THE TECHNOLOGY AND ECOLOGY OF WILDLIFE HABITAT SELECTION RESEARCH

By

Robert A. Montgomery

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Fisheries and Wildlife

2012

ABSTRACT

THE TECHNOLOGY AND ECOLOGY OF WILDLIFE HABITAT SELECTION RESEARCH

By

Robert A. Montgomery

Habitat selection research is devoted to understanding how organisms make use of their environment. Moving beyond mere documentation of habitat that organisms use, this field is defined by striving to understand why an organism selects a particular habitat and to determine the mechanisms that drive a population of organisms to inhabit certain areas. Assessments of this type depend on the ability to reliably locate animals in their environment. Two methods for evaluating the location of animals in space are telemetry technology and discrete animal locations (e.g., carcasses). In this dissertation I demonstrate how to derive ecological inferences from data collected by each of these methods. First, I assess the influence of telemetry error on habitat selection models (Chapters 1 and 2). Results from this research indicate that the accurate of wildlife habitat selection models is conditional on the interaction of telemetry error, covariate resolution, and patch size characteristics inherent to the study area. For instance, higher accuracies are expected in larger patch sizes. However, for imprecise telemetry systems (mean telemetry error = 174 m, SD = 130 m) complete accuracy (1.00) was not attained until patches sizes were unusually large (> 450 ha). Large patch sizes (> 200 ha) were also necessary to achieve complete accuracy for highly resolute telemetry systems (1-5 m telemetry error). These results articulate that non-point based techniques (e.g., utilization distributions, state space models) should be employed in habitat selection research. I next provide an overview of habitat selection research focusing on the methodological techniques employed to understand animal-habitat associations (Chapter 3). This chapter serves as a guide for conducting habitat selection research. Finally, I demonstrate the influence of individual body conditions on animal decision-

making using the location of predator-killed animals (Chapters 4 and 5). These two chapters document that the body condition of the individual, in combination with prevailing abiotic and biotic factors, affects habitat selection. Furthermore, this effect on prey habitat selection can generate specific landscape-level patterns in predation which have important ecological consequences. My research presents a template by which others can evaluate the effect of telemetry error and individual body conditions on habitat selection. I broadly illustrate the means by which habitat selection research can inform ecology through analyses of organism-habitat associations.

ACKNOWLEDGMENTS

My research was supported by the National Science Foundation Graduate Research Fellowship Program. I also received fellowships from The Graduate School and the College of Agricultural and Natural Resources at Michigan State University, The Rocky Mountain Goats Foundation, Safari Club International, the Future Academic Scholars in Teaching, and the Bailey Scholars Program. Thanks to my committee members Drs. Kelly Millenbah, Gary Roloff, Michael Nelson, and John Vucetich for their helpful critique of this dissertation and their encouragement throughout the duration of my degree. I am indebted to 'The Boss' for accepting me into the Ph.D. program in the Department of Fisheries and Wildlife and for making my experience such a positive one. I thank Team Millenbah and the Roloff laboratory for their support, advice, and collegiality over these last four years. I would also like to acknowledge the contribution of my co-authors on the publications that have resulted from my dissertation research. Thanks are due to Drs. Jay Ver Hoef, Joshua Millspaugh, and Rolf Peterson.

This dissertation would literally not have been possible without the guidance and grace of my beautiful wife Dr. Georgina Montgomery. And finally…to our exceptional daughter Olly, who has turned my world upside down in the most magical way.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Evidence of human interest in wildlife dates back to 30,000 BC. with Paleolithic cave drawings depicting predators, prey, and the habitat in which they reside (Kalof 2007). These paintings in the mountains of southwest France demonstrate a keen interest in animal observation. One of the most well-known of the early naturalists was Aristotle. Aristotle was a keen wildlife observer and made many notations of the habitat that various species used (Morrison et al. 2006). Though artists carefully scrutinized the natural world to capture the elegance and brutality of animal-habitat associations and human-animal interactions, there is little evidence of naturalistic observation between Aristotle's time and the 17th – 18th centuries (Morrison et al. 2006). It was during the 17th and 18th centuries that naturalistic observation was dominated by the development of naming conventions and classifications for plants and animals (Blunt 2004). The period between the middle of the 18th century and the middle of the 19th century was defined by naturalism in its purest form, with a focus on qualitative description, as eminent naturalists such as Charles Darwin and Alfred Russel Wallace developed the concepts of speciation and evolution by natural selection (Browne 2010). Since Darwin's publication of the *Origin of Species* (1859) there has been a vast succession of technological innovations to support ever more complex quantitative assessments of animal behavior, population ecology, and habitat selection (Kingsland 1995).

One of the most important technological advancements occurred in the middle of the 20th century when researchers at the University of Minnesota adopted telemetry technology for use in wildlife research (Benson 2010). Telemetry, which literally translates to *remote measurement*, was utilized by the US Government during the Cold War and was retrofitted for animal observation (Benson 2010). This technique allowed scientists to non-invasively track animals through the wilderness documenting animal presence at various intervals by relocating the radio frequencies associated with small tags or collars attached directly to the animal subject. In 1960, Dwain Warner and John Tester were field testing Very High Frequency (VHF) radio tags on ruffed grouse (*Bonasa umbellus*). Shortly thereafter John and Frank Craighead fitted radio collars to grizzly bears (*Ursus horriblis*) in the Greater Yellowstone Ecosystem, a feat which earned notoriety through *National Geographic* coverage and a CBS documentary (Benson 2010). The Craighead's research led to publications in major peer-reviewed journals and a 1979 book titled *Track of the Grizzly*. The depth of this research and the attention it garnered propelled telemetry technology to the forefront of habitat selection research. As a result, telemetry has developed into one of the main techniques used to study habitat selection. This technology was an improvement on the animal tracking and habituation efforts which were time consuming and regularly yielded little to no information due to the wariness of many animals for humans (Montgomery 2005). However, this unparalleled telemetry technology was not without its drawbacks.

Animal locations acquired from VHF telemetry technology could be imprecise (errors from 10's to 1000's of meters; White 1985, Nams and Boutin 1991) because of interference associated with weather, topography, animal movement, technology, and vegetation structure (Moen et al 1997, Moen et al. 2001, Gantz et al. 2006, Hebblewhite et al. 2007). These telemetry errors increase the probability of misidentifying wildlife habitat selection (Garton et al. 2001, Kenward 2001). Seminal publications highlighted the importance of quantifying this error and explicitly incorporating it into the study design (White and Garrott 1990, Saltz 1994). Techniques for incorporating telemetry error include 1) ignoring the error, 2) rescaling covariate surfaces to exceed the error, 3) mean sampling within the mean error buffer around each locations, 4) majority sampling within a mean error buffer, and 5) bivariate-weighted sampling within the maximum error buffer. While each of these techniques was based on sound logic, the ability of these techniques to accurately incorporate error was never evaluated. Chapter 1 of my dissertation explores this topic. In this chapter I create virtual environments and simulate animal locations, typical of those captured from VHF telemetry, within these environments. I induce these locations with error, evaluate the ability of each technique to incorporate that error, and examine the consequences of that error for ecological inference. I also apply an assessment of data from a ‘real environment’ with actual VHF telemetry locations collected on elk in Custer State Park, South Dakota, USA.

By the late 20th century the field of habitat selection research advanced once again with the development of Global Positioning System (GPS) technology. This new technology is more precise than VHF with telemetry errors commonly less than 12 m (Cargnelutti et al. 2007). Because these errors were often considered minor in comparison to those associated with VHF telemetry, researchers would regularly ignore the error altogether and continue with their study design. The second chapter of my dissertation assesses the consequences of ignoring telemetry errors typical of GPS technology. I simulate a range of telemetry errors consistent with GPS telemetry technology and reveal the effects of ignoring such errors on ecological inference.

While the first two chapters of my dissertation explore the influence of technology on habitat selection research, the third chapter acts as a bridge between technology and ecology. There are many other techniques, much apart from those that relate to telemetry technology, used to study wildlife habitat selection. These include direct visual observation, visual or auditory surveys, trapping (both physical and camera), and other evidence of occurrence including animal tracks, scat, and carcass locations. Moreover, there are a number of models developed to describe animal-habitat associations. In Chapter 3, I perform a thorough review of techniques used to collect and analyze locations of animals in space. I frame the importance of these techniques in their ability to make valid ecological inferences. I also discuss some of the limitations on inference that relate to technological and methodological issues.

In the final two chapters of my dissertation I focus my efforts on the interactions of wolves (*Canis lupus*) and moose (*Alces alces*) in Isle Royale National Park, Lake Superior, USA. My research aimed to reveal the importance of individual body conditions on animal decision-making, expressed through habitat selection. The wolf-moose research on Isle Royale has been one of the longest running studies of predator-prey dynamics anywhere in the world (Wilmers et al. 2006). As such, I accessed an extensive dataset describing the location of wolf-killed moose on the island over 50 years (1959-2008). The objectives of this analysis were to assess the relative influence of individual body conditions (age category, sex, and incidence of pathology) and environmental factors (moose density, predation risk, and winter severity in both year *t* and *t-1*) on the habitat selection of moose.

In Chapter 5, I evaluate whether specific landscape-level patterns are associated with areas where wolves kill moose with differing individual condition. I modeled a broad set of environmental features associated with areas where wolves killed moose at two spatial scales; scale 1 = scale typical of a moose home range, scale 2 = scale typical of daily within home range moose habitat selection. My motivation was to assess whether moose with certain individual body conditions (i.e., senescent-associated pathology or not) would select a specific set of environmental features directly before dying from wolf predation. My interest also extended to whether wolves were capable of successfully hunting moose with differing individual body conditions in environmental space.

The results of my dissertation have relevance to the entire discipline of habitat selection research. They speak to both the technological and ecological sides of this research area and make an important contribution to the understanding of error and individual body conditions in habitat selection research. In particular, my dissertation makes specific implications for the arenas of management and ecology. Managers can use the methods and results presented in Chapters 1 and 2 to identify the ramifications of telemetry error. This process could yield more accurate habitat selection models, or at the very least, models that carefully present their ecological inferences in relation to the prevailing telemetry error. The review of methodological considerations associated with habitat selection research presented in Chapter 3 should be of broad interest to students and professionals alike. Chapters 4 and 5 should help ecologists recognize the importance of conditions specific to the individual in habitat selection research. Consideration of conditions such as senescence and senescence-associated pathology may account for important sources of variation in habitat selection research. It is my hope that researchers across the broad spectrum of animal behavior and habitat selection research will find my dissertation of direct utility to their work.

CHAPTER 1

CAN WE ACCURATELY CHARACTERIZE WILDLIFE RESOURCES USE WHEN TELEMETRY DATA ARE IMPRECISE?

ABSTRACT

Telemetry data have been widely used to quantify wildlife habitat relationships despite the fact that these data are inherently imprecise. All telemetry data have positional error and failure to account for that error can lead to incorrect predictions of wildlife resource use. Several techniques have been used to account for positional error in wildlife studies. These techniques have been described in the literature, but their ability to accurately characterize wildlife resource use has never been tested. I evaluated the performance of techniques commonly used for incorporating telemetry error into studies of wildlife resource use. This evaluation was based on imprecise telemetry data (mean telemetry error = 174 m, SD = 130 m) typical of field-based studies. I tested 5 techniques in 10 virtual environments and in one real-world environment for categorical (i.e., habitat types) and continuous (i.e., distances or elevations) rasters. Technique accuracy varied by patch size for the categorical rasters, with higher accuracy as patch size increased. At the smallest patch size (1 ha), the technique that ignores error performed best on categorical data (0.31 and 0.30 accuracy for virtual and real data, respectively), however as patch size increased the bivariate-weighted technique performed better (0.56 accuracy at patch sizes >31 ha) and achieved complete accuracy (i.e., 1.00 accuracy) at smaller patch sizes (472 ha and 1,522 ha for virtual and real data, respectively) than any other technique. I quantified the accuracy of the continuous covariates using the mean absolute difference (MAD) in covariate value between true and estimated locations. I found that average MAD varied between 104 m (ignore telemetry error) and 140 m (rescale the covariate data) for the continuous covariate surfaces across virtual and real data sets. Techniques that rescale continuous covariate data or use a zonal mean on values within a telemetry error polygon were significantly less accurate than other techniques. Although the technique that ignored telemetry error performed best on categorical rasters with smaller average patch sizes (i.e., ≤31 ha) and on continuous rasters in my study, accuracy was so low that the utility of using point-based approaches for quantifying resource use is questionable when telemetry data are imprecise, particularly for small-patch habitat relationships.

INTRODUCTION

Telemetry data are widely used to locate wildlife in spatial and temporal dimensions. These data enable scientists to detect animal carcasses (Mech 1967), locate bird nests and mammal dens (Craighead and Craighead 1970), and conduct population assessments (White and Shenk 2001). Wildlife telemetry has also advanced our understanding of animal behavior (Cooper and Millspaugh 1999), animal movement paths (Pace 2001), and wildlife resource use (Johnson et al. 2008a). Models for wildlife resource selection typically compare environmental features that intersect estimated wildlife locations to those that are available (Johnson 1980, Manly et al. 2002, Christ et al. 2008). Some have questioned whether telemetry data can reliably inform these models because inherent telemetric error often masks true animal locations (Heezen and Tester 1967, Saltz 1994, White and Garrott 1990). Locations estimated from Global Positioning Systems (GPS) can be tens to hundreds of meters in error of true animal locations (Ills et al. 1986; Moen et al. 1996, 1997). Very high frequency (VHF) systems may have locational error that exceeds thousands of meters (Mech 1983, White 1985, Chu et al. 1989, Nams and Boutin 1991). These positional errors can be caused by canopy cover (Chu et al. 1989, Rempel et al. 1995, Dussault et al. 1999), topography (Mech 1983, Gantz et al. 2006), technological differences (Saltz and Alkon 1985, Carrel et al. 1997, Hebblewhite et al. 2007), user error (Hoskinson 1976, Kenward 2001), animal movements (Schmutz and White 1990, Moen et al. 1996, 2001), and weather (Hupp and Ratti 1983, Moen et al. 1997). Failure to recognize and incorporate positional error of telemetry data decreases the power of statistical tests (White and Garrott 1986) and increases the potential for incorrectly predicting resource use (Samuel and Kenow 1992, Garton et al. 2001, Kenward 2001).

Accuracy was rarely evaluated during the early years of telemetry use (Nams 1989). More recently the importance of error quantification has been highlighted (Lee et al. 1985, Saltz 1994). Estimates of positional accuracy are produced by locating geo-referenced transmitters in conditions that emulate field data collection. The geo-referenced, or known location, is compared to the location acquired using the telemetry system and an offset distance is determined. The process is repeated over time under various field conditions resulting in a mean accuracy for the telemetry system and corresponding study design (White 1985, Garrott et al. 1986, White and Garrott 1990). Therefore, telemetry accuracy is often portrayed as the mean distance between estimated and true locations (Rempel et al. 1995, Withey et al. 2001). The accuracy assessment thus provides a method to explicitly quantify and incorporate positional error into subsequent analyses to reduce the chances of Type I statistical errors (Saltz 1994, Johnson and Gillingham 2008).

Generally 5 techniques are used to address positional telemetry error in wildlife resource use studies. The first technique (ignore) is to neglect the error and assume that the estimated telemetry location is the best approximation (Robel et al. 1970, Wallestad 1971). The ignore technique was widely used during the inception of telemetry studies and less so thereafter (Hupp and Ratti 1983), although it continues to be a common approach. The second technique (rescale) alters the resolution of covariate data to align with the mean telemetry error (Koehler and Hornocker 1989, Servheen and Lyon 1989, Telesco and Van Manen 2006). The rescale technique explicitly incorporates telemetry error into the resource use analysis, but the covariate data are generalized and as such important fine scale habitat relationships may go undetected (Roloff et al. 2009). The third technique (zonal mean) recognizes that the error around telemetry locations can be portrayed as polygons (e.g., Heezen and Tester 1967). The zonal mean technique uses an average of the covariate data that intersects with the error polygon (Dickson and Beier 2002). The fourth technique (zonal majority) is also based on the error polygon, but in this case the most frequently occurring covariate value is assigned to the telemetry location (Mace et al. 1996, 1999). The fifth technique (bivariate-weighted) utilizes a half-normal decay function to weight covariate values intersecting the error polygon (e.g., McKelvey and Noon 2001, Findholt et al. 2002, Copeland et al. 2007). The half-normal decay results in a weighted covariate value, with weighting based on proximity to the estimated telemetry location. Covariate values closer to the estimated location are weighted heavier than those farther away and a mean of these weighted covariates is assigned to the telemetry location. Despite the availability of each technique, no evaluation has examined the efficacy of these techniques for incorporating positional error of wildlife telemetry data.

White and Garrott (1990:200) stated that wildlife resource use models “require a precise estimate of an animal’s location so that it can be correctly placed in a habitat type.” This contention is logical but assessments of telemetry precision and subsequent impacts to resource use remain untested, likely because of our inability to know true animal locations from telemetry data (Heezen and Tester 1967). My objectives were to evaluate the accuracy and precision of commonly used techniques for incorporating telemetry error into wildlife resource use studies. I conducted this evaluation by constructing virtual environments and generating categorical and continuous covariate rasters with patchiness and continuity that emulated realistic conditions. I then simulated true wildlife locations, added error to create estimated wildlife locations, and tested the ability of each technique to accurately characterize resource use across the virtual environments. I also applied this process to real data using elk (*Cervus elephus*) telemetry and covariate data from Custer State Park, South Dakota.

METHODS

I reviewed 100 scientific studies of terrestrial wildlife resource use that utilized telemetry data to guide the selection of a virtual study area size. These articles were published in 15 peer-reviewed journals since 1995 with most from the *Journal of Wildlife Management* (n = 75). Median study area size (560 km2) from this review defined the extent of my virtual environments (Figure 1a). I generated 10 virtual environments to serve as replicates in my analysis. I subsequently generated categorical (Figure 1b) and continuous (Figure 1c) rasters at a commonly used spatial resolution (30 m) within each virtual environment.

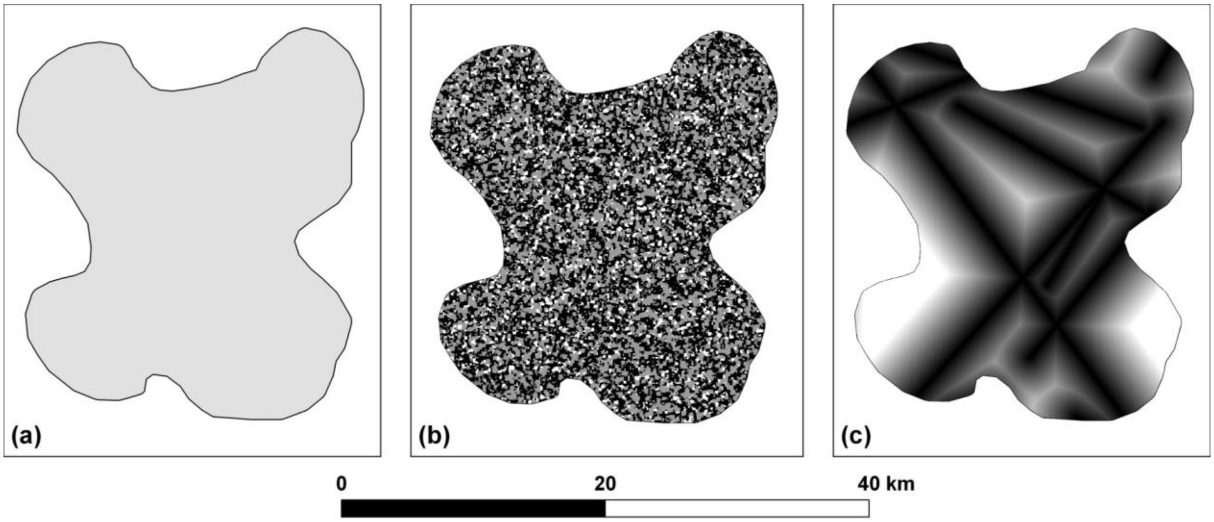


Figure 1. A virtual environment (1 of 10) created for evaluating effects of telemetry error on assigning covariate values to telemetry locations. (a) Outline of the virtual environment with a study area size of 560 km2 (b) Categorical covariate raster simulating habitat type (c) Continuous covariate raster representing distance to a linear feature.

Covariate Rasters

I generated covariate rasters to portray predictor variables commonly used in wildlife resource modeling. I intended the categorical rasters to represent landcover types. I generated categorical rasters of differing patch sizes to assess the influence of patch size on accuracy of the telemetry error techniques. I intended the continuous raster to represent any continuously depicted environmental variable like distance or elevation.

I developed a process in ArcGIS 9.2 to create the categorical (landcover) rasters (*n* = 10). The first step in this process was the creation of a random raster using a Poisson distribution function with a mean range of 35 to 100. I next used a series of boundary cleaning tools (no sort, descend, and ascend) and filters (majority and expand) from the Spatial Analyst extension to aggregate cells into patchy rasters (e.g., Figure 1b). I iterated this process to produce 10 unique rasters with 7 to10 landcover categories each. These 10 categorical rasters contained patches that varied in number (count) and size (min., max., $\bar{x}$, and SD; Table 1).

I developed continuous covariate rasters (*n* = 10) representing distance to a linear feature (e.g., Figure 1c). To randomize the nature of the linear features I randomly generated 50 points inside the study area boundary for each virtual environment and used a random number generator to assign a unique identification value to each point. I then converted these points to lines by sequentially connecting their identification values and calculated Euclidean distance to line rasters.

