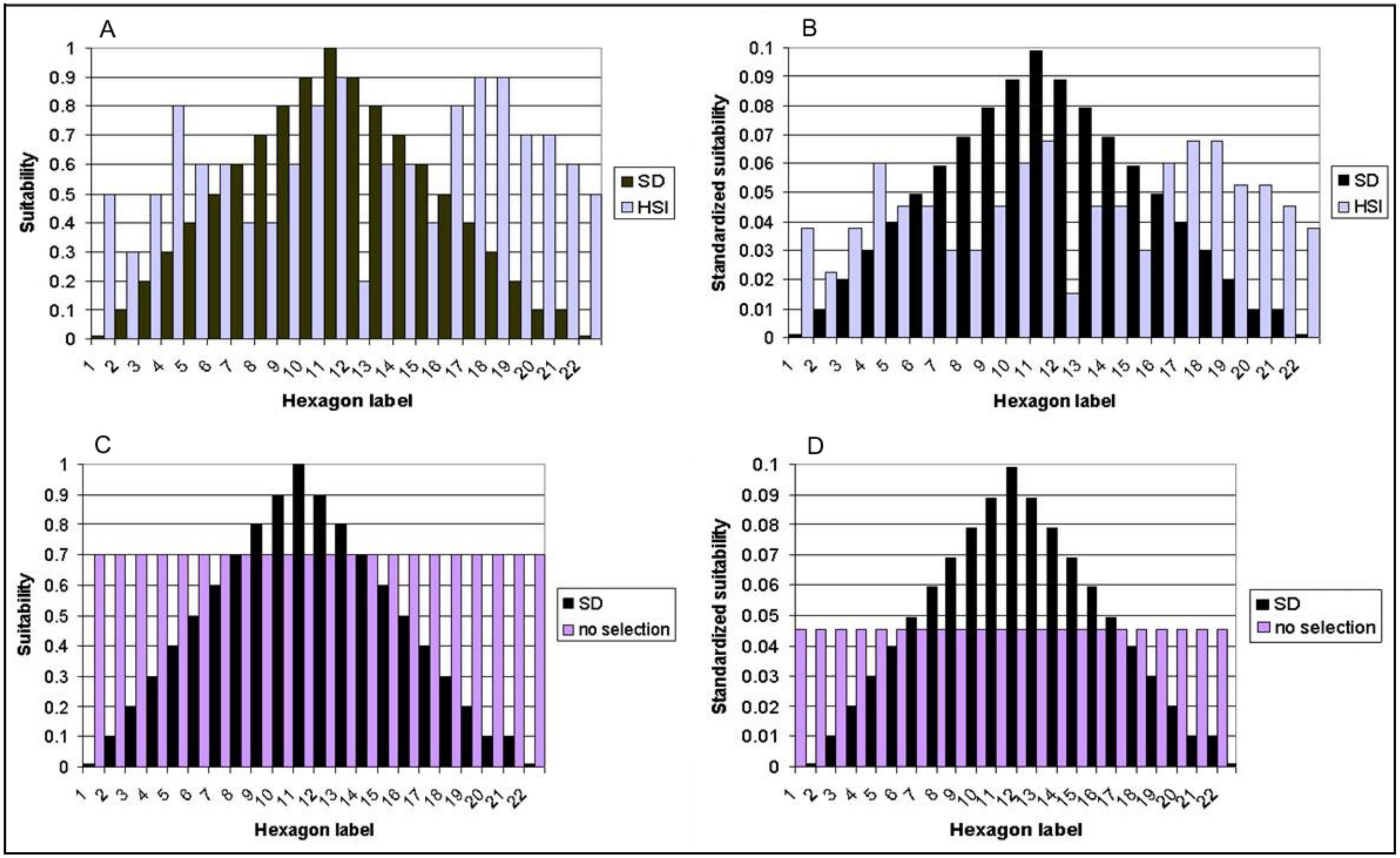

Figure 1. Two dimensional representation of an unstandardized SD and HSI model (A), standardized SD and HSI model (B), unstandardized SD and 'no selection' (C) and standardized SD and 'no selection' (D). The HSI model deviates in shape from the animal's SD. Each bar represents a hexagon and bars within the same hexagon label represent overlapping hexagons. Data from Appendix Table 2.