Table 1. Patch size statistics for the virtual categorical landcover rasters. Count refers to the number of patches per raster, whereas the minimum, maximum, $\bar{x}$, and SD values are patch size statistics measured in hectares (ha). Consistency among minimum patch size values was a byproduct of the spatial resolution, 30 m (0.09 ha), of the rasters.

Categorical raster	**Count**	**Min.**	**Max.**	$\bar{x}$	**SD**
1	1,875	0.09	741.78	30.55	60.70
2	3,367	0.09	1,393.38	17.01	51.66
3	6,438	0.09	3,066.84	8.90	78.50
4	9,097	0.09	1,452.60	6.30	36.86
5	8,939	0.09	700.56	6.41	18.20
6	8,006	0.09	857.25	7.16	25.82
7	7,514	0.09	7,042.86	7.62	92.55
8	8,140	0.09	413.82	7.04	15.38
9	3,190	0.09	8,347.23	17.96	153.60
10	3,468	0.09	1,369.89	16.52	55.95

True and Estimated Animal Locations

I randomly generated 1,000 points per virtual environment that represented true animal locations. I assigned categorical and continuous covariate values to each true location using the Intersect Point Tool in Hawth’s Analysis Tools (Beyer 2004).

I added error to true animal locations to generate estimated locations. These estimated locations were analogous to data collected during typical telemetry studies. I used this sample of

100 published telemetry studies to calculate a mean positional error. Telemetry error is traditionally under-reported (Saltz and Alkon 1985, Saltz 1994, Withey et al. 2001) and, consistent with that observation, only 50 of the studies in my sample reported positional accuracy around the telemetry location. These values were reported as a mean (*n* = 28), median (*n* = 2), range (*n* = 9) and upper error range (*n* = 2), and area (*n* = 8) and upper error area (*n* = 1). In cases where range was provided, I used the upper end of the error range in this analysis and when telemetry error was expressed as an area, I calculated the corresponding radius. From these studies I generated a mean error radius of 174 m (SD = 130 m) for use in this analysis.

With the telemetry error identified, I needed to determine whether a half-normal or exponential model better fit the distribution of these data (mean telemetry error = 174 m, SD = 130 m). I let a random variable *X* be distributed as a normal distribution with mean zero and variance δ^2; $X \sim N(0,\delta^2)$. I then obtained the half-normal by taking *Y* = |*X*|, (a special case of a folded normal distribution, Johnson et al. [1994:170]), and the mean of *Y* is $\mu = E(Y) = \delta\sqrt{2/\pi}$, and the standard deviation of *Y* is $\sigma = \sqrt{\text{var}(Y)} = \delta\sqrt{1-2/\pi}$. Given these calculations, I can use the mean and standard deviation of the telemetric error to get 2 estimates of δ in the half-normal. First, I can solve

$$174 = \delta\sqrt{2/\pi} \Rightarrow \delta = 218.0767$$

Alternatively, I can solve

$$130 = \delta\sqrt{1-2/\pi} \Rightarrow \delta = 215.6566$$

These values are similar, implying that the half-normal is a reasonable model for these data. For an exponential distribution for *Y* with parameter θ, the mean of *Y* is $\mu = E(Y) = \theta$ and the standard deviation of *Y* is $\sigma = \sqrt{\text{var}(Y)} = \theta$. The magnitude of difference in θ ($\bar{x}$ $\theta = 174$ and

SD $\theta = 130$) demonstrates that the half-normal is a better model for the error distribution in my data. I might also consider 2-parameter models, such as the weibull and gamma distributions, but given the solutions for the single parameter model using the half-normal are similar, I selected the simpler model (half-normal) which is consistent with the expected distribution of telemetry error (Springer 1979). I used $\delta = 217$ as the parameter estimate, drew from a $N(0, 217)$ normal distribution, and took the absolute value to simulate the radius of the telemetry error. I then randomly selected a bearing angle and generated a point at the radial distance from the true point.

The orientation and shape of a VHF error polygon is influenced by triangulation method, azimuth angle, equipment type, and distance to the animal (Mech 1983). Similarly, the shape of GPS error (though variable by GPS unit and satellite fix; Moen et al. 1997) is generally circular (Ills et al. 1986). Thus, my assumption that a circle radius can be used to portray the shape of an error polygon is reasonable (e.g., Nams 1989, Rettie and McLoughlin 1999, Visscher 2006), though I acknowledge that telemetry error may exhibit directional bias in some studies.

Error Techniques

The ignore technique neglects the inherent telemetric positional error. I used the Intersect Point Tool to assign categorical and continuous covariate values to the estimated locations for the ignore technique.

I utilized the majority function in the Resample Tool of ArcGIS to rescale the categorical and continuous rasters from a spatial resolution of 30 m to 174 m, matching the mean telemetry error in my study. Once I rescaled the covariate data I again assigned covariate values using the Intersect Point Tool.

Zonal mean is based on the average of covariate values that intersect with the error polygon. The zonal majority is based on the most frequently occurring covariate value within the error polygon. I buffered each estimated location by the mean error of 174 m and calculated these zonal statistics for the covariate values within the error polygons.

Several techniques have been developed to weight covariate data within the error polygon by the half-normal decay. The half-normal decay translates to a higher probability of the true animal location being towards the center of the error polygon than to its periphery. The periphery of the error distribution used in this analysis was at 714 m, corresponding to the distance that contains 99.9% of the error distribution. I buffered the estimated locations by 714 m to create an error polygon. I populated the error polygon with an array of points spaced 30 m apart (matching the spatial resolution of the covariate data) using the Point Sampling Tool in Hawth's Analysis Tools. I calculated the distance (*d*) of these points from the polygon center and converted these distances to probabilities based on the half-normal distribution using the following equation.

$$\exp(-(\frac{d^2}{2*217^2})),$$

I assigned covariate data for categorical rasters by calculating cumulative totals of the weights by category within the error polygon and selecting the category with the largest value. I created the bivariate-weighted value for the continuous rasters by weighting covariate values with the half-normal distribution and calculating a weighted mean.

Parameter Averaging

I modeled the effect of patch size by first evaluating the relationship between patch size (abscissa) and proportion correct (ordinate) using scatterplots. I used a logarithmic function (general form $y = \beta_0 + [\beta_1 * Log10(Patch\ Size)]$) to represent these relationships for all 10 virtual environments and the elk data. I averaged the beta coefficients to generate a mean logarithmic function of technique performance. I subsequently used these average logarithmic functions to compare error technique performance across patch sizes that varied from 1 to 10,001 ha.

Elk Data

I used telemetry data collected on 21 females and 7 male adult elk in Custer State Park, South Dakota (Figure 2a). Millspaugh et al. (1995) detailed the methods used for capture, anesthetizing, and collaring elk. Each elk was fitted with a mortality-sensing Lotek VHF radiocollar. Elk were located several times weekly by triangulation and visual observation. Surveys were conducted throughout the day and during all seasons using surface triangulation methods (Mech 1983). Observations were collected >28 hours apart to minimize temporal autocorrelation (Swihart and Slade 1985*a*,*b*). The resultant dataset included >12,000 elk locations, but I limited the dataset to 10,000 as some locations were beyond the extent of the covariate rasters. I treated these 10,000 elk locations as true and induced positional error to create estimated locations using the aforementioned process. For comparative purposes to the virtual analysis, I assumed a mean telemetry error of 174 m with a standard deviation of 130 m. The mean telemetry error estimate was comparable to mean error measured during the elk study (176 m; Roloff et al. 2001*a*).

I used a 30-m land cover raster (Figure 2b) that included classes such as deciduous trees, ponderosa pine (*Pinus ponderosa*), low cover grassland, and others (Roloff et al. 2001*a*). Patch sizes ranged from 0.09 - 6038 ha. For a continuous covariate raster (Figure 2c) I generated a distance to primary road raster. Custer State Park has 103 km of primary road and I created a

Euclidean raster by calculating distance to these linear features. I assigned covariate values for each error technique using the same methodologies as previously described.

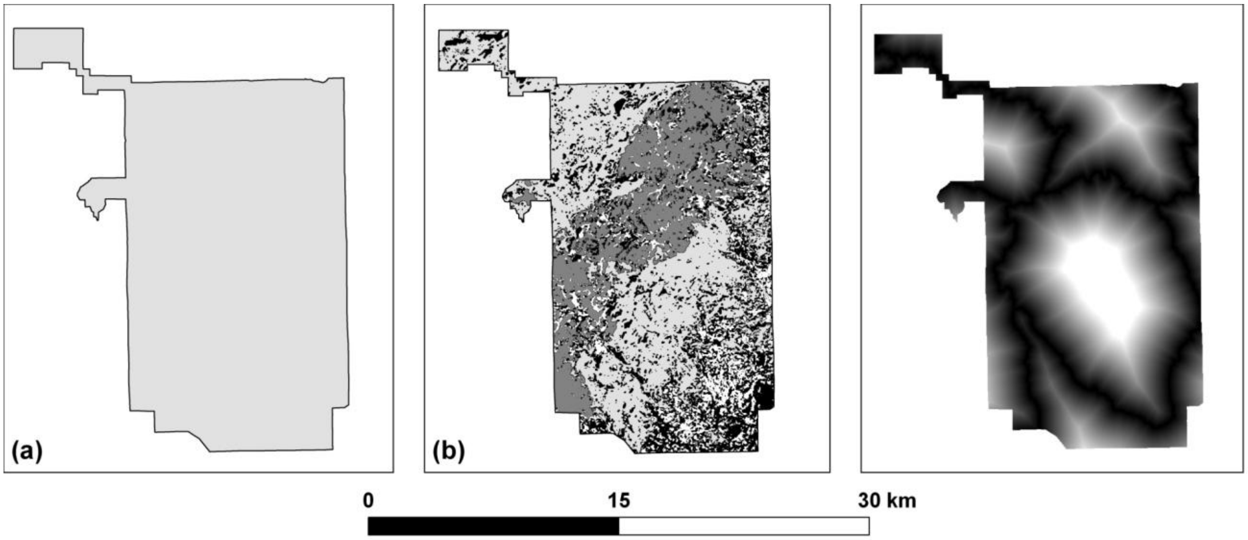


Figure 2. Data from Custer State Park, South Dakota. (a) Outline of the park, which is 286 km2 (b) Categorical covariate raster depicting landcover classes as derived from photo interpretation (Roloff et al. 2001) (c) Continuous covariate raster portraying distance to primary road.

Statistics

Statistics for my analysis varied by covariate raster. For categorical rasters I compared the true (T_i) to the estimated (E_i) values by calculating the proportion correctly identified. For continuous rasters, I calculated the mean absolute difference (MAD) between true values for the *i*th location (T_i) and estimated values for the *i*th location (E_i):

$$\text{MAD} = \frac{1}{n}\sum_{i=1}^{n} | E_i - T_i |,$$

where n = total number of locations. Mean absolute difference ranges from zero (no errors) to infinity, with the magnitude of the statistic corresponding to magnitude of the error in map units.

RESULTS

Categorical Data

Accuracy of the techniques for incorporating telemetry error varied by virtual environment and this variability appeared to associate with mean patch size of each environment (Figure 3). Although performance of telemetry error techniques varied among the virtual environments (ranging from 0.42 to 0.66 proportion correct), for any single environment performance was consistently within 0.10 for all techniques (Figure 3). These results indicate that performance of any telemetry error technique is influenced by raster patch properties. Average logarithmic functions indicated that the ignore technique had the highest accuracy (0.31) at the smallest patch size (1 ha; Figure 4a) but accuracy for ignore at larger patch sizes was lowest among the techniques evaluated (Figure 4b). In contrast, the bivariate-weighted technique performed worst (0.00 accuracy) at the smallest patch size (Figure 4a), but outperformed all other techniques as patch size increased (Figure 4b). Bivariate-weighted became a better technique than ignore in my simulated environments as patch sizes exceeded 31 ha (Figure 4a). Coefficient averaging suggests that the bivariate-weighted technique is completely accurate (i.e., 1.00 accuracy) at patch sizes >471 ha, whereas the ignore technique did not reach 1.00 accuracy (max. = 0.95) at any of the patch sizes I evaluated (1–10,001 ha; Figure 4b). The zonal majority and rescale techniques performed comparably, with zonal majority slightly more accurate (Figure 4b), but neither technique was completely accurate for the range of patch sizes I evaluated. My results for categorical covariates indicate that techniques for incorporating telemetry error into wildlife resource use models are only completely accurate for large (i.e., >471 ha) patch sizes.

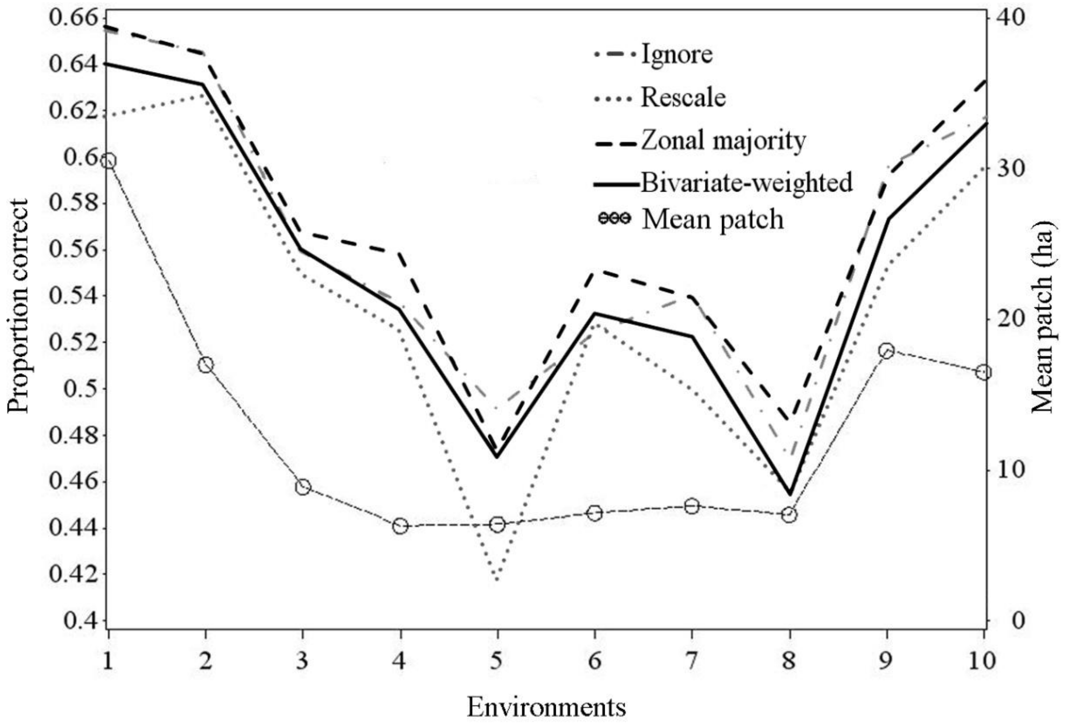


Figure 3. Proportion of estimated locations correctly classified across categorical covariates for each technique of incorporating telemetry error by virtual environment. Mean patch size of each virtual environment is portrayed as a second y-axis.

Similar to the virtual environments, patch size influenced performance in the elk data. At the smallest patch size (1 ha), ignore (0.30 accuracy) outperformed the other error techniques (0.10 to 0.28 accuracy; Figure 4c). Consistent with the results from the virtual environments, the bivariate-weighted technique outperformed other techniques as patch size increased (Figure 4d). Specifically, bivariate-weighted produced higher accuracy estimates than the other techniques when patches sizes were >39 ha (Figure 4c). Logarithmic modeling for the bivariate-weighted technique indicated that this approach was accurate (1.00) at patch sizes >1,521 ha (Figure 4d). My results for the elk data verify the trends in technique performance observed from the virtual environments, i.e., that none of the error techniques are accurate at patch sizes that are commonly used to map habitat classes.

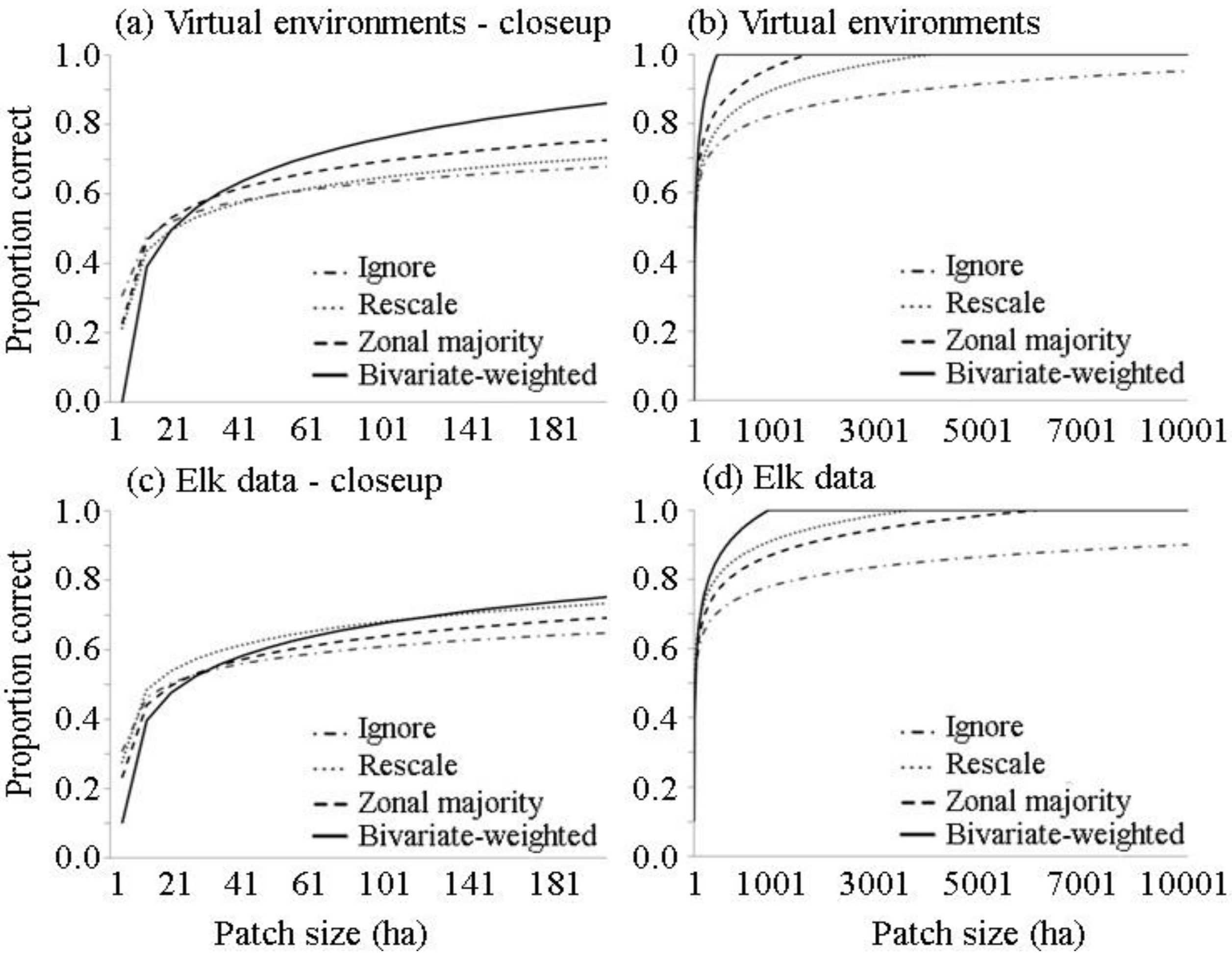


Figure 4 Trends in accuracy with increasing patch size for the categorical covariates as represented by averaged logarithmic models for virtual environment (n = 10) patch sizes (a) 1–201 ha and (b) 1–10,001 ha, and as represented by the logarithmic model for Custer State Park elk data for patch sizes (c) 1–201 ha and (d) 1–10,001 ha.

Continuous Data

The best performing techniques for addressing positional error on continuous data across the virtual environments were ignore (MAD = 104 m) and zonal mean (MAD = 105 m), followed by bivariate-weighted (MAD = 107 m), zonal majority (MAD = 130 m), and rescale (MAD = 140 m; Table 2). The environment was less influential on the average accuracy of telemetry error technique (Figure 5) than I observed for categorical data (Figure 3), indicating that spatial characteristics (e.g., gradients in distance measures) of the individual virtual environments had less influence on technique performance. My analysis indicated that continuous covariate value assignment was ≥104 m in error of the true covariate value across the virtual environments. In Custer State Park the ignore technique was again the top performer with 105 m of error, followed by bivariate-weighted (MAD = 108 m), then zonal mean (MAD = 126 m). Zonal majority and rescale were tied with 139 m of error.

Table 2. Descriptive statistics of the mean absolute difference (MAD) between true and estimated values for the virtual continuous covariates (representing distance in [m] in my analysis) and the elk data collected in Custer State Park. I present SD values and 95% confidence intervals for the replicated virtual environments (*n* = 10).