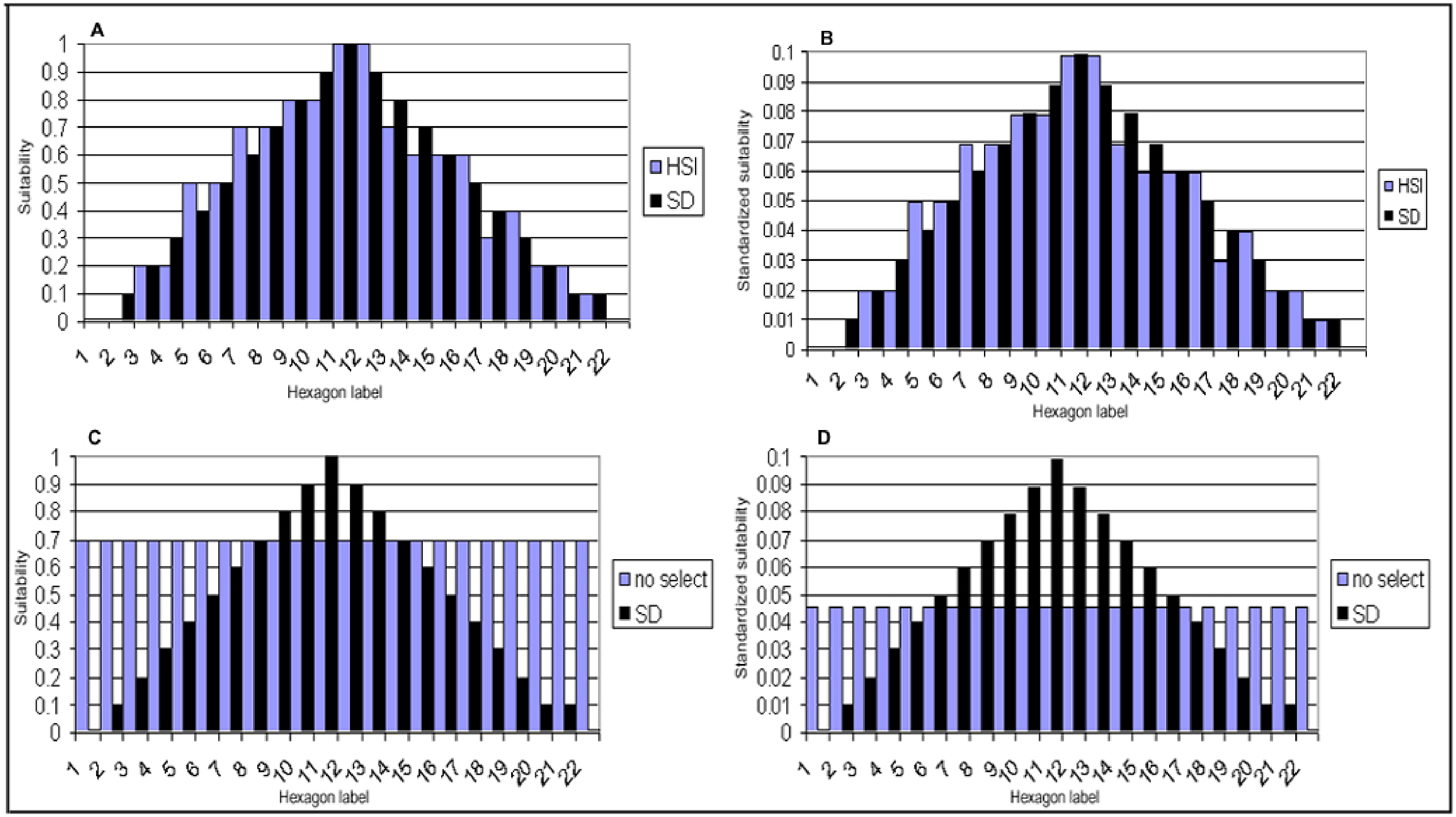

Figure 2. Two dimensional representation of an unstandardized SD and HSI model (A), standardized SD and HSI model (B), unstandardized SD and 'no selection' (C) and standardized SD and 'no selection' (D). The HSI model shows a similar shape to the animal's SD. Each bar represents a hexagon and bars within the same hexagon label represent overlapping hexagons. Data from Appendix Table 3.