	Virtual environments *n* = 10			**Elk data**
Technique	**MAD**	**SD**	**95% CI**	**MAD**
Ignore	104	3.3	102.0-106.0	105
Rescale	140	5.0	137.1-143.3	139
Zonal majority	130	4.8	127.3-133.3	139
Zonal mean	105	3.5	102.7-107.1	126
Bivariate-weighted	107	3.1	105.3-109.1	108

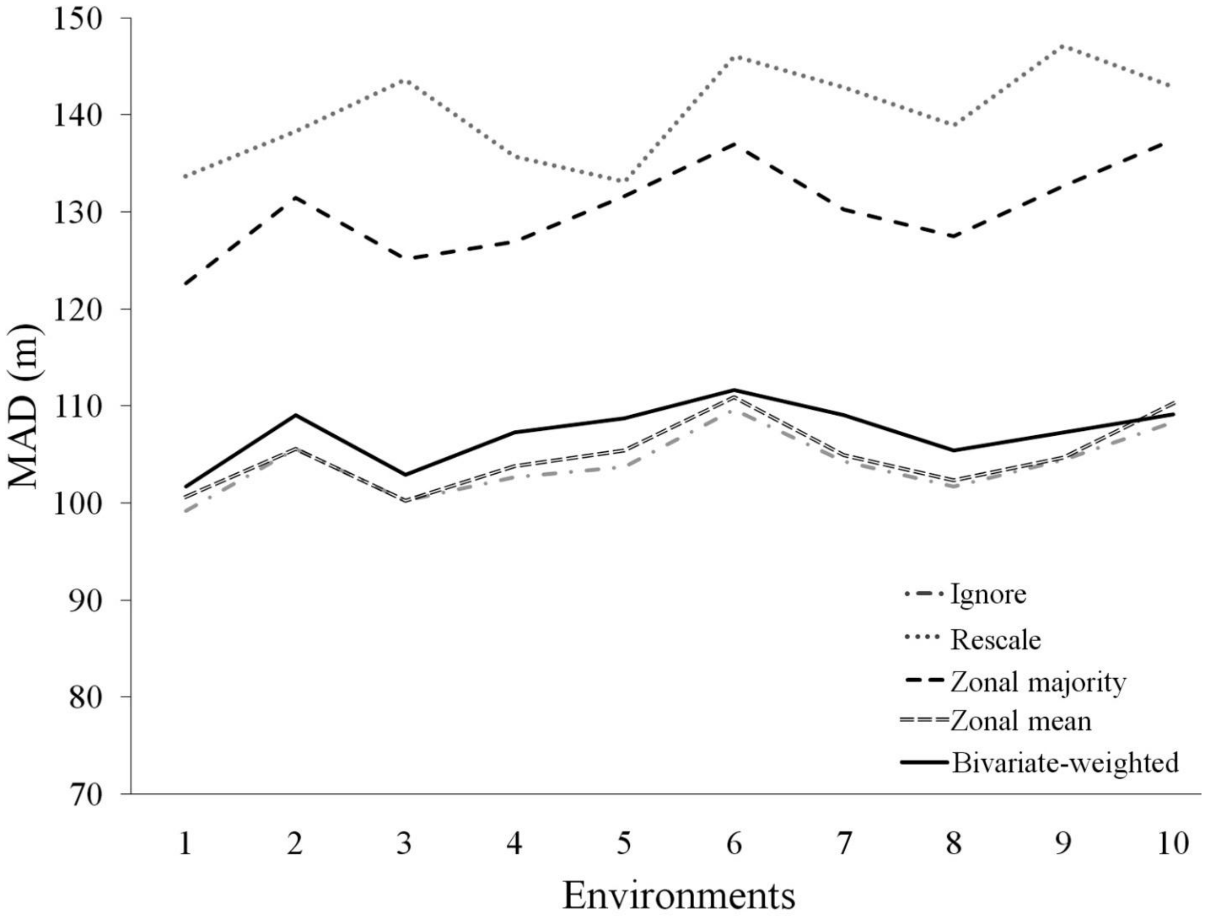


Figure 5. Mean absolute differences (MAD) among telemetry error techniques between true values and estimated values for continuous covariates by virtual environment.

DISCUSSION

Variation in environmental patchiness can substantially influence resource use studies that rely on telemetry data (Samuel and Fuller 1994). Consistent with my findings, smaller patches increase the likelihood of misidentification (Findholt et al. 1996). When analyzed across multiple patch sizes, the ignore technique performed best at smaller patch sizes. In my study, patch sizes needed to be substantially larger (50× virtual landscape, 160× for elk landscape) than the mean error polygon to be completely accurate. Due to inherent error associated with telemetry data, it is doubtful that resource use studies can be accurate except in situations where patches consistently encapsulate the telemetry error polygon (Saltz 1994, Rettie and McLoughlin 1999). However, this generality overlooks the tendency of some wildlife species to purposefully position themselves near patch edges. My results indicate that patch sizes must be large and blocky enough so that the potential for inclusion of multiple landcover categories within the error polygon is low. I caution that my simulated patch shapes tended to be blocky and thus poor representations of cover types that are long and linear (e.g., riparian areas). However, I expect accuracy to be lower in less blocky patches and my results likely portray optimistic accuracy estimates.

Continuous covariate data are commonly used in wildlife resource use modeling (e.g., Mladenoff et al. 1995, Ager et al. 2003). My analysis demonstrated that when telemetry data are imprecise the best technique was ignore (Table 2). I showed that the commonly used techniques for incorporating telemetry error into wildlife resource use models do not produce accurate results when telemetry error was approximately 6× the size of my continuous covariate resolution (mean telemetry error = 174 m, spatial resolution = 30 m). I hypothesize that the ratio between telemetry error and covariate resolution has direct implications for defining the spatial bounds of inference for telemetry-based wildlife resource use studies. For example, in the virtual simulations inference on biological processes operating <104 m from a linear feature would not be appropriate. I contend that telemetry studies with imprecise telemetry data relative to continuous covariate data resolution cannot accurately detect small scale wildlife responses (Roloff et al. 2009).

Our inability to reliably characterize wildlife resource use when telemetry data are imprecise leads us to question how best to evaluate wildlife resource use with telemetry data. Some have suggested removing locations with unacceptable error from the analysis (Saltz and

Alkon 1985, Kenward 1987, White and Garrott 1990). This approach decreases model power (Nams 1989, McKelvey and Noon 2001) and potentially biases the analysis in favor of those areas or landscape locations that tend to produce low telemetry error (e.g., unvegetated areas, flat areas; Rettie and McLoughlin 1999). I have identified 2 methods that show promise for using imprecise telemetry data to characterize wildlife-habitat relationships. The first method is a hierarchical model, or state-space model (Cressie et al. 2009), that does not try to attach covariate values but rather works directly with a likelihood that includes measurement error. This approach has been used by Johnson et al. (2008*b*) for pure movement models but has not yet been adapted to handle covariates. The second method incorporates telemetry error into a utilization distribution (UD) or kernel home range (Quinn 1995, Cox et al. 2006, Hebblewhite and Merrill 2007, Land et al. 2008, Rittenhouse et al. 2008). The UDs map the probability of an animal occurrence in space (Kernohan et al. 2001, Millspaugh et al. 2006). Moser and Garton (2007) found that when sample sizes are large, telemetry error is not likely to have a negative effect on fixed kernel density estimates. After a UD is generated, covariate assignment to locations is based on all raster cells that intersect the UD for species with smaller home ranges (e.g., Marzluff et al. 2004) or a random or systematic sample for species with large home ranges. Researchers should strive to use the maximum number of cells encompassed by the UD, but processing times for species with large home ranges may warrant a sampling approach.

MANAGEMENT IMPLICATIONS

I caution that my results are unique to the telemetry precision, patch spatial characteristics, and data resolution used to inform my analysis. My work demonstrates the importance of understanding the interaction between telemetry error and how habitat covariates are classified and mapped. When telemetry data are imprecise, models derived from covariates assigned to animal locations are suspect. Most telemetric-based wildlife studies are designed to minimize locational error but field conditions often result in errors ranging from tens to hundreds of meters (both VHF and GPS systems; Ills et al. 1986; Moen et al. 1996, 1997; Coulombe et al. 2006). As such, researchers must incorporate locational imprecision into resource use analyses. For categorical data, the ignore technique outperformed other error techniques at smaller patch sizes (i.e., <40 ha). However, I caution the use of ignore (and the other error techniques) because accuracy is low for small patches. Similarly, accurate assignment of continuous covariate data values is difficult when telemetry data are imprecise and I caution researchers against inferring fine scale ecological relationships without understanding data reliability. The importance of collecting precise telemetry data and quantifying telemetry error in support of wildlife resource use studies cannot be overstated. I recommend that researchers and managers evaluate their telemetry and covariate data using the methods I described to better understand limitations on inference.

CHAPTER 2

IMPLICATIONS OF IGNORNING TELEMETRY ERROR ON INFERENCE IN WILDLIFE RESOURCE USE MODELS

ABSTRACT

Global Positioning System (GPS) and very high frequency (VHF) telemetry data redefined the examination of wildlife resource use. Researchers collar animals, relocate those animals over time, and utilize the estimated locations to infer resource use and build predictive models. Precision of these estimated wildlife locations, however, influences the reliability of point-based models with accuracy depending on the interaction between mean telemetry error and how habitat characteristics are mapped (categorical raster resolution and patch size). Telemetry data often foster the assumption that locational error can be ignored without biasing study results. I evaluated the effects of mean telemetry error and categorical raster resolution on the correct characterization of patch use when locational error is ignored. I found that the ability to accurately attribute patch type to an estimated telemetry location improved non-linearly as patch size increased and mean telemetry error decreased. Furthermore, the exact shape of these relationships was directly influenced by categorical raster resolution. Accuracy ranged from 100% (200-ha patch size, 1−5-m telemetry error) to 46% (0.5-ha patch size, 56−60-m telemetry error) for 10-m resolution rasters. Accuracy ranged from 99% (200-ha patch size, 1−5-m telemetry error) to 57% (0.5-ha patch size, 56−60-m telemetry error) for 30-m resolution rasters. When covariate rasters were less resolute (30-m vs 10-m) estimates for the ignore technique were more accurate at smaller patch sizes. Hence, both fine resolution (10-m) covariate rasters and small patch sizes increased probability of patch misidentification. My results help frame the scope of ecological inference made from point-based wildlife resource use models. For instance,

to make ecological inferences with 90% accuracy at small patch sizes (≤5 ha) mean telemetry error ≤5 m is required for 10-m resolution categorical rasters. To achieve the same inference on 30-m resolution categorical rasters, mean telemetry error ≤10 m is required. I encourage wildlife professionals creating point-based models to assess whether reasonable estimates of resource use can be expected given their telemetry error, covariate raster resolution, and range of patch sizes.

INTRODUCTION

Technological advancements in telemetry systems and remote sensing have increased the spatial and temporal resolution of ecological data and theoretically improved our ability to infer wildlife habitat relationships (Cagnacci et al. 2010). Point-based models, which can rely upon the intersection of telemetry data and remotely sensed categorical covariate data, often provide the basis for constructing wildlife resource selection functions (e.g., Atwood et al. 2009, Chetkiewicz and Boyce 2009, Long et al. 2009, Houle et al. 2010). These functions use estimated wildlife locations to portray animal behavior, animal movement, and resource use (Frair et al. 2005, Hebblewhite and Haydon 2010, Merrill et al. 2010, Morales et al. 2010). There is an expectation that greater spatial and temporal resolution of telemetry and covariate data should translate into improved resource selection functions, however, telemetry and covariate error can substantially affect the probability of correctly assigning a covariate value to an estimated wildlife location (Goodchild 2003, Stehman et al. 2003, Montgomery et al. 2010). As such, using imprecise telemetry data as the basis for resource selection functions can negate benefits derived from utilization of more resolute covariate data.

Telemetry data are subject to variations in precision as a result of topography (Gantz et al. 2006), weather (Hupp and Ratti 1983, Moen et al. 1997), animal movement (Schmutz and White 1990, Moen et al. 2001), technology (Carrel et al. 1997, Hebblewhite et al. 2007), and canopy cover (Dussault et al. 1999). Telemetry error is expressed through spatial differentiation of the estimated wildlife location and the true wildlife location (Heezen and Tester 1967). This difference between estimated and true can be tens to thousands of meters in the case of very high frequency (VHF) data (White 1985, Nams and Boutin 1991) and is commonly <100 m in the case of Global Positioning System (GPS) data (though <12 m is obtainable with 3-dimensional fixing; Rempel et al. 1995, D'Eon et al. 2002, Cargnelutti et al. 2007). Telemetry error is problematic because it increases the probability of misidentifying resource use, leading to errors in statistical inference (Garton et al. 2001, Kenward 2001, Johnson and Gillingham 2008, Frair et al. 2010).

The importance of quantifying, reporting, and incorporating telemetry error into wildlife resource use studies has been widely noted (Lee et al. 1985, Saltz 1994). Quantification of error commonly occurs when transmitters are placed in known locations throughout a study area and relocated in conditions that are representative of the overall sampling design (White 1985, Garrott et al. 1986, White and Garrott 1990). This process is repeated over time, the difference between true and estimated locations is measured, and these measures are averaged to produce a mean telemetry error (Rempel et al. 1995, Withey et al. 2001). Several techniques have been developed to explicitly incorporate telemetry error into wildlife resource use models. These techniques include ignoring the error (Robel et al. 1970, Wallestad 1971), rescaling the covariate data to match the mean error (Koehler and Hornocker 1989, Telesco and Van Manen 2006), calculating a zonal mean (Dickson and Beier 2002) or a zonal majority (Mace et al. 1996, 1999) of the covariate values that intersect with the mean error polygon, or weighting the covariate values inside of the error polygon by the bivariate normal distribution (McKelvey and Noon 2001, Findholt et al. 2002, Copeland et al. 2007). Montgomery et al. (2010) evaluated the accuracy of these techniques and determined that when telemetry data are imprecise ($\bar{x}$ error = 174 m, SD = 130 m) none could reliably characterize true wildlife resource use at scales commonly used by managers (i.e., tens of hectares).

Recent improvements to GPS and VHF telemetry systems have resulted in more precise estimates of wildlife locations (Cagnacci et al. 2010, Hebblewhite and Haydon 2010). Precision of these telemetry data often exceed the resolution and accuracy of conventional covariate data (Urbano et al. 2010). The perception of high precision in estimated wildlife locations and remotely sensed covariate data often foster the assumption that telemetry error can be ignored without analytical consequence (see Springer 1979, Hupp and Ratti 1983, Saltz 1994, Nams 1989, Whithey et al. 2001). This assumption fails to consider the complex interactions between telemetry error, animal movement or behavior, and how environmental characteristics are described and mapped; namely the resolution and patch configuration of categorical rasters.

Montgomery et al. (2010) found that ignoring telemetry error was the most accurate technique for characterizing wildlife resource use at small patch sizes ($\leq$1 ha), though accuracy was <31%. Given that the ignore technique is commonly used by wildlife biologists, and that it most accurately characterizes habitat use at small patch sizes when telemetry data are imprecise (Montgomery et al. 2010), I sought to better understand the relationship between telemetry error and patch size using the ignore technique. My goal was to examine the ramifications on inference for resource use models that depend upon the intersection of point-based wildlife locations and categorical covariate data. Within this context I 1) quantified accuracy of patch identification using the ignore technique for a range of telemetry errors and patch sizes and 2) evaluated how categorical raster resolution influences the accuracy relationship between telemetry error and patch identification.

METHODS

I conducted my analysis by generating virtual environments in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA). I reviewed 100 scientific studies of terrestrial wildlife resource using telemetry data to guide the selection of a virtual study area size. These articles were published in 15 peer-reviewed journals since 1995 with most from the *Journal of Wildlife Management* (n = 75; Montgomery et al. 2010). The median study area size (560 km^2) from this review defined the extent of my virtual environment (Figure 6a). I subsequently generated (n = 10) categorical rasters at a resolution of 10 m (Figure 6b) and another set (n = 10) at a resolution of 30 m (Figure 6c), consistent with categorical raster resolutions commonly used in wildlife resource use studies (e.g., Boyce et al. 2003, Fortin et al. 2005, Rittenhouse et al. 2010). Each categorical raster had unique patch characteristics (Table 3) created using a 2-step process. I first generated a random raster in ArcGIS by controlling the mean values of a Poisson distribution, which ensured a separate and distinct configuration of cells for each raster. I then utilized a suite of tools from the Spatial Analyst extension (boundary clean, majority filters, and expand filters) to merge neighboring cells into patch types (see Montgomery et al. 2010).

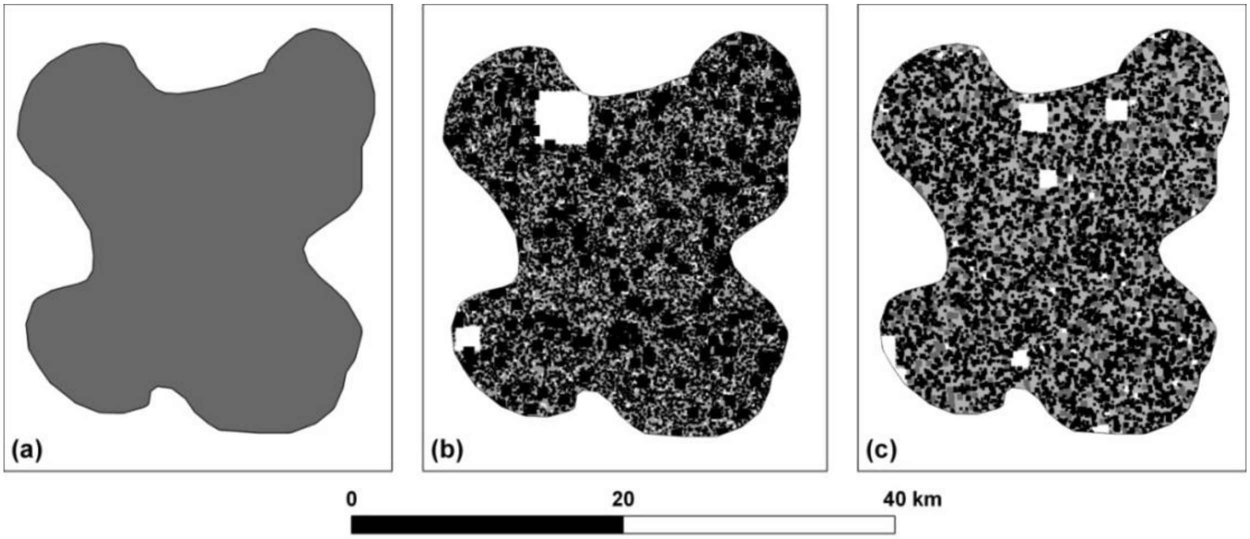


Figure 6. Example of a virtual environment and categorical rasters created for evaluating the effects of telemetry error on assigning habitat patches to telemetry locations; (a) outline of the virtual environment with an area of 560 km2 (b) a categorical raster (1 of 10) at the 10-m resolution (c) a categorical raster (1 of 10) at the 30-m resolution.

Table 3. Patch characteristics for categorical rasters created at 10-m and 30-m resolution.

Resolution	Categorical raster	Patch count	Patch size (ha) Min.	Max.	$\bar{x}$	SD
10-m	1	14,042	0.01	281.82	4.08	11.41
	2	5,238	0.01	1,450.33	10.94	43.54
	3	18,847	0.01	7,207.16	3.04	66.31
	4	25,275	0.01	2,094.63	2.27	32.81
	5	539,840	0.01	17.26	0.11	0.30
	6	17,263	0.01	3,874.07	3.32	58.93
	7	1,082	0.01	5,104.68	52.94	302.15
	8	24,769	0.01	6,114.33	2.31	46.53
	9	17,010	0.01	9,088.07	3.37	113.72
	10	112,466	0.01	6,127.02	0.51	18.70
30-m	1	1,875	0.09	741.78	30.55	60.70
	2	3,367	0.09	1,393.38	17.01	51.66
	3	6,438	0.09	3,066.84	8.90	78.50
	4	9,097	0.09	1,452.60	6.30	36.86
	5	8,939	0.09	700.56	6.41	18.20
	6	8,006	0.09	857.25	7.16	25.82
	7	7,514	0.09	7,042.86	7.62	92.55
	8	8,140	0.09	413.82	7.04	15.38
	9	3,190	0.09	8,347.23	17.96	153.60
	10	3,468	0.09	1,369.89	16.52	55.95

I evaluated 36 mean telemetry errors ranging from 3.5 m to 60 m for 10-m and 30-m resolution categorical rasters. I chose this range of telemetry precision to mimic the locational error often produced by sophisticated telemetry systems and because I previously showed that highly imprecise telemetry data are of limited value for predicting small-scale habitat use (Montgomery et al. 2010). I randomly distributed 1,000 true wildlife locations per categorical raster and subsequently paired each true location to an estimated location. Estimated locations were drawn from a circular bivariate normal distribution centered on the true location, resulting in a higher probability of estimated locations being closer to the true location (Montgomery et al. 2010). Mean telemetry error was controlled by the variance parameter of the bivariate normal. I intersected true and estimated locations with the categorical rasters and assigned patch type and patch size to each location. I quantified accuracy by calculating the proportion of points correctly classified for each categorical raster. This approach resulted in patch identification accuracies for each mean telemetry error at discrete patch sizes for each categorical raster.

To examine accuracy across all mean telemetry errors and patch sizes by categorical raster resolution (i.e., 10 m, 30 m), I modeled accuracy (ordinate) against patch size (abscissa) as a logarithmic function (general form $E[y] = \beta_0 + [\beta_1 \times Log10(Patch\ Size)]$). I modeled each combination of telemetry error and categorical raster and averaged estimated beta coefficients across all corresponding categorical rasters (n = 10 for each telemetry error) by raster resolution. This process resulted in 36 averaged logarithmic functions, one for each unique telemetry error that I evaluated per raster resolution. Based on similarities in model coefficients for sequential telemetry errors I aggregated the results into telemetry error bins for presentation purposes. Hence, each bin consisted of averaged estimated beta coefficients from 3 mean telemetry errors (e.g., 11-15-m bin included results from 11 m, 13 m, and 15 m).

RESULTS

Patch shapes in the virtual environments tended to be blocky (Figure 6b,c), an artifact of the raster generation process. For 10-m resolution rasters, the number of patches in the virtual environments ranged from 1,082 to 539,840 and average patch sizes ranged from 52.94 ha to 0.11 ha (Table 3). Patch counts for the 30-m resolution rasters ranged from 1,875 to 9,097 with corresponding mean patch sizes of 30.55 ha and 6.30 ha (Table 3). Average patch sizes were highly variable, with standard deviations ≥2 times the means (Table 3). Thus, the virtual environments included both fine- and coarse-grained patches consistent with the range of patch sizes often observed in wildlife resource use studies.

As patch size increased, correct identification of patch use increased nonlinearly (Figure 7). In contrast, as telemetry error increased, the ability to accurately assign patch use decreased nonlinearly (Figure 7). Also, the form of these relationships depended on categorical raster resolution. Coarser rasters (i.e., 30-m) resulted in higher accuracies at smaller patch sizes over all telemetry errors examined (Figure 7). With small telemetry errors (1−5-m) accuracy was consistently high (>0.90) across all patch sizes (Tables 4, 5).

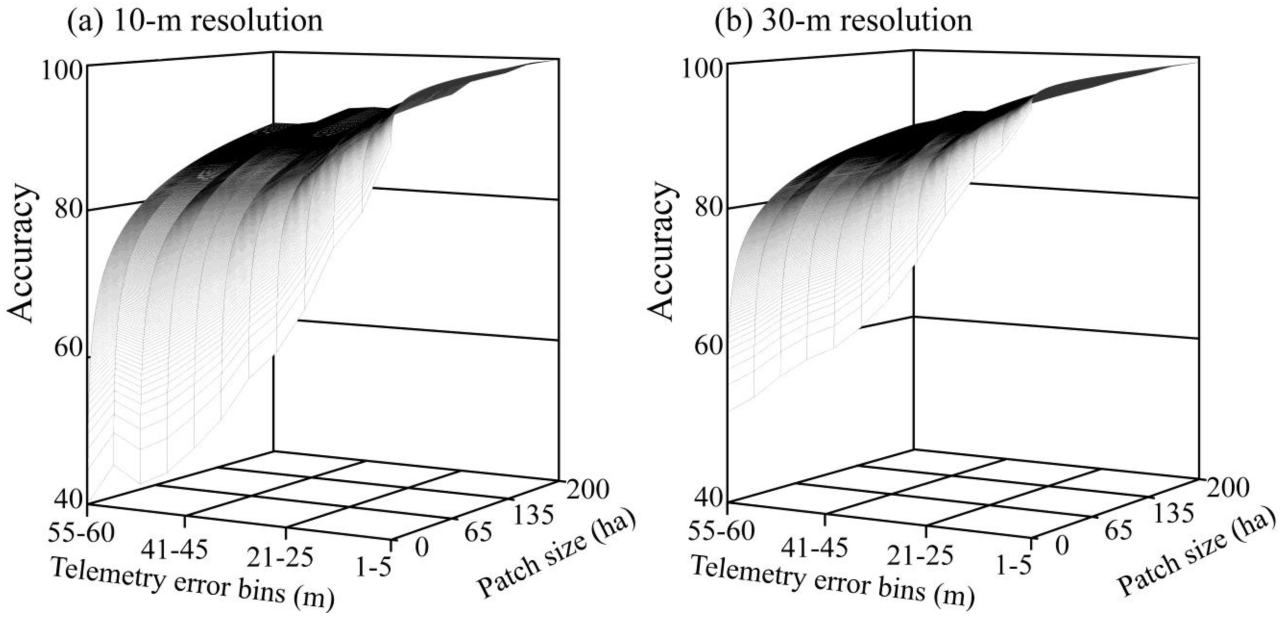


Figure 7. Trends in accuracy for telemetry error bins and patch size. (a) 10-m resolution categorical rasters and (b) 30-m resolution categorical rasters.

These results should allow researchers to identify an acceptable level of accuracy based on the mean telemetry error and patch size inherent to their analysis. For example, to make inferences on use of small patches (≤5 ha) with 90% accuracy, telemetry error ≤5 m is required for the 10 m categorical raster (Table 4) and telemetry error ≤10 m is required for the 30 m categorical raster (Table 5). If >70% accuracy is deemed acceptable, telemetry error ≤20 m and ≤30 m is required for 10-m and 30-m covariate surfaces, respectively (Tables 4, 5). My results indicate that accuracy declines quickly for patch sizes <20 ha and also for mean telemetry errors >20 m for the 10-m categorical rasters (Figure 7a). Accuracy declines quickly for patch sizes <10 ha and also for mean telemetry errors >30 m for the 30-m categorical rasters (Figure 7b). These results highlight the importance of quantifying and reporting both telemetry error and patch sizes for categorical rasters and using that information to limit the scale of ecological inference to those patch sizes with some minimum acceptable accuracy.

Table 4. Accuracy (%) of patch identification for telemetry error bins across a variety of patch sizes I evaluated on categorical rasters created at a 10-m resolution. These accuracies portray the ability of estimated locations to correctly characterize true locations at discrete patch sizes.

	Telemetry error bins (m)											
Patch size (ha)	1-5	6-10	11-15	16-20	21-25	26-30	31-36	37-40	41-45	46-50	51-55	56-60
0.5	92	84	80	73	67	64	58	55	52	50	52	46
1	93	86	82	76	70	67	62	59	56	54	56	51
2	94	88	84	78	73	71	66	64	61	59	60	56
3	95	89	85	80	75	73	69	66	64	62	63	59
4	95	90	86	81	77	74	70	68	66	64	65	61
5	95	90	87	82	78	75	71	69	67	65	66	63
10	96	92	89	85	81	78	75	74	72	70	70	68
20	97	94	91	88	84	82	79	78	76	74	75	73
30	98	95	92	89	86	84	81	80	79	77	77	76
40	98	95	93	91	87	85	83	82	81	79	79	78
50	98	96	94	92	88	86	84	84	83	81	81	79
100	99	98	96	94	91	90	88	88	87	85	85	84
200	100	99	98	97	94	93	92	92	92	90	89	89

Table 5. Accuracy (%) of patch identification for telemetry error bins across a variety of patch sizes I evaluated on categorical rasters created at a 30-m resolution. These accuracies portray the ability of estimated locations to correctly characterize true locations at discrete patch sizes.

	Telemetry error bins (m)											
Patch size (ha)	1-5	6-10	11-15	16-20	21-25	26-30	31-36	37-40	41-45	46-50	51-55	56-60
0.5	96	91	88	83	77	73	69	66	65	62	59	57
1	96	92	89	85	79	76	72	69	68	66	63	61
2	97	93	90	86	82	78	75	72	71	69	66	65
3	97	93	91	87	83	80	76	74	73	71	68	67
4	97	94	91	88	84	81	78	75	74	72	70	68
5	97	94	91	88	84	82	78	76	75	73	71	69
10	98	95	93	90	86	84	81	79	78	77	75	73
20	98	96	94	91	88	87	84	82	81	80	78	77
30	98	96	94	92	90	88	86	84	83	82	80	79
40	98	97	95	93	90	89	87	85	84	83	82	80
50	99	97	95	93	91	90	88	86	85	84	83	82
100	99	98	96	95	93	93	91	89	88	88	86	85
200	99	99	97	97	95	95	93	92	91	91	90	89

DISCUSSION

During the early years of wildlife VHF telemetry quantification of telemetry error rarely occurred (Nams 1989). The importance of quantifying telemetry error was later emphasized (Lee et al. 1985, White and Garrott 1990) and a suite of methods were developed to explicitly incorporate telemetry error into models of wildlife resource use (Mace et al. 1996, Dickson and Beier 2002, Findholt et al. 2002, Telesco and VanManen 2006, Copeland et al. 2007). The more recent application of GPS technology to wildlife biology has generally resulted in the same sequence of events. The power of GPS technology that enables researchers to remotely examine relatively precise estimates of wildlife locations (Hebblewhite and Haydon et al. 2010) has again contributed to the idea that telemetry error can be ignored without analytical consequences. My study demonstrates that regardless of telemetry system precision, ignoring telemetry error when quantifying resource use from categorical rasters can lead to error in patch identification. My study clearly shows that telemetry error, patch size, and categorical raster resolution interact to inform the scale of defensible inference.

Accuracy in assigning wildlife resource use to a categorical habitat covariate depends on the magnitude of telemetry error and characteristics of the raster (i.e., resolution and patch sizes). A positive nonlinear relationship exists between accuracy and patch size, with telemetry error becoming less relevant at larger patch sizes (i.e., >200 ha). Unfortunately, wildlife professionals often make habitat management decisions at considerably smaller scales (i.e., tens of hectares) and thus, resource selection functions that are accurate only at large scales are of limited utility. I encourage quantitative ecologists to scrutinize the relationship between telemetry error, patch sizes of categorical rasters, and covariate resolution to identify a minimum patch size below which reliable inference cannot be drawn. I note that there was always classification error (from

4 to 8%) with the smallest patches I evaluated (<0.5 ha), even for the finest telemetry error (telemetry error bin = 1−5-m), a level of telemetry precision seldom observed even in the most advanced GPS systems. This persistent misclassification likely prevents accurate characterization of wildlife use in small (McLoughlin et al. 2002, McKenzie et al. 2009) or rare habitat patches (Frair et al. 2010). Inability to detect the importance of these patch types could lead to conservation and management strategies that fail to protect the full range of habitats used by a particular species.

I caution that accuracy estimates in this analysis are likely overestimates. I attribute this bias to the lack of linear features in the categorical rasters. McKenzie et al. (2009) found that telemetry error leads to underestimating use of linear features (e.g., roads, riverine habitats) by increasing the probability of Type I errors. Linear patch configurations are common to many natural ecosystems but difficult to simulate in a virtual environment (White and Garrott 1986, Montgomery et al. 2010) and hence my results should be viewed optimistically.

I note that my analysis examined the effects of telemetry error on categorical rasters exclusively. Thus, accuracy was binary with the estimated location either matching or not matching the covariate value of the true location. An emerging area of wildlife resource use studies converts categorical data to continuous metrics, which alleviate the challenges of working with discrete data (Alldredge and Dasgupta 2003, Conner et al. 2003, Alldredge and Griswold 2006). Under a continuous data scenario, estimated wildlife locations no longer intersect covariate categories, but rather a quantitative measure (e.g., distance) is assigned to the location. This approach does not remove error from the analysis but it does allow for quantification of error effects in measurable units (Montgomery et al. 2010).

My analysis provides further evidence that results from point-based estimation of wildlife resource use can be questionable (Johnson and Gillingham 2008, McKenzie et al. 2009, Montgomery et al. 2010). Montgomery et al. (2010) advocated for the use of area-based techniques to help ameliorate the effects of telemetry error. Various home range estimators (e.g., minimum convex polygons, kernel density, and utilization distributions) are largely impervious to the effects of telemetry error (Moser and Garton 2007). I encourage researchers to further develop innovative techniques for modeling wildlife resource use through the application of area-based estimators (see Marzluff et al. 2004, Millspaugh et al. 2008) or likelihood-based methods with models that incorporate telemetry error (see Johnson et al. 2008a, Hooten et al. 2010).

I found that resolution of categorical rasters substantially affected the accuracy of assigning a covariate value to an estimated wildlife location. Others have suggested that the relationship between telemetry error and resolution needs to be examined to understand the effect of raster resolution on model accuracy (Frair et al. 2010, Urbano et al. 2010). I demonstrated that telemetry systems were more accurate for coarser resolution rasters (30-m versus 10-m) likely because the minimum patch size (i.e., minimum mapping unit) is determined by the resolution (landscape grain) of categorical rasters (Turner et al. 2001). Inherently, a 10-m resolution categorical raster has smaller patch sizes than a 30-m resolution categorical raster, and smaller patch sizes increase the probability of misidentifying resource use (Samuel and Kenow 1992, Findholt et al. 1996, Montgomery et al. 2010). This result does not suggest that rescaling covariate surfaces is a wise option (see Montgomery et al. 2010), but it does suggest that finer resolution covariate surfaces are not inherently better. When the scale of the categorical raster exceeds the precision of the estimated wildlife locations misidentification of resource use is compounded.

My results and the methodologies I presented depend on telemetry errors that exhibit a bivariate normal distribution. When sufficient sampling is conducted, telemetry errors are thought to be bivariate normally distributed (Samuel and Kenow 1992, Jerde and Visscher 2005), though other distributions (e.g., uniform, Laplace) have also been observed and utilized in telemetry studies (Dickson and Beier 2002, McKenzie et al. 2009). Sufficient sampling of telemetry error includes an ample sample size (to estimate model parameters with adequate precision), collection of error data from portions of the landscape representative of the habitats the organism of interest uses, and collection of error data under appropriate canopy cover, weather, topographical, and technological conditions.

MANAGEMENT IMPLICATIONS

Categorical raster resolution and patch size interact with telemetry error to influence the accuracy of assigning covariate values to estimated wildlife telemetry locations. Telemetry errors up to 60 m will generally have >50% probability of being correct for all patch sizes, but accuracies >90% tend to be restricted to small telemetry errors (<10 m) or intermediate telemetry errors (>10 m and <36 m) at larger patch sizes (20−200 ha). I invite wildlife professionals to evaluate their telemetry studies using my results as a general guide. I advise against making small-scale inferences when patch identification accuracies are unacceptably low. I encourage wildlife professionals to acknowledge the inherent deficiencies in the logic of ignoring telemetry error and accept that Type I and Type II errors are common when the ignore technique is utilized on categorical rasters, regardless of telemetric precision. Wildlife professionals must continue to revise their ecological questions when faced with telemetry errors and justify their scale(s) of ecological inference (Cagnacci et al. 2010, Frair et al. 2010). I provided metrics and a replicable methodology by which researchers and managers can identify the relative accuracy of wildlife models given mean error of their telemetry system and the patch size characteristics of their study area. This approach will allow researchers and managers to adequately defend the methodologies that are utilized in their analysis and should lead to a more critical evaluation of the ecological question and the inferences that are possible.

CHAPTER 3

HABITAT SELECTION

INTRODUCTION

Habitat is a theoretical construct used to describe the living space of an organism. As such, habitat includes the suite of interacting abiotic (e.g., weather, soils, topography, hydrology) and biotic (e.g., vegetation structure and composition, inter- and intra-specific competition, prevalence of diseases) elements that influence whether an organism uses a particular location. Habitat selection is the act of choosing the combination of available abiotic and biotic elements for the purpose of fulfilling the life history events of the organism (e.g., mating, raising young, and avoiding death). An organism's selection of habitat varies across space and time as certain needs are fulfilled and others pursued. The objective of habitat selection research is to describe why organisms use various combinations of environmental (abiotic and biotic) variables, an understanding of which informs population or species conservation. The concept of habitat selection can be extended to plants and fungi but animals are the most common research subject.

When discussing the concept of habitat selection it is important to differentiate among habitat use, habitat selection, and habitat preference because each concept has important management and conservation implications. Habitat use refers to organisms occurring in an area, not necessarily by choice. Habitat selection implies that an organism made a choice about occurring in a particular location, i.e., the organism had multiple options and for some reason (presumably to efficiently satisfy a life history event) chose to occur at a particular location. Habitat preference is applied at the species-level and refers to the habitat that the species prefers above all others, even if that habitat is unavailable in the landscape where a local population resides. Habitat preference is the most difficult concept to quantify because in most areas organisms are not free to choose among an unrestricted set of environmental variables. Thus, researchers tend to focus their efforts on quantifying habitat selection and use. Knowledge of preferred habitat may elude researchers because of the inability to comprehend the exact combination of environmental variables that would be selected if all were available. This reality has conservation implications which could potentially compromise organism, population, or even the species persistence into the future.

The origin of habitat selection research is based on the observation of animals by naturalists. One of the earliest documented naturalists was Aristotle who took a keen interest in animal-habitat associations (Morrison et al. 2006). Since Aristotle, both informally and formally trained naturalists and ecologists have studied how organisms use their environment. This was certainly of concern to 19th century naturalists who examined the morphology and relatedness of certain species as the basis for concepts like biogeography and speciation (Wallace 1876). These naturalists realized that the selection of habitat had important evolutionary ramifications (Darwin 1859). The interaction of an organism with habitat was later framed as the ecologic niche (Grinnell 1917). Niche theory developed into a research area unto itself with ecologists being principally concerned with how organism-habitat interactions shape fitness (Petren 2001).

The 20th century saw an expansion in research methodologies used to study habitat selection. The collective goal of these methodologies was to identify the location of organisms across spatial and temporal dimensions and to examine the environmental variables associated with those locations. Habitat selection research broadly consists of two phases; 1) documenting habitat used by an organism of interest and 2) making inferences on why habitat was selected (usually based on a comparison of habitat use and availability). The first step in quantifying habitat use is to map organism locations. Multiple techniques are used to locate organisms in space including direct visual observation, conducting visual or auditory surveys, using traps or other evidence of occurrence (i.e., scat, tracks, and carcasses), and telemetry technology. Each of these techniques results in animal location(s) that can be related to a suite of environmental variables which collectively define habitat. Once animals are located and the environmental variables of interest are measured, habitat selection can be quantified.

GLOSSARY

Habitat**:** An area where an organism resides comprised of abiotic and biotic elements.

Habitat selection: The act of choosing the combination of available abiotic and biotic elements for the purpose of fulfilling the life history events of the organism.

Environmental variables: Abiotic and biotic elements of an area including vegetation, soil, topography, species competition, geology, prevalence of diseases and hydrologic characteristics, among others. Habitat selection can be positively or negatively related to these environmental variables.

Habitat patch: A spatially contiguous area in which environmental variables are similar.

Hierarchical habitat selection: This concept recognizes that an organism's selection of habitat occurs at varying spatial and temporal scales. The scale at which different selections occur are ordered; First-order (habitat selections defining the species range), Second-order (selections defining the placement of an individual's home range within the species range), Third-order (within home range selections), and Fourth-order (fine-scale daily habitat selections).

MEASUREMENT OF ANIMAL LOCATIONS

Direct Visual Observation

Directly observing animals in their habitat is the oldest technique used to measure habitat selection. This process involves researchers following single or multiple animals through environmental space while making notations about the environmental variables that are used to satisfy various life history events (Figure 8a). Though visual observation might appear to be a relatively simplistic means of evaluating habitat use, increasingly complex methods of sampling have been employed in animal behavior research (Altmann 1974). Ad-libitum sampling, focal animal sampling, and all occurrence sampling are common direct visual observation techniques used to assign the location of an organism with the environmental variables that describe habitat.

Ad-libitum sampling is a form of visual observation where the researcher documents habitat use in an *ad-lib*, or opportunistic fashion. As such, ad-libitum sampling most aptly describes the technique used by early naturalists. A field notebook is commonly used to record environmental variables chosen by the organism of interest. This sampling scheme is notoriously difficult to quantify with reliability because of the opportunistic fashion in which the data are recorded. Thus this technique has been criticized for being more anecdotal than empirical (Altmann 1974, Mann 1999). However, ad-libitum sampling can be useful in pilot studies or in situations where a researcher is attempting to document the variety of environmental variables used by an organism over limited spatial and temporal dimensions (Altmann 1974).

Focal animal sampling involves the detailed observation of a single organism at specified intervals over a period of time. For instance, a researcher would identify an individual to observe and would follow that individual wherever it goes recording all behaviors, including environmental variables that are used. The researcher notes the type of behavior, the duration of the performed behavior, whether or not the behavior involved interactions with other individuals or organisms, and any other environmental variables that were used. This type of sampling would continue for a specified interval (e.g., 5 minutes, 15 minutes, 1 hour) at which point the researcher would break from recording data.

With all occurrence sampling, the researcher focuses on a specific behavior (such as selection of an environmental variable) and records any time that the behavior is performed throughout the sampling interval. This technique is widely employed in animal behavior research because it provides an estimate of occurrence rate for a particular behavior. With this sampling technique the researcher can estimate how often a particular food item is selected, for instance, or how often cover habitat is selected per unit of time. All occurrence sampling can be useful in determining the relative dependence that an organism has for a particular environmental variable.

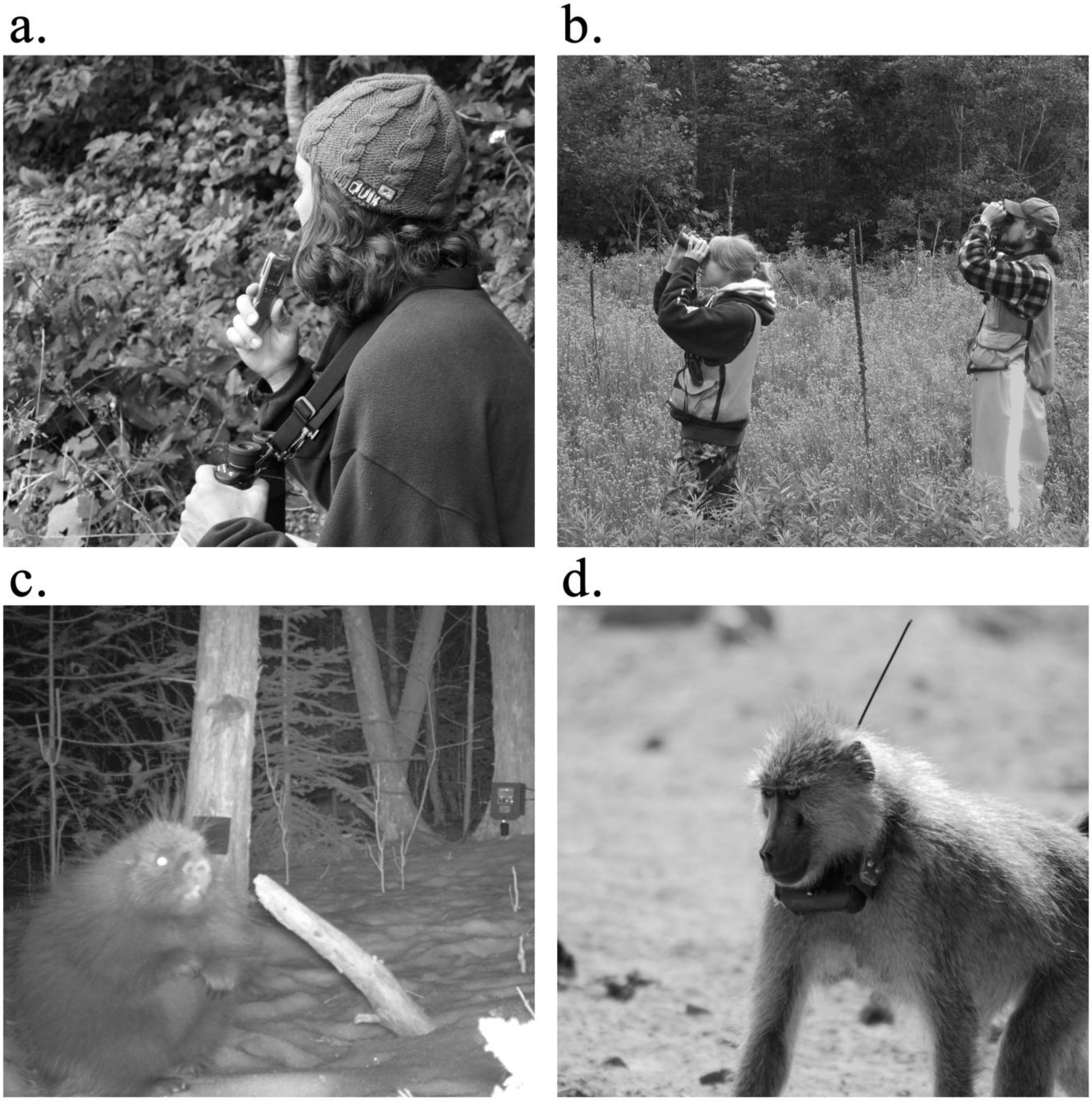


Figure 8. Four techniques used to locate organisms in environmental space, a.) direct visual observation, b.) visual surveys, c.) trapping (camera trapping), and d.) telemetry.

Visual and Auditory Surveys

Another set of research methodologies developed to identify the location of organisms in space at a particular time involves visual or auditory surveys (Figure 8b). Visual and/or auditory detection have been used to estimate species richness, produce population estimates, and characterize habitat selection. Several different methodologies exist but these can be categorized into two broad types; visual encounter surveys and auditory surveys.

Visual encounter surveys are widely utilized in ground, air, and ship-board capacities. In these cases the researcher scans the environment to visually identify individuals of the focal species. Various methods are used to conduct these surveys including line transects, randomized walk designs, and patch-based searches. Line transect surveys involve the designation of routes that researchers follow while searching for organisms (e.g., Otto and Roloff 2011). Typically, the researcher limits the sampling to an area where organisms can be reliably detected. In random walk surveys the researcher follows a random path, while searching for organisms, for a specified distance (e.g., Gregory et al. 2006). Upon reaching that distance, another random path is selected and followed after which the process is repeated. The advantage of this technique is that it can be an effective method for searching large areas, if the focal organism can be reliably observed. Patch-based surveys involve sampling all environmental variables within a given area. For example, if the goal of a survey is to identify birthing sites and the abundance and distribution of Hawaiian monk seals (*Monachus schauinslandi*) patch-based surveys would sample all beaches in the Hawaiian archipelago searching for females and their young during and directly after the pupping season (Baker and Johanos 2004).

To conduct an auditory survey the researcher relies on sounds to identify and locate different organisms or species. Auditory surveys are particularly useful for vocal organisms like some birds and amphibians and include point counts and calling surveys. When employing point count surveys a number of locations or stations are identified where the researcher remains stationary listening for calls (e.g., Ralph et al. 1993, Seavy et al. 2009). The researcher stays on station for a specific period of time, documenting species occurrence through auditory and in some cases visual detection. The stations are typically spread across several different environmental variables that are relevant to the species of interest. Calling surveys involve surveyors searching certain areas with the goal of detecting where different organisms reside. These surveys are predicated on the idea that there are spatial and temporal conditions where certain species vocalize. Frogs and toads are common subjects of calling surveys (Pellet and Schmidt 2005). The result of these surveys is the identification of environmental variables used by organisms of one or multiple species. These surveys are designed to detect organisms, assign organism locations, and associate organism locations to specific environmental variables.

Trapping and Other Evidence of Occurrence

Another technique used to measure animal locations in the environment involves trapping (Figure 8c). There are a wide variety of trapping methodologies that include, but are certainly not limited to, baited traps (e.g., Cypher et al. 2009), drift fences (e.g., Otto and Roloff 2011), and pitfall traps (e.g., Müller and Brandl 2009) that restrain animals so their presence, abundance, and location can be documented. Trapping can also be done in non-invasive fashions through the collection of images (photographs or video; e.g., Soisalo and Cavalcanti 2006, Thorn et al. 2009) or DNA (hair snares; e.g., Gardner et al. 2010). Trapping designs can include a grid, transect, or web network of traps, with traps spaced accordingly to increase the probability of detecting organisms (i.e., spacing based on home range size or known movement patterns). Like direct visual observation and visual or auditory surveys, trapping techniques can be used to associate organism locations with environmental variables on the landscape.

There are some concerns with trapping. With baited traps, in particular, it is possible that certain organisms will become conditioned to and potentially attracted to the trap. Within this context, study results would be biased if the researcher is repeatedly capturing the same individual or a cohort of individuals that are vulnerable to trapping. Conversely, if organisms associate a negative experience with being trapped, they may purposefully avoid traps and similarly bias study results. Furthermore, if multiple species are captured in the same trap it is possible to have competition and predation events where the presence of one species is being masked because it is consumed by another species. For example, it is Ill known that some species, such as shrews (family *Soricidae*) and opossums (family *Didelphidae*), will prey upon other animals and insects captured in the same trap (Jurzenski and Hoback 2011).

Researchers are increasingly using non-invasive techniques such as motion-activated cameras to photographically *capture* organisms or hair snares to collect DNA samples (Cutler and Swann 1999, Gardner et al. 2009; Figure 8c). The design of camera traps is quite similar to the aforementioned trapping procedures. Cameras are placed in a variety of environmental variables throughout the study area with the intention of documenting species occurrence or to produce population abundance estimates using mark-recapture on individuals. Individual identification of organisms is possible through visual acuity or with computer software programs which assist in the recognition of pelage patterns, markings, and other morphological characteristics specific to individuals. These methods effectively eliminate the necessity of restraining organisms and have the benefit of non-invasively documenting organism-habitat associations, although baited camera and hair snare traps are subject to the same biases described in the preceding paragraph for other baited trapping approaches.

Several additional techniques can be used to identify the position of organisms in space. These include locations where evidence of organism presence persists including scat, tracks, and carcasses, among others. In these cases researchers are generally interested in describing specific life history events and collect data to describe those events. For instance, a researcher may be interested in quantifying the environmental variables that are characteristic of areas where organisms are subject to predation. All areas in the study can be searched in opportunistic or structured fashions to identify predator-killed carcasses (Kauffman et al. 2007, Bump et al. 2009). Once located, carcass sites can be associated with different environmental variables to determine the abiotic and biotic elements that correlate with predation events.

Increasingly complex forms of collecting organism locations are continually employed in habitat selection research. Remote sensing, satellite imagery, and infrared technology are now being used to study habitat selection in new and interesting ways. For instance, to document the distribution and abundance of harbor seals (*Phoca vitulina*) researchers are using aircraft fit with infrared technology to locate heat signatures of seals on ice flows (London and Richmond 2010). This technology enables researchers to cover vast areas with increased reliability in the estimates of organism-habitat associations. Radar technology, typically used for describing the weather, is now being used to map concentrations of migratory birds (Bonter et al. 2008). Large concentrations of birds at stopover sites along migratory pathways are viewed as selection for the environmental variables that coincide with these aggregations.

Telemetry

Both VHF and Global Positioning System (GPS) telemetry depend on fitting an organism with a tag that transmits a signal and relocating that tag across space and time. For VHF telemetry data organisms are located through triangulating the radio signal (Mech 1983). ToIr-mounted, vehicle-mounted, or hand-held receivers are used to detect the tag signal and once detected a 3-dimensional fix is sought to improve precision in the location. Collecting VHF telemetry locations can be time consuming and logistically challenging. GPS technology has largely alleviated the time-intensive procedures associated with VHF by allowing for more frequent locations (provided that a fix can be acquired) and automated or remote data download. With GPS technology, the radio tag communicates with satellites at pre-set intervals. Like VHF, at least a 3-dimensional fix is required for GPS to precisely locate the radio tag. Regardless of the telemetry system used, the goal is to accurately locate the organism in space and connect the location to the environmental variables that describe habitat.

The main advantages of telemetry technology are the opportunities to seemingly study animal behavior in a non-invasive fashion. The close observation of organisms, characteristic of direct visual observation and some visual and auditory survey methodologies, has been scrutinized for the potential influence of the researcher’s presence on *natural* behavior (see Strum and Fedigan 2000 for review). Similarly, potential bias associated with trapping can limit inference on habitat selection. In theory, telemetry technology permits collection of data via remote radio towers or portable telemetry units that minimize observer effects on individual organisms. However, in some instances the weight and resistance associated with telemetry tags have been shown to influence both organism behavior and survivability (Marcström et al. 1989, Swenson et al. 1999, Barron et al. 2010). A common limitation of telemetry studies is the ability to capture and instrument enough animals for sound ecological inference on habitat selection.

MEASUREMENT OF ENVIRONMENTAL VARIABLES

The characterization of habitat selection depends not only on the identification of organism locations but also the intersection of these locations with the environmental variables that define habitat. Environmental variables can be collected using field-based sampling or digital remote sensing. With some of the organism location methodologies described above (visual observation and some survey or trapping designs) environmental variables can be collected at the time the organism is located (e.g., Gutzwiller et al. 1994). Though direct observation and measurement of environmental variables is still widely used in habitat selection research, another common technique for describing environmental variables at certain locations is digital remote sensing.

Digital data portraying environmental variables are now widely available for download from numerous reputable governmental and non-governmental organizations. These data include digital elevation models, bathymetry data, hydrology, soil type, geologic features, vegetation cover, landuse data, climate, and many others. Therefore, some components of habitat can be compiled with relative ease using modern, often freely-available data. Caution must be exercised when using widely available digital data so that the research question is properly framed and issues of scale are reconciled (Roloff et al. 2009). For example, the data vintage must be consistent with the spatial and temporal position of the organism location (Roloff et al. 2009). If vintage of the environmental data are not considered, then the researcher will potentially describe environmental variables that the organism of interest was not necessarily selecting. Furthermore, spatial and temporal resolutions are also important factors to consider (Roloff et al. 2009). As discussed below (see section Issues of Scale and Resolution) the resolution of the environmental data can limit the ability to make valid inferences. Spatial resolution refers to the minimum mapping unit in the data layer. Temporal resolution refers to the frequency of data collection or update. Regardless of the technique used for acquiring or compiling data on environmental variables, the resolution of the data must align with the spatial and temporal scales of selection for the organism of interest.

ANALYTICAL TECHNIQUES

Measurement of habitat use through mapping of animal locations and associated environmental variables is only the first part of describing habitat selection. The next step is to make inferences, or reach conclusions on the basis of evidence and reasoning. Numerous analytical techniques have been used to infer habitat selection. Models have been the cornerstone of habitat selection research for the last 30 years. Common modeling techniques can be based on organism presence/ or abundance and the relationship between environmental covariates and organism locations, utilization distributions as calculated from organism locations, or animal movements.

Linear and Logistic Regression Models

A common analytical approach in habitat selection research is to regress environmental variables (i.e., predictor variables) against a response variable that is either continuous (linear regression) or binary (logistic regression). Linear regression models typically take the form;

$$Y_i = \mathbf{x}_i' \boldsymbol{\beta} + Z_i$$

where Y is the response variable at location i, x is a vector of the environmental variables at location i, β is a vector of the regression parameters, and Z accounts for the random error term. The random error term can have spatial and temporal dependencies that should be accounted for

(Ver Hoef et al. 2001). A common response variable in linear regression models is a count of the individuals that occupy an area. Within these models there is a tacit assumption that more individuals in an area represent greater selection for the corresponding environmental variables associated with that area. The interpretation of the parameter estimates that are output from these models is based on the expected amount of change in the response (organism count) given unit changes in the environmental variables.

Logistic regression is generally used to model the relationships between presence or absence of an organism and environmental variables. Logistic regression models take the form;

$$P(y = 1 \mid x) = \frac{\exp(\beta' x)}{1 + \exp(\beta' x)}$$

where the binary response variable is modelled given a value of 1 (presence or used), x is a vector of the environmental variables, and β is a vector of the regression parameters. Presence or use is based on measured organism locations while absence is often estimated. The creation of absence locations is a topic that has been widely scrutinized (see section How is Available Habitat Defined?). Absence locations in available habitat tend to be estimated via a random or stratified sampling design (Keating and Cherry 2004). For example in a random design, absence is randomly assigned to locations in a study area, with the assumption that these locations are not used by the organism or that the locations portray what is available to the organism for selection. In a stratified design, absence is assigned to different locations based on some pre-determined stratification, perhaps by vegetation or soil type. Selecting the sampling strategy that best suits the data depends upon the research question, the species of interest, and the composition of environmental variables within the study area. Regardless of the technique that is selected, at each presence and absence location environmental variables are measured and model parameters are fit. For more information on regression modelling see Elith and Franklin (2011).

A specific type of regression modelling is referred to as resource selection functions. The goal of resource selection functions is to develop probabilities of relative use of environmental variables within the study area (Manly et al. 2002). The classic use versus availability exponential model is expressed as;

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 ... \beta_k x_k)$$

where x is a vector of k environmental variables and β is a vector of the coefficients at each location. This model is calculated with a regression based on maximum likelihood estimation. The environmental variables can be either continuous or categorical, though similar to logistic regression, resource selection functions are subject to critique for the exact methodology employed to generate available locations (Boyce 2006).

Utilization Distributions

Utilization distributions (UDs) have been used to model habitat selection by departing from strict point-based modeling (Marzluff et al. 2004). Essentially, UDs stretch the probability of an animal occurrence across space and time. This technique improves upon traditional home range estimators (e.g., minimum convex polygons) by recognizing that organisms use habitat non-uniformly. UDs enable the researcher to quantify those environmental variables that are used more often than others.

The creation of a UD is initially informed by the collected organism locations. The organism locations are used to develop density estimates of relative use across spatial and temporal dimensions. Researchers typically divide their dataset of organism locations based on biological relevance and the question being asked (e.g., sex, season, year). The latitude (Y) and longitude (X) coordinates from organism locations are mathematically analyzed to develop the Z dimension in the UD, which represents the probability of space use. This probability of use can then be manipulated to function as the response variable in any modelling design. A variety of techniques can be implemented to measure the environmental variables within the utilization distribution. For instance Marzluff et al. (2004) developed a resource utilization function based on the entire UD. However, this procedure could prove computationally challenging for extremely large UDs. Another option is to implement a strategy for sampling the environmental variables within the UD (Marzluff et al. 2004).

Animal Movement Models

One emerging area of modelling habitat selection is animal movement models. Given the potential for fine-scale temporal sampling from GPS telemetry tags, consecutive organism locations can be linked to simulate animal movement paths. Innovative new models incorporate temporal autocorrelation and can also be modified to integrate habitat availability within the context of an animal's utilization distribution while estimating model parameters via a Bayesian framework (Christ et al. 2008). Furthermore, animal movement models can be fit using data collected at regular or irregular intervals (Johnson et al. 2008b). Animal movement models represent an exciting area of habitat selection research and have thus far proved integral to understanding migration patterns, responses to various time-sensitive phenomena (Weather, temperature, disturbance events), and use of edge habitat (Schick et al. 2008, Forester et al. 2009, Morales et al. 2010).

INFERENCE

Among the scientific community, the term inference is used to describe the process of reaching logical conclusions based on evidence and reasoning. In habitat selection research inference is based on animal location and associated environmental variable data in an effort to understand organism decision-making. Inference from habitat selection research has resulted in formulation of multiple theories and concepts including niche theory (Petren 2001, Hirzel and Le Lay 2008), habitat suitability (Hirzel et al. 2006), and specificity of habitat use (Devictor et al. 2008). These theories and concepts have collectively added to our understanding of ecology.

The foundation of niche theory and resource partitioning includes a seminal publication by Joseph Grinnell in 1917 on the organism-habitat relationship for California thrashers (*Toxostoma redivivum*). Grinnell referenced a specific set of environmental variables that California thrashers were adapted to as “critical conditions”. These conditions included humidity, slope, elevation, and composition of shrubbery. Grinnell (1917) posited that California thrashers were adapted to a specific set of environmental conditions and that the availability of these conditions limited distributional range, thereby defining niche. Later (in 1957), G. Evelyn Hutchison formally articulated the multivariate components of habitat as an n-dimensional niche, where the n-dimensions correspond to different environmental variables that are used by the organism (Morrison et al. 2006). Niche theory has been a useful construct to guide development of analytical tools for habitat selection research.

The concept of habitat suitability is based on Grinnell’s notion that some portions of the niche are better suited for organism fitness than others, and that habitat selection can help reveal those relationships. The concept of suitability contends that habitat varies in quality, i.e., some habitat is more conducive to occupancy, reproduction, and survival than others. Numerous analytical approaches have been used to portray habitat quality, including linear and logistic regression, resource selection functions, UDs, and an expert-opinion-based modelling approach called habitat suitability modelling (Singh et al. 2009). These techniques portray disproportionate habitat use, with the assumption that areas receiving more use or having a higher probability of occupancy or use correspond to higher quality. However, animal density or occurrence is not always a reliable correlate to habitat quality (Van Horne 1983) and researchers have emphasized the importance of using fitness (often quantitatively expressed as viability) as the best indicator of quality (e.g., Roloff and Haufler 2002, Mosser et al. 2009)

Habitat suitability modelling has been conducted on a variety of species. One Ill-known example was performed in the mid 1990's. At that time it became clear that the wolf (*Canis lupus*) population in the Great Lakes region of the United States was growing rapidly. Concerned citizens, stakeholders, and scientists wanted to determine how widely wolves could potentially range. Mladenoff et al. (1995) developed a model that was used to map habitat suitability for wolves throughout the Great Lakes region. The model was built from habitat selection data collected on a population of Ill-studied wolves in northern Minnesota. The model was subsequently extrapolated to other areas in the Great Lakes region to estimate where wolves might colonize and survive. The research of Mladenoff et al. (1995) demonstrated, amongst other things, that wolves were capable of traversing large areas of unsuitable habitat in search of areas that provided the right mix of favorable habitat characteristics, a habitat use pattern that has been realized as wolf populations recovered in this region (Mladenoff et al. 2009).

The occurrence, abundance, and fitness of some species are closely linked to specific environmental variables whereas other species exhibit more latitude in habitat selection. This observed difference in habitat specificity among species has resulted in 2 broad categories; habitat-specialists and habitat-generalists. Habitat-specialists are so suited to a specific set of environmental variables that they are vulnerable if these variables are altered. Habitat-generalists are more malleable in their dependence on specific environmental variables and can potentially thrive in disturbed habitat. In a world that is rapidly changing as a result of anthropogenic disturbance including human population growth, development, exploitation of natural resources, and accelerated climate change, habitat-specialists can experience significant population losses from habitat disturbance while habitat-generalists are more capable of adjusting to environmental change (Brook et al. 2003).

Although the broad categories of habitat specialist and generalist imply autonomy, recent research has demonstrated that habitat functionality also depends on the composition of different species that occupy similar space and time. The term trophic cascade, for instance, describes an event where predators, at the top of the food chain, influence the vegetative community at the bottom of the food chain (Carpenter et al. 1985, Ripple and Beschta 2007). At the system level, predators are known to influence nutrient cycling through consumptive and non-consumptive means (Bump et al. 2009, Schmitz et al. 2010). Furthermore, habitat heterogeneity and species diversity are positively associated (Tews et al. 2004). Essentially, more varied environmental variables result in more potential niches and hence, greater species richness.

LIMITATIONS ON INFERENCE

How is Selection of Habitat Defined?

Point-based habitat selection models are built on the assumption that organism locations represent the full suite of selection decisions. In reality, sampling and technological shortcomings often limit, sometimes in a biased manner, the animal locations that are collected. For example, Beyer and Haufler (1994) demonstrated that inference on habitat selection by elk (*Cervus elaphus*) was different depending on whether the sample contained night-time locations. Technological advances, like modern GPS telemetry technology, have helped alleviate some of the logistical constraints associated with sampling. Indeed, use of GPS technology has revealed new insights into environmental variables that are infrequently used but nonetheless important(e.g., transitory areas between more highly used areas; Beyer et al. 2010). However, GPS telemetry data do not represent a guaranteed solution as vegetation cover, weather, animal movement, and topography affect the likelihood of triangulating a position and the precision of the organism location. For example, topography is known to influence the ability of GPS to triangulate a location (Gantz et al. 2006) and thus, resultant animal locations are biased to those areas where topography did not limit functionality of the GPS technology. By assuming that all organism locations in a data set represent the full suite of selection decisions, the importance of certain environmental variables is likely exaggerated while the value of others is likely diminished (Marzluff et al. 2004). Hence, it is important for researchers to critically evaluate their animal location data, understand the spatial and temporal dimensions of the data, and adjust the scope of inference accordingly.

Another factor that limits our ability to make inference from habitat selection studies is the assumption that organisms are making selections for habitat that is ideal (i.e., organisms are free to choose among the full range of habitat conditions). Fretwell (1972) and Fretwell and Lucas (1969) described this process as the ideal free distribution. The concept implies that organisms are ideal in their perception of habitat and that they are free to choose among habitats. In reality, individuals are likely selecting less-than-ideal habitat because external pressures (e.g., dispersal constraints, intra and inter-species competition, source-sink dynamics, and human encroachment on habitat) limit the ability to perceive or move into ideal habitat. By studying organisms that are not behaving according to an ideal free distribution researchers risk identifying less than ideal habitat as ideal. This misidentification can have significant conservation ramifications if management activities inadvertently focus on less than ideal habitat. Herein lays the importance of using fitness as a metric of habitat suitability. Fitness should be highest in ideal habitats.

How is Available Habitat Defined?

Many logistic regression models and resource selection functions require the designation of available or presumably unused habitat. Because of the coarse temporal resolution characteristic of almost all animal sampling efforts, it is difficult to say with certainty that available habitat were unused. For instance, an animal may make use of available habitat between sampling intervals. Thus, the naming convention representing the binary response is traditionally used versus available habitat. It is important to note that this is a problem which does not pertain to the habitat selection research of plants and fungi. Within this context it is possible to identify true absence locations by visiting various habitat and confirming plant presence or absence (Turner et al. 2003). Methods for estimating available habitat in animal habitat selection research have been scrutinized (MacKenzie 2005, Boyce 2006). One technique for estimating available habitat is based on randomly sampling locations from the study area where organisms were not recorded (Edge et al. 1987, Aebischer et al. 1993). Another technique uses the organism locations to create a home range, and then samples available habitat within the home range (Anderson et al. 2005, Christ et al. 2008) (Figure 9). The aforementioned techniques are similar, yet the latter limits the generation of available habitat to only that within the organism's home range while the former allows sampling throughout the study area without considering the organism's site fidelity. The problems associated with identifying available habitat are often based on the delineation of the spatial and temporal boundaries of what is considered available.

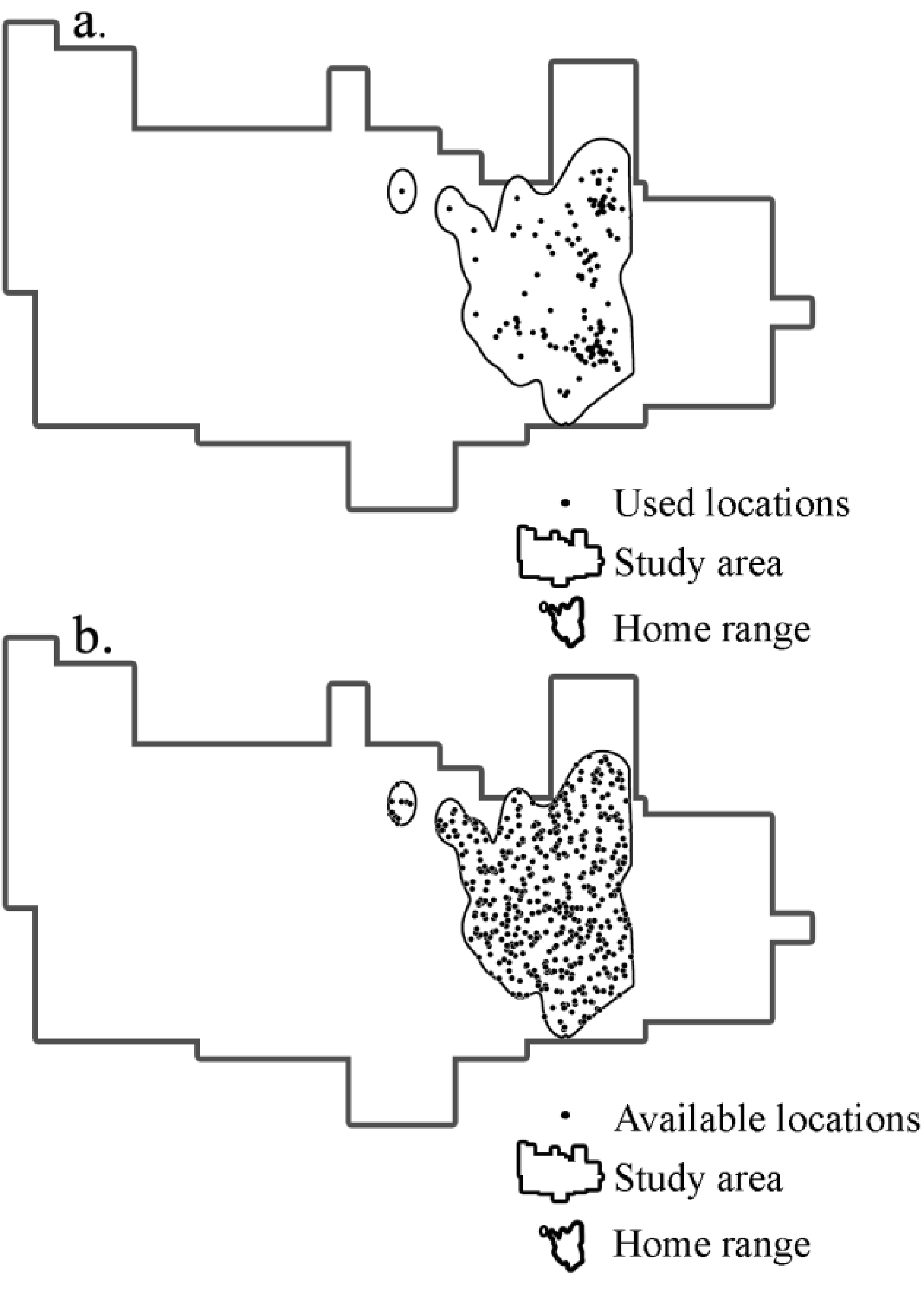


Figure 9. Example of a use versus availability design with a random sample of available habitat drawn from within the home range; a.) shows the organism locations collected by the researcher that were used to create the home range, while b.) displays the available locations which resulted from a random sample of all available habitat within the home range.

Depending on the method used to identify available habitat, the ability to infer ecological relationships can vary substantially. Porter and Church (1987) found that results from the same habitat model could contradict depending on the manner in which available habitat was portrayed. This facet of traditional experimental designs for assessing habitat use and availability injects uncertainty into the inferences derived from this research. The problem is that decisions on how to define habitat availability are commonly made *a priori*. Study area boundaries are identified as a result of funding, logistics, or the delineation of political demarcations, none of which may be relevant to the biology of an organism. Despite this reality, study areas are one of the primary means by which habitat is considered available.

There is also an assumption that areas without recorded animal locations represent unselected habitat. The limitations of different organism location techniques (e.g., organisms can only be observed during certain times of day, measurement error), coarse temporal resolution of some telemetry data, and problems with detection probability influence whether the researcher is able to definitively designate available habitat as definitively unused. While measuring habitat selection, the probability of detecting organisms of interest can vary. Historically, researchers have assumed that detection probability was reliable and constant. In reality, conditions during measurement of habitat selection (vegetation cover, weather, animal behavior, observer bias) can influence the researcher’s ability to detect an organism. Failure to account for imperfect detection probability can impact inferences derived from habitat selection research (MacKenzie et al. 2006). For instance, the importance of habitat where an organism is readily detected can be overestimated while habitat where the organism occurred but was not detected would be undervalued. However, once the probability of detecting an organism is calculated, this probability can be incorporated into models developed to quantify habitat selection (MacKenzie et al. 2006). Regardless, near-continuous telemetry sampling or intense visual observation would be required to completely assuage this critique associated with how available habitat is defined.

Furthermore, there is an important spatial and temporal component to identifying what should be considered available habitat which can be referred to as habitat accessibility (Buskirk and Millspaugh 2006). For example, if a sedentary organism is selecting habitat in the far western portion of its home range, then habitat 5 km away cannot be simultaneously considered available. Researchers must explicitly consider both habitat availability and accessibility in their habitat selection research to increase the validity of their inferences. For a further discussion of the issues associated with habitat availability see Elith and Franklin (2011).

Issues of Scale and Resolution

Scale is critical to any examination of habitat selection. The components of scale include extent and resolution. Extent defines the boundary of the analysis; resolution refers to the smallest identifiable unit (also referred to as grain and minimum mapping unit). Inference derived from habitat selection research can vary depending on extent (as discussed above for defining available habitat) and resolution (e.g., see Roloff et al. 2009). Thus, an understanding of scale as it relates to the biology of the study organism and the research question is critical for valid inference (Turner et al. 2001, Roloff et al. 2009). Furthermore, ecological processes exhibit spatial and temporal variability and the results and inferences derived from habitat selection research directly depend on the scale of the analysis (Boyce 2006).

Johnson (1980) articulated that organisms perceive their environment at varying scales and make decisions to satisfy certain life history events in orders that depend on these scales (Figure 10). The first-order represents a selection of habitat that defines the range of the species.

Selection of habitat by individuals for the placement of home ranges within the species range occurs at the second-order. The third-order of the hierarchy represents within home range selections, for example denning, feeding, or roosting areas, while the fourth-order addresses fine-scale (e.g., microsite, daily) habitat selections.

As organisms use their environment at varying spatial and temporal scales, failure to explicitly consider scale can distort inference. In a habitat modelling framework, scale affects the relationship between the response variable(s) and the environmental variables that describe the habitat. For instance, certain habitat selection studies divide the study area (extent) into a network of polygons, called habitat units (e.g., a grid lattice of polygons delineated at a specific resolution) (Servheen and Lyon 1989, Boyce et al. 2003). When habitat selection research depends upon concepts like habitat units, identifying the scale of those units must be done in careful consideration of the research question, the biology of the organism, and the patterns and processes of the environment. Furthermore, it is recommended that several different scales be examined and model selection methods be utilized to identify the best-approximating model (Anderson et al. 2005, Boyce 2006).

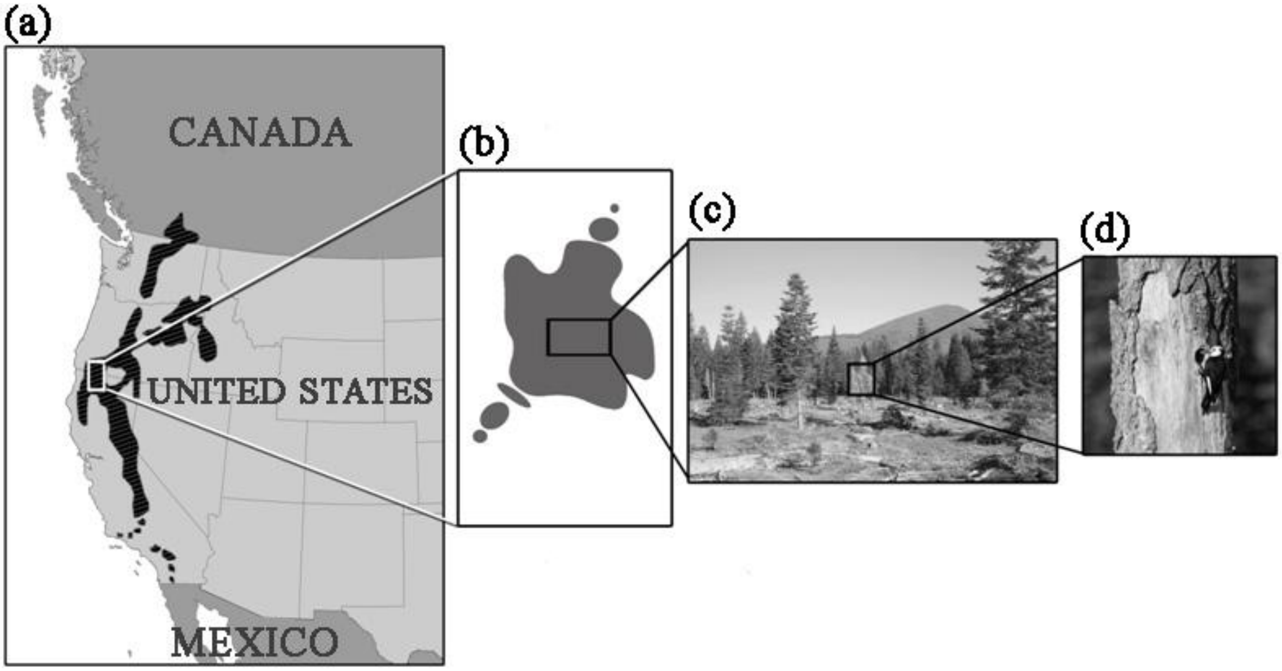


Figure 10. The four orders of hierarchical habitat selection outlined by Johnson (1980); a.) the first-order selection represents habitat selection that defines the range of the species, in this case the range of the white-headed woodpecker (*Picoides albolarvatus*)* adapted from Garrett, K. L., Martin, G.R. and Dixon, R.D. (1996). White-headed woodpecker (*Picoides albolarvatus*). In Poole, A. (ed) The birds of North America online. Ithaca, NY. USA, b.) in the second-order selection an individual white-headed woodpecker makes a selection for the placement of their own home range within the species range, c.) the third-order selection correspond to within-home range habitat selection, and d.) the fourth-order selection relate to fine-scale daily habitat selection.

Spatial and Temporal Autocorrelation

Spatial and temporal autocorrelation are two factors that influence the measurement of habitat selection. Autocorrelation can be viewed as the similarity among observations as a function of the space or time separation among them. Regression models have a statistical structure that requires independence of the environmental variables. As environmental variables (e.g., elevation, vegetation type, and soil structure) are more similar to one another in space and time the fine-scale sampling protocols associated with acquisition of some animal location techniques (e.g., direct visual observation, GPS telemetry) will yield data that exhibit correlated, directional dependencies. Failure to account for these inherent dependencies is a violation of regression model assumptions.

The issue of autocorrelation in space and time has direct ramifications on inference because failure to account for dependencies amongst the environmental variables imputes bias into the model design, potentially inflating the significance of certain relationships. The problem is that a researcher could infer an organism-habitat relationship that is stronger than it is in actuality, simply because a facet of the modelling design was neglected. However, regression models and RSFs can be structured to account for autocorrelations. As mentioned, a progressive area of habitat selection research involves the integration of autocorrelation within animal movement models. When autocorrelation is explicitly included into the likelihood method of estimating model parameters more accurate interpretations of ecological relationships become possible (Boyce et al. 2010).

Locational Imprecision

The unprecedented depth and scope of our ability to locate organisms, particularly with telemetry systems have fostered the assumption that measured organism locations are precise. In actuality, locational data can have considerable amounts of measurement error which is problematic for habitat selection research. In 1990, Gary White and Robert Garrott published an important book which, amongst other things, demonstrated the necessity of explicitly incorporating measurement error into habitat selection models. Given that habitat selection research strives to understand which habitat patches an individual is using in relation to those that are available, measurement error limits our ability to accurately detect true organism-habitat associations. White and Garrott summed up this sentiment when they wrote that habitat selection models “require a precise estimate of an animal’s location so that it can be correctly placed in a habitat type" (White and Garrott 1990:200). Without precise locations habitat selection models have the potential to produce erroneous results. Following White and Garrott (1990) numerous methods (e.g., ignoring the error, rescaling environmental variables, majority sampling, and bivariate-weighted techniques) were developed to explicitly incorporate measurement error into habitat selection models. For several decades these techniques were applied to habitat selection research. However, the ability of these techniques to ameliorate the error associated with organism locations had rarely been tested.

Montgomery et al. (2010) demonstrated that commonly used techniques for incorporating error into habitat selection studies were largely incapable of accurately portraying habitat use. However, by 2010 the primacy of VHF technology had been usurped by GPS telemetry data. GPS data are, on the whole, more accurate than VHF data with errors that are commonly <12 m, depending on topography, canopy cover, and geographic location (Cargnelutti et al. 2007). Because of this documented precision, a common approach was to simply ignore the measurement error and proceed with the modelling design assuming that the organism locations were near perfect. Montgomery et al. (2011) examined the effects of ignoring measurement error consistent with GPS telemetry systems. Their analysis discovered that ignoring measurement error from precise telemetry systems could have considerable ramifications on the ability to make valid habitat selection inferences. Regardless, new models and analytical methodologies are frequently being designed to portray habitat selection with as little bias as possible. The progression of telemetry technology from the 1950's forward demonstrates that habitat selection research is ever-evolving, constantly advancing upon what has been done previously with new techniques and innovative methodologies.

CHAPTER 4

THE INFLUENCE OF SENESCENCE ON HABITAT SELECTION AMONG MOOSE EXPOSED TO WOLF PREDATION

ABSTRACT

Climate, forage availability, and predation risk are known to influence habitat selection. Less appreciated is how habitat selection is influenced by individual body condition, especially senescence. I assessed the possibility of such an influence for wolf-killed moose (*Alces alces*) during a 50-year period in Isle Royale National Park, USA. I developed habitat models which indicate that during severe winters prime-aged moose had a tendency to die closer to Isle Royale's shoreline, where foraging opportunities and predation risk tend to be greater. By contrast, senescent-aged moose tended to die farther from shore during severe winters. The same model also indicated that moose tended to die in riskier, shoreline habitats during years when predation risk had been lower in the preceding year. These results show how an individual's body condition can affect habitat selection and how predation dynamics may be complicated by habitat selection based on characteristics of the preceding year.

INTRODUCTION

Most habitat selection research focuses on understanding how selection is influenced by abiotic and biotic factors (e.g., Pimm and RosenzIig 1981, Morris and MacEachern 2010). Habitat selection is also influenced by an individual's vulnerability to predation (Winnie and Creel 2007) which can be affected by an individual's body condition (Peterson 1977, Wright et al. 2006). These relationships suggest that habitat selection may also be affected by an individual's body condition. Nevertheless assessments of such an effect on habitat selection are rare (Sinclair and Arcese 1995, Heithaus et al. 2007).

Some fundamental changes in body condition over the lifetime of an individual are predicted by and understood through life history theory (Mangel 2008). In particular, the life history of many organisms involves senescence. From a physiological perspective, senescence is the decline in body condition with increasing age (e.g., Doherty 2003). Within evolutionary ecology, this deterioration in condition ultimately results in a decline in vital rates. Much insight has been gained by understanding how senescence influences population dynamics (e.g., Nussey et al. 2008; Tuljapurkar et al. 2009). Here I assess how habitat selection, a fitness-related behavior (McLoughlin et al. 2006), is influenced by an important life history change for many species, the transition from prime condition to senescent.

Wolf-ungulate systems are especially Ill suited for examining how senescence affects prey vulnerability and corresponding habitat selection. For instance, the presence of wolves (*Canis lupus*) causes ungulates to select habitat that offers better protection from predation (Creel et al. 2005), and ungulates in poorer nutritional condition seem to select different habitats than animals in better nutritional condition (Winnie and Creel 2007). These patterns may be attributable to wolves' tendency to selectively kill senescent ungulates (Wright et al. 2006). In this study I assess how winter severity, predation risk, and moose body condition affect moose (*Alces alces*) habitat selection and where wolves (*Canis lupus*) kill moose.

MATERIALS AND METHODS

I evaluated winter habitat selection of moose living in Isle Royale National Park (544 km^2), an island ecosystem in Lake Superior, USA. The moose population is typically comprised of 700–1100 individuals (1.4–2.4/km^2) (interquartile ranges) (Vucetich et al. 2002). During most winters wolf predation accounts for more than 80% of moose deaths (e.g., Vucetich and Peterson 2011), and the mean annual predation rate for the moose population (>9 months of age) is 9.9%

(Vucetich et al. 2011). Growth rate of the moose population is negatively influenced by severe winters (Vucetich and Peterson 2004a) and high rates of predation (McLaren and Peterson 1994; Wilmers et al. 2006; Vucetich et al. 2011). Neither wolves nor moose have been subjected to human hunting pressure.

Between 1959 and 2008, I found and necropsied the carcasses or skeletal remains of moose that had been killed by wolves during winter (Figure 11). Most carcasses were located during aerial surveys that tracked the movement of wolves through the snow during a 7-week field season conducted each January and February. Some additional carcasses were also discovered during summer ground surveys that involved extensive off-trail hiking. Because most carcasses in this sample were located from light fixed-wing aircraft in conjunction with estimating kill rate, few moose that died during the field season were missed (Vucetich et al. 2002). For carcasses discovered in winter, necropsies were conducted as soon as possible after wolves finished feeding on a carcass and left the area, typically within 7 days of the moose’s death (Vucetich et al. 2012).

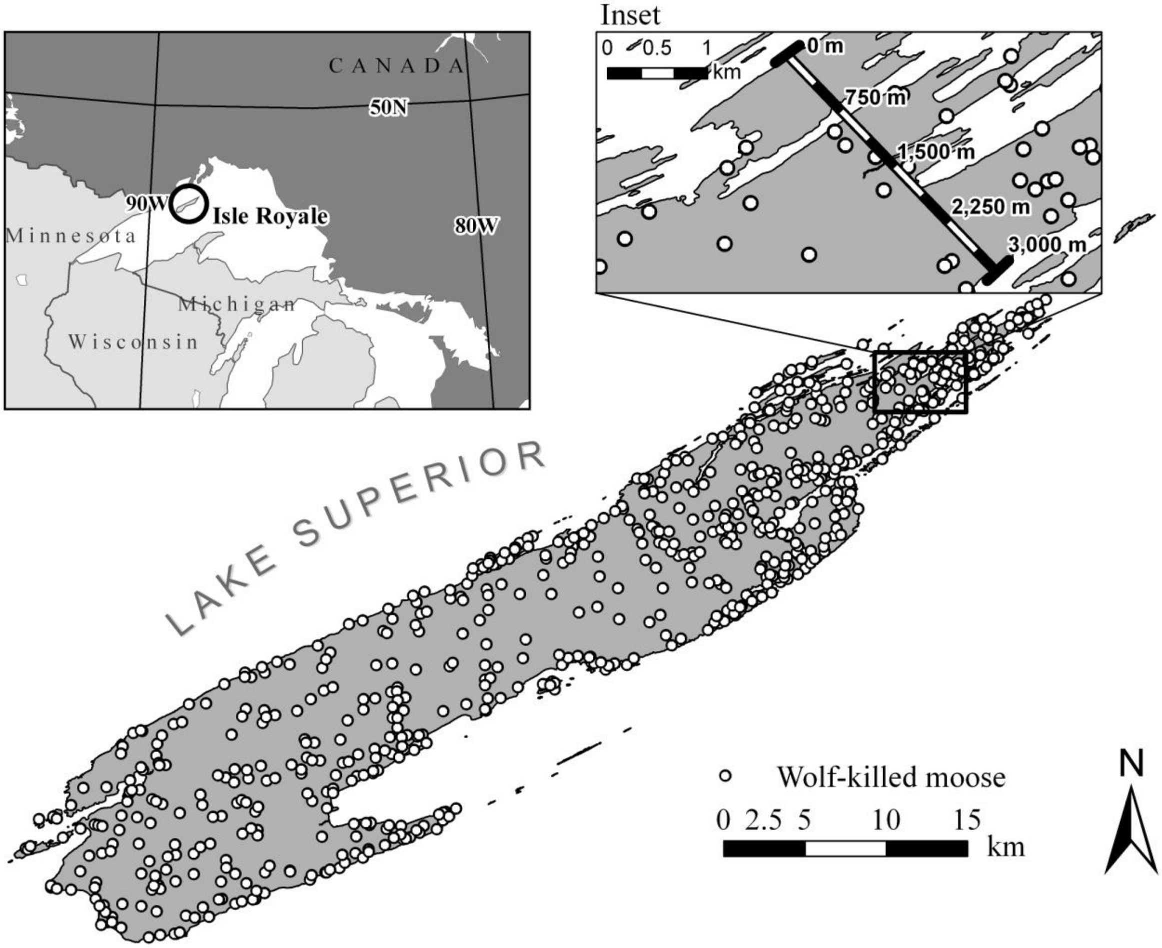


Figure 11. The location of Isle Royale National Park within Lake Superior (upper panel) and the distribution of moose killed by wolves during the winter (N = 732) in Isle Royale National Park, USA, 1959 - 2008. The inset provides a scale to help interpret the response variable depicted as the *y*-axis of Figures 12 and 13.

Necropsies included inferring the cause of death from field sign (e.g., blood on trees, signs of a chase, and signs of struggle including broken branches). For carcasses discovered during the summer, season of death was also inferred from field sign (e.g., degree of decomposition, presence of adult ticks which exist only in winter or early spring). Necropsies also involved recording the sex and location of the carcass. I estimated age at time of death by counting annual cementum lines in the teeth (Bubenik 1997), and I recorded osteoarthritis (Peterson et al. 2010) and periodontal disease (Peterson 1977) as being absent, mild, moderate, or severe.

Habitat Characterization

The shoreline habitat of Isle Royale is characterized by conifer-dominated forests (i.e., *Abies balsamea*, *Picea glauca,* and *Thuja occidentalis*) which moose prefer in winter (Puttock et al. 1996, Jordan et al. 2000; see Figure A.1 in Appendix A). With increasing distance from the shore, deciduous species (especially, *Populus spp.*, *Acer spp*., and *Betula spp.*) become more common (Krefting 1974, Jordan et al. 2000). Because Isle Royale moose prefer A. *balsamea* and *T. occidentalis* during the winter (Vucetich and Peterson 2005), habitat closer to shore represents the best of the available foraging opportunities, with consideration for predation risk, energy expenditure, and forage intake (Geist 1982, Edwards 1983, Peterson and Page 1993). Conifer-dominated forests are also associated with lower snow depth, which favors moose mobility, and greater horizontal structure of vegetation, which favor escape from predation (Peterson 1977). These habitat qualities are associated with moose density being greater in habitats that are closer to the shore (e.g., Vucetich and Peterson 2011). However, wolves also travel and forage more frequently in shoreline habitats (see Figure A.2 in Appendix A). Thus, habitat near to the Lake Superior shore provides moose with better forage, but may also correspond to riskier habitat. For these reasons, distance to shore represents important changes in moose habitat selection on Isle Royale.

I calculated the distance from each carcass location (in meters) to the Lake Superior shore. Moose carcass locations are representative of habitat selection because moose make daily movement decisions at relatively small scales (10's – 100's of meters) (Phillips et al. 1973) and chase distances of wolves for moose tend to average < 100 m (Wikenros et al. 2009). Moose killed by wolves on shore ice were assigned a distance value of 0 m, meaning that they were considered to be on shore. In the majority of these cases, the moose would have been on the shoreline and chased onto the ice by wolves. The accuracy of these carcass locations is reasonably high (given the context, i.e., distance from Lake Superior shore, whose range is [0, 5.4 km]) because a carcass located from the air must also be found, on a later date, by a ground crew (to conduct the necropsy). Doing so in a forested environment requires the aerial observer's location to be plotted very accurately.

Predictor Covariates

I assessed whether distance from shore could be predicted from two biotic covariates (ratio of moose to wolf abundance and moose density), one abiotic covariate (North Atlantic Oscillation Index [NAO]), and three individual body condition covariates (sex, age-class, and pathologic condition). The ratio of moose to wolf abundance (RATIO) is an important indicator of predation risk (Vucetich et al. 2011), and ungulate density (MOOSE) is an important indicator for a variety of density-dependent processes including intraspecfic competition for forage (Patterson and Power 2002, Vucetich and Peterson 2004a).

Winter severity and its effect on ecological processes are complicated. Consequently, large-scale, seasonal indices of climate spanning several months can be better indices of winter severity than local climatic factors for ungulate populations (Hallett et al. 2004), including Isle Royale moose (Vucetich and Peterson 2004a). In particular, NAO is an index of winter severity for many ungulate populations (Ottersen et al. 2001), including Isle Royale moose (Vucetich and Peterson 2004a). I used annual NAO values reported by Hurrell (1995) and annual estimates of moose and wolf abundance reported in Vucetich et al. (2011).

I categorized moose as prime-aged if they were 1-10 years old and senescent-aged if they were >10 years old (AGE). This classification corresponds to the age when survival and reproduction begin to decline in moose (Ericsson and Wallin 2001, Ericsson et al. 2001, Vucetich and Peterson unpublished data). I categorized moose as pathologic if they exhibited either of two senescence-associated pathologies (PATH). Specifically, a moose was categorized as pathologic if it exhibited moderate or severe periodontal disease and/or moderate or severe osteoarthritis. Moose were otherwise categorized as non-pathologic. Because moose habitat selection commonly differs between sexes (Dussault et al. 2005), I also included sex as a predictor covariate (SEX). I standardized the continuous predictors to have a mean value of 0 and a standard deviation of 1 to facilitate comparison of the regression coefficients.

Model Development

My model building procedure was based on nine predictor variables; three individual body condition predictors (AGE, SEX, PATH) and three environmental predictors (RATIO, MOOSE, NAO) that could be assessed for their influence during the current year (t) and the previous year (t-1). I tested for multicollinearity among these predictor covariates and found that RATIO and MOOSE correlated ($R = 0.79$; $P < 0.01$). Despite the degree of correlation, the variance inflation factor for these two predictors was small (VIF = 2.62) suggesting that multicollinearity was not problematic (O'Brien 2007). However, I did not evaluate any models that included both RATIO and MOOSE.

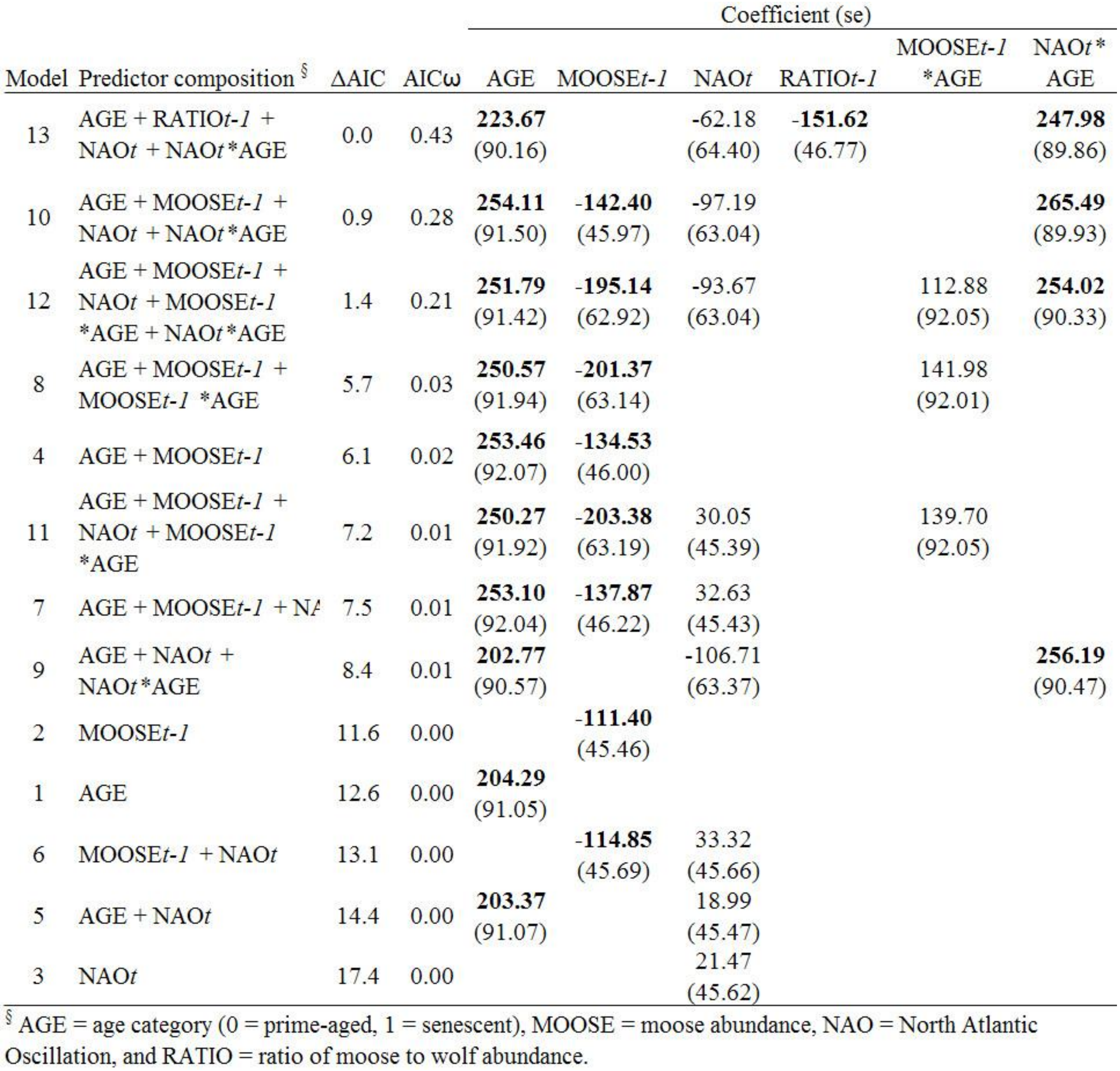
I began the model selection procedure by using backward elimination to assess which of the three body condition covariates were significant predictors of the location where moose died (Table 6). That procedure indicated that AGE was significant, but SEX and PATH were not. Next I assessed how the influence of AGE might be modulated by environmental covariates. To do so, I applied backward elimination to a set of candidate predictors representing all the interaction terms that included AGE and each of the environmental predictors for year *t* or *t*-1 (Table 6). This application of backward elimination indicated that MOOSE*t-1**AGE and NAO*t**AGE were important predictors. The next step of my model selection procedure was to construct models representing every possible combination of predictors (see models 1-12 in Table 7), with the restriction that every model with an interaction term would also include those covariates as main effects. I compared these models using Akaike's Information Criterion (AIC) and ranked model performance with AIC weights (AICw) (Burnham and Anderson 2002). The top-ranking model featured MOOSE in year *t*-1 (Table 7). Due to collinearity between MOOSE and RATIO, I also evaluated a model where RATIO*t-1* replaced MOOSE*t-1* (see model 13 in Table 7).

Table 6. The removed and retained predictor covariates for models predicting the distance from Isle Royale's shoreline where wolf-killed moose died between 1959 and 2008. Predictors were removed in iterative fashion until all retained predictors were $P < 0.05$.

	Individual body conditions		Interactions terms	
	Predictor[§]	P-value	Predictor[§]	P-value
Removed predictors	SEX	0.87	NAOt-1*AGE	0.81
	PATH	0.57	RATIOt-1*AGE	0.80
			RATIOt*AGE	0.05
			MOOSEt*AGE	0.43
Retained predictors	AGE	0.03	NAOt*AGE	0.02
			MOOSEt-1*AGE	0.01

[§] SEX = 0 for males and 1 for females, PATH = pathology category (0 = non-pathologic, 1 = pathologic), AGE = age category (0 = prime-aged, 1 = senescent), NAO = North Atlantic Oscillation, RATIO = ratio of moose to wolf abundance, and MOOSE = moose abundance.

Table 7. Rankings of the models developed to evaluate the habitat selection of moose in relation to the Lake Superior shore in Isle Royale National Park, USA, 1959-2008. Coefficients significant at α = 0.025 level are highlighted in bold type face.



				Coefficient (se)					
Model	Predictor composition §	ΔAIC	AICω	AGE	MOOSE*t-1*	NAO*t*	RATIO*t-1*	MOOSE*t-1* *AGE	NAO*t* * AGE
13	AGE + RATIO*t-1* + NAO*t* + NAO*t* *AGE	0.0	0.43	**223.67** (90.16)		-62.18 (64.40)	**-151.62** (46.77)		**247.98** (89.86)
10	AGE + MOOSE*t-1* + NAO*t* + NAO*t* *AGE	0.9	0.28	**254.11** (91.50)	**-142.40** (45.97)	-97.19 (63.04)			**265.49** (89.93)
12	AGE + MOOSE*t-1* + NAO*t* + MOOSE*t-1* *AGE + NAO*t* *AGE	1.4	0.21	**251.79** (91.42)	**-195.14** (62.92)	-93.67 (63.04)		112.88 (92.05)	**254.02** (90.33)
8	AGE + MOOSE*t-1* + MOOSE*t-1* *AGE	5.7	0.03	**250.57** (91.94)	**-201.37** (63.14)			141.98 (92.01)	
4	AGE + MOOSE*t-1*	6.1	0.02	**253.46** (92.07)	**-134.53** (46.00)				
11	AGE + MOOSE*t-1* + NAO*t* + MOOSE*t-1* *AGE	7.2	0.01	**250.27** (91.92)	**-203.38** (63.19)	30.05 (45.39)		139.70 (92.05)	
7	AGE + MOOSE*t-1* + NA	7.5	0.01	**253.10** (92.04)	**-137.87** (46.22)	32.63 (45.43)			
9	AGE + NAO*t* + NAO*t* *AGE	8.4	0.01	**202.77** (90.57)		-106.71 (63.37)			**256.19** (90.47)
2	MOOSE*t-1*	11.6	0.00		**-111.40** (45.46)				
1	AGE	12.6	0.00	**204.29** (91.05)					
6	MOOSE*t-1* + NAO*t*	13.1	0.00		**-114.85** (45.69)	33.32 (45.66)			
5	AGE + NAO*t*	14.4	0.00	**203.37** (91.07)		18.99 (45.47)			
3	NAO*t*	17.4	0.00			21.47 (45.62)			

§ AGE = age category (0 = prime-aged, 1 = senescent), MOOSE = moose abundance, NAO = North Atlantic Oscillation, and RATIO = ratio of moose to wolf abundance.

These models were fit using a linear regression in SAS PROC MIXED (version 9.2, Cary, NC). My models took the form:

$$Y_i = x_i'\beta + Z_i$$

where Y_i represents distance to shore at the *i*th carcass location, $x_i'\beta$ are the vectors of the predictor covariates or the fixed effects parameters, and Z_i represents the random error term.

RESULTS

Between 1959 and 2008 aerial and ground surveys located 732 winter wolf-killed moose for which age, sex, and pathology (peridontal disease and osteoarthritis) could be assessed (Figure 11). Among this dataset, 309 were males, 423 were females, 340 were not pathologic, and 392 were pathologic. Furthermore, 347 moose were prime-aged and 385 moose were senescent-aged. Senescent-aged moose died, on average, significantly closer to the Lake Superior shore than did prime-aged moose ($t = 2.20$, $P = 0.01$).

The top-ranking model included AGE ($P = 0.01$), RATIO*t-1* ($P < 0.01$), NAO*t* ($P = 0.19$), and NAO*t**AGE ($P < 0.01$; Table 7). This model (AICw = 0.43) was more than 1.5 times as likely to be the best approximating model when compared to the next ranking model (AICw = 0.28; Table 7). The second-best performing model included the same covariates as the best-performing model, except MOOSE*t-1* replaced RATIO*t-1*, these covariates are also correlated, and the coefficients for each of these predictors were similar (Table 7). Moreover, RATIO explains 62% percent of the variation in predation rate (see Vucetich et al. 2011), and MOOSE explains 52% of the variation in predation rate (Vucetich and Peterson 2011). Collectively, these considerations suggest RATIO and MOOSE are both useful indicators of predation risk on moose habitat selection. The parameter estimates indicate that moose tended to die closer to the shore, where foraging opportunities were better and predation risk was likely greater, when the ratio of moose to wolf abundance (i.e., predation risk) had been lower in the preceding year (Figure 12). The interaction term indicates that the effect of winter severity in year *t* on habitat selection depended on the age class of the moose. Specifically, prime-aged moose had a tendency to die farther from shore during mild winters and much closer to shore during severe winters (Figure 13a). By contrast, senescent-aged moose tended to die farther from shore during severe winters (Figure 13b).

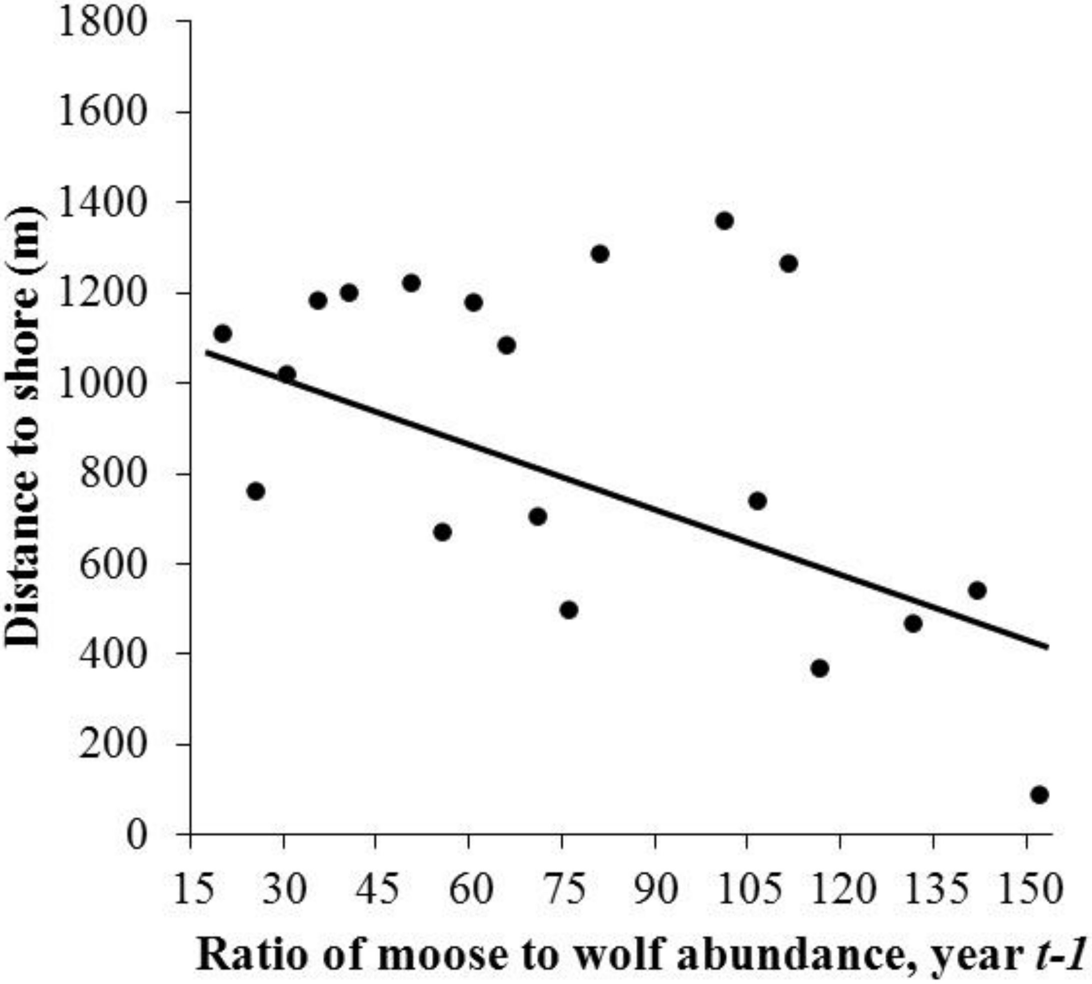


Figure 12. The influence of predation risk, indexed by the ratio of moose to wolf abundance (RATIO) in year *t*-1, on the location of wolf-killed moose in relation to Isle Royale's Lake Superior shore. The regression line displays the expected location, as predicted by the top-ranking model in Table 2. Each circle represents the mean location pooled across years with similar values of RATIO (i.e., every 5 units along the x-axis). I pooled data across years because some individual years were associated with relatively small sample sizes. The inset in Fig. 1 offers a basis for interpreting the scale of the y-axis. Low values of RATIO correspond to high predation risk.

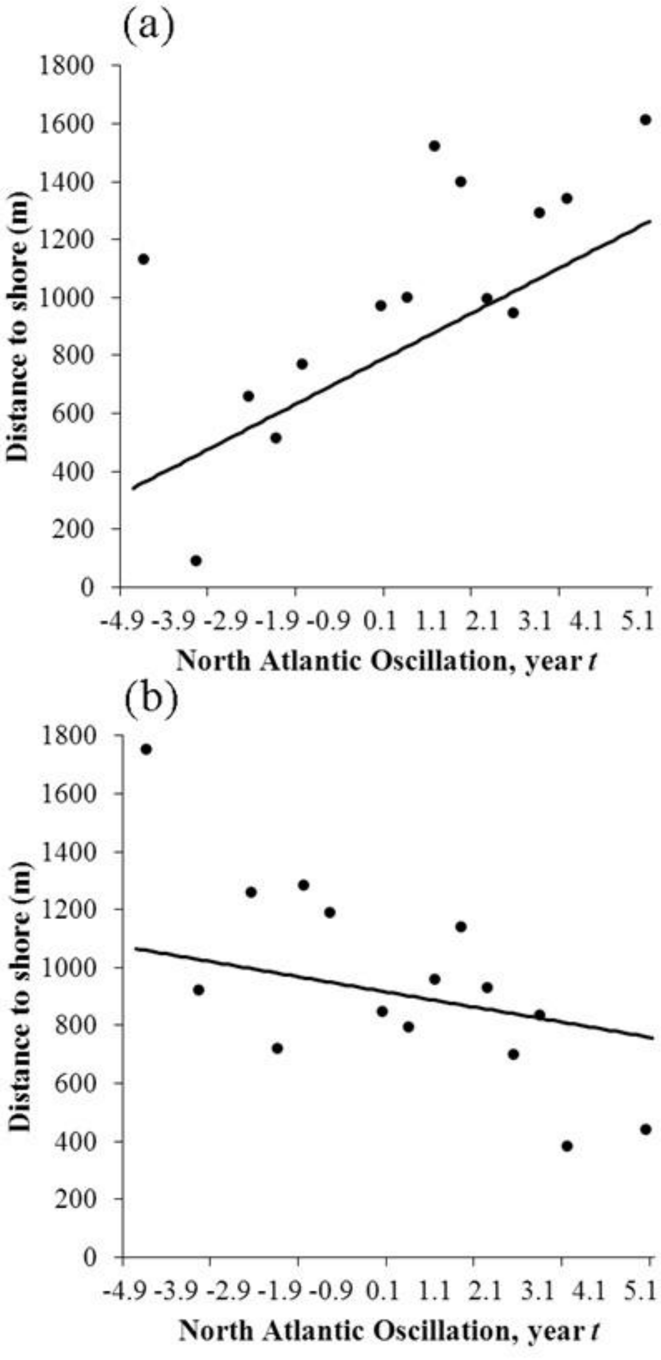


Figure 13. The influence of winter severity, indexed by the North Atlantic Oscillation (NAO) in year *t*, on the location of wolf-killed moose in relation to Isle Royale’s shore. Panel (a) represents prime-aged moose, and panel (b) represents senescent-aged moose. Regression lines represent the expected location, as predicted by the top-ranking model in Table 2. Each circle represents the mean location pooled across years with similar values of NAO (i.e., every 0.25 units along the x-axis, see Fig. 2 legend for details). Low values of NAO represent more severe winters.

DISCUSSION

Locations of moose carcasses reflect decisions about where moose select habitat and where wolves decide to hunt (and successfully kill) moose. Thus, the two processes are inextricably linked and carcass locations represent a reasonable basis for concluding that decisions about habitat used by moose and wolves are influenced by the life history state and body condition of moose. In particular, habitat selection is influenced by the decline in reproductive success associated with senescence (Fig. 3). Generally, and regardless of winter severity, senescent-aged moose that end up being killed by wolves, tend to die closer to the Lake Superior shoreline than do prime-aged moose ($t = 2.20$, $P = 0.01$). Because the frequency of senescent individuals in a population varies over time and among populations, senescence also manifests its influence at the population level, affecting processes such as growth rate and predator kill rate (Coulson et al. 2001; Peterson et al. 2010). My work suggests that a population’s age structure may also affect habitat selection, which could in turn influence spatial patterns in ecosystem processes such as herbivory. While the details of such relationships remain unevaluated, my work highlights a critical relationship between life history and habitat-related behaviors whose influences are also likely manifest in population-level processes.

The habitat selection of prey is a complicated dynamic involving the quality of forage in various habitat types, the state-dependence of the prey (Berger-Tal et al. 2010), and decisions made by predators which alter the predation risk experienced by prey (Creel et al. 2005, Kotler et al. 2010). For example, wolves tend to select landscape features where ungulates, such as elk (*Cervus elaphus*), are more vulnerable to predation (Bergman et al.2006). Elk also select grassland habitat, which is preferred for forage, when predators are not immediately present, but move into forested habitat when wolves are present (Creel et al. 2005), just as is predicted by predation sensitive foraging theory (Lima and Dill 1990). My work adds to these insights by showing how moose habitat selection varies from year to year with changes in predation risk (Figure 12). Specifically, moose tended to avoid near-shore habitat, where wolves tend to forage (see Figure A.2), when predation risk was high in the preceding year. Moose appear to be more sensitive to recent predation risk than current predation risk.

Winter severity influences ungulate population dynamics (Stenseth et al. 2002, Vucetich and Peterson 2004a), diet (Christianson and Creel 2007), and behavior (Mysterud and Østbye 2006, Creel and Christianson 2009). My observations extend the understanding of winter severity's influence by showing how it also affects habitat selection (Figure 13). In particular, during severe winters, prime-aged moose tended to die closer to shore, where foraging opportunities and predation risk are greater (Figure 13a). By contrast, senescent-aged moose tended to die farther from shore during severe winters (Figure 13b). These patterns suggest that senescent-aged moose sacrifice foraging opportunities for lower predation risk, when compared to the habitat selection of prime-aged moose. These patterns also suggest that prime-aged moose may be less sensitive to the effect that winter severity has on predation risk (cf., Figures 13a and 13b). This result is more complex than theoretical models which predict that animals in poor condition (e.g., a hunger state) are expected to be riskier in their pursuit of quality forage (McNamara and Houston 1986). These results also suggest that climate change is likely to affect habitat selection of large mammals.

Wolves have long been considered to be highly selective in their pursuit of prey (Mech 1970, Wright et al. 2006). My work further suggests that wolves not only have the ability to select for individuals with various body conditions within the prey population but they also have the ability to target these individuals in environmental space. Thus, my study substantiates that wolf hunting patterns correspond to the habitat decisions of their primary prey (Jędrzejewski et al. 2001, Bergman et al. 2006, Kauffman et al. 2007). My results also suggest that the interaction of moose senescent condition with winter severity may be, in part, a product of wolf hunting tendencies. For instance, per capita kill rates by wolves tend to be greatest during severe winters (Nelson & Mech 1986, Huggard 1993, Hebblewhite, Pletscher & Paquet 2002). This tendency is likely associated with moose nutritional condition and their corresponding ability to forage (Gasaway et al. 1983). Consequently, the habitat decisions of a moose likely depend on climatic conditions, their body condition, as well as wolf hunting strategies.

Conclusions of this study, based on locations of a large number of wolf-killed moose examined over a 50-year period, allude to some of the subtleties that likely pervade wolf-prey interactions, exhibited in changing habitat decisions as a moose approaches the most vulnerable life stage. Future research involving detailed study of individual moose should evaluate my finding that previous year risk is significant in current year habitat selection.

CHAPTER 5

SPATIAL PATTERN IN AREAS WHERE WOLVES KILL MOOSE WITH SENESCENT-ASSOCIATED PATHOLOGY

ABSTRACT

I document two landscape patterns in predation, each occurring at a separate spatial scale and each arising from a different cause. At the larger spatial scale, corresponding to the scale at which moose disperse or establish home ranges, subtle changes in geology and vegetation structure give rise to prey refugia. I suggest that these spatial patterns in predation can be attributed to spatial variation in resources. Isle Royale has a three-trophic level system of balsam fir (*Abies balsamea*), moose (*Alces alces*) density, and wolf (*Canis lupus*) density. The distribution of balsam fir, the preferred winter forage of moose, is largely confined to the east end of the island where there are moose and correspondingly more wolves. Thus, predation risk is greater on the east end of the island and lower on the west end where habitat heterogeneity seems to give rise to prey refugia. Refugia resulting from habitat heterogeneity can stabilize the interactions of predators and prey over vast temporal resolutions. At the smaller spatial scale, corresponding to the scale at which moose make within home range selections, I show how subtle changes in life history give rise to a different set of landscape patterns in predation whereby moose with senescent-associated pathology die in some areas and moose without pathology die in other areas. These results highlight that moose rely upon different landscapes to support their decision making in different states of their life history. Though similar observations have been made for animals residing in other systems (e.g., marine fish and insects), comparable results have not yet been documented among large mammals.

INTRODUCTION

Spatial variation in predation is a critical feature of predation ecology. Anthropogenic changes in landscape structure can create spatial variation in predation rates for a broad array of species (Rodewald 2002, Andruskiw et al. 2008, Perfecto and Vandemeer 2008). Spatially patterned predation has also been attributed to variation in climate (Stenseth et al. 2004), relative predation risk (Creel and Winnie 2005), habitat heterogeneity (Birkhofer et al. 2010), and trophic interactions mediated by landscape structure (McCoy et al. 2009). Furthermore, these patterns have been observed across both vast (Stenseth et al. 1998, Sundell et al. 2004) and narrow (Birkhofer et al. 2011) spatial scales. Extensive theory suggests that complex spatial dynamics in predation may be an emergent property of local population processes such as dispersal (e.g., Howeth and Leibold 2010).

Some insects and marine fish exhibit intricate spatial variation in predation dynamics that arise from complicated life history patterns, such as prey relying on different habitats during various states of their life (e.g., McCoy et al. 2009). Most mammals do not exhibit such dramatic changes over the course of their life history. Consequently, complicated life history patterns would not seem to be an important basis for spatial variation in predation dynamics among mammals. However, recent evidence has shown that moose (*Alces alces*), a large terrestrial mammal, living in Isle Royale National Park (Lake Superior, USA) exhibit variation in habitat selection with individual body condition (Montgomery et al., in review). Specifically, senescent-aged moose differed in their habitat selection in relation to prime-aged individuals. Another recent study, motivated to better understand the fertilizing effects of moose killed by wolves (*Canis lupus*) on large scale patterns in nutrient cycling, also found spatial patterns in the distribution of moose carcasses on Isle Royale (Bump et al. 2009). These observations suggest the value of investigating whether subtle changes in the life history of large mammalian prey in relation to their primary predators can result in spatial patterns in predation.

I assess this possibility by looking for spatial patterns in the landscape covariates associated with the distribution of wolf-killed moose in different states (e.g., those with senescent-associated pathology and those without). Theory also suggests that spatial variation in predator-prey dynamics can arise from spatial variation in resources that supply prey populations (Hopcraft et al. 2010). The nature of these dynamics relies greatly on the magnitude and spatial scale of resource variation. In particular, predation dynamics could depend on whether influential variation in resources occurs at scales that are larger than or smaller than the scale at which local predator-prey population dynamics occur. Therefore, I also show how spatial patterns is predation correspond to spatial patterns in resources occurring at spatial scales that relate to within home range selections and the distances at which moose disperse or establish home ranges (Labonté et al. 1998).

STUDY SITE AND FIELD METHODS

Isle Royale National Park (544 km2) is located in Lake Superior, USA (48^{o}N, 89^{o}W). The island is essentially a single-predator single-prey system (Peterson and Page 1988) that is largely closed to moose and wolf immigration and emigration (Adams et al. 2011). The moose population is typically comprised of 700–1100 individuals (1.4–2.4/km2) (ranges are interquartile ranges) (Vucetich et al. 2002) and averaged between 0.5 and 3.8 moose/km2 during the study period (Figure 14a). The population dynamics of moose are influenced by winter severity (Vucetich and Peterson 2004a) and predation risk (McLaren and Peterson 1994, Wilmers et al. 2004, Vucetich et al. 2011). During most winters wolf predation accounts for more than 80% of moose deaths (e.g., Vucetich and Peterson 2011), and the mean annual predation rate among moose (>9 months of age) is 9.9% (Vucetich et al. 2011). From 2000 to 2008 the wolf population averaged between 0.0 and 0.1 wolves/km2 (Figure 14b).

Between 2000 and 2008, I located carcasses of moose that were wolf-killed in winter (Figure 15). The majority of these carcasses were located during a 7-week winter study period involving extensive aerial surveys of the island (Jan. – Feb.). A minority of the carcasses were located by field crews conducting backcountry expeditions during the summer months (May – Aug). Those carcasses located during winter were necropsied directly following wolf abandonment of the carcass (generally within 7 days if moose death; Vucetich et al. 2011). Very few wolf-killed moose carcasses would have been missed during the winter aerial surveys because of the efficiency of the light aircraft and the necessity to precisely calculate wolf kill rate (Vucetich et al. 2002).

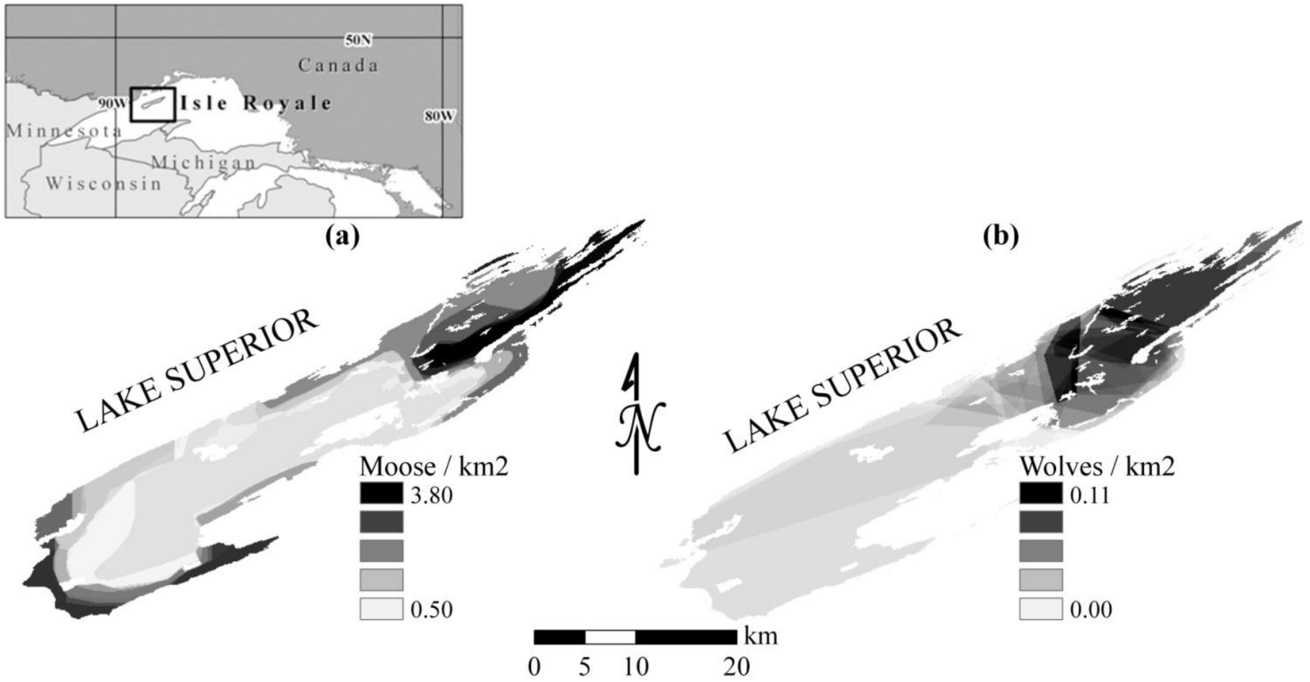


Figure 14. Average population dynamics for A) moose and B) wolves within Isle Royale National Park, Lake Superior, USA, 2000-2008.

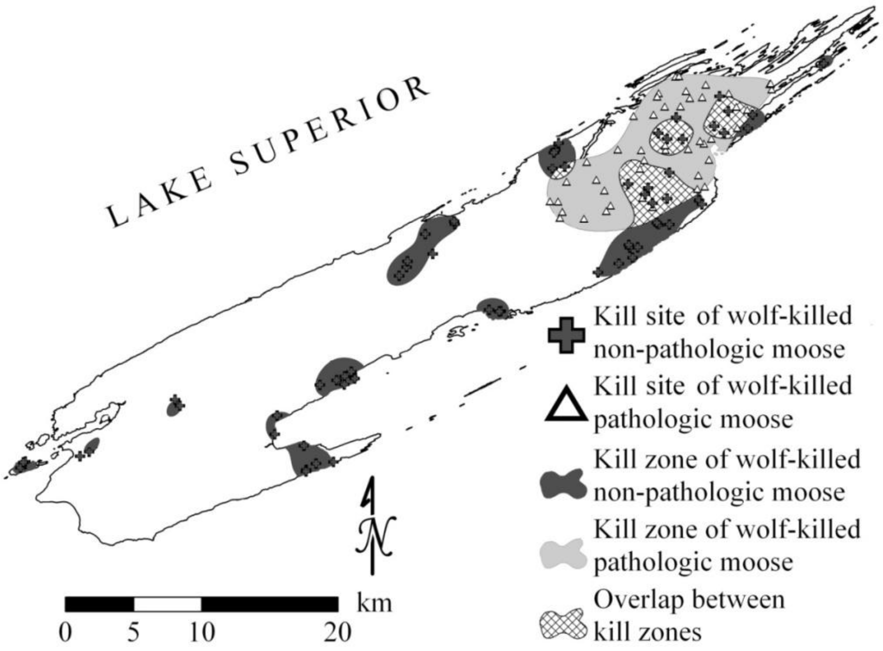


Figure 15. Kill zones of wolf-killed pathologic and non-pathologic moose and the corresponding kill sites in Isle Royale National Park, Lake Superior, USA, 2000-2008.

During the necropsies cause of death was identified from field sign (e.g., blood patterns, wolf chase sign, and evidence of struggle). Degree of decomposition and adult tick presence were used to identify season of death for moose carcasses discovered in the summer months. I also identified senescent-associated pathology based on the degree of osteoarthritis (Peterson et al. 2010) and periodontal disease (Peterson 1977) in the moose carcasses. I classified a moose as being *pathologic* if the carcass showed signs of moderate to severe osteoarthritis or periodontal disease. If the carcass had none to mild osteoarthritis or periodontal disease the moose was *non-pathologic*. The presence of pathology in this population of moose is senescent-associated. From an examination of 2,652 moose carcasses collected on Isle Royale between 1959 and 2008 the mean age of non-pathologic individuals was 3.90 years while the mean age of pathologic individuals was 12.02 years (Montgomery et al. unpublished data).

ANALYTICAL METHODS

I conducted a preliminary assessment of six landscape covariates associated with moose carcass locations to determine whether these sites were spatial patterned. More precisely I assessed whether the spatial patterns of these landscape covariates for combined pathologic and non-pathologic moose and pathologic moose and non-pathologic moose considered separately deviated from random (Table 8). The minimum mapping unit for this analysis was 30 m. Two of these landscape covariates (% canopy cover and % conifer cover) were derived from the U.S. Geologic Survey’s National Land Cover Database (NLCD; Homer et al. 2007), which is based on data remotely sensed between 2001 and 2006. Percent canopy cover represented the proportion of each raster cell that was covered by canopy. Percent conifer was calculated as the proportion of each raster cell that was covered with a forest type dominated by conifer trees (i.e., evergreen forest, mixed forest, and palustrine forested wetland). The percent canopy cover layer has an estimated accuracy >81% (Wickham et al. 2010), and the conifer distribution layer has a forest-type classification accuracy of >91% (NLCD 2006 metadata, <http://www.csc.noaa.gov/crs/lca>, accessed on 1 Dec 2010). I also used the National Elevation Dataset to portray elevation and calculate slope. The last two landscape covariates that I assessed were distance to inland lakes and distance from Lake Superior. I mapped these two rasters because ungulates are particularly vulnerable to wolf predation on inland ice (Carbyn 1983) and the shoreline of Isle Royale is associated with increased wolf use in winter (Montgomery et al. in review).

Kill Zones

I used locations of wolf-killed moose and kernel density estimates (KDE) to identify the location and extent of moose carcasses at two spatial scales (kill zones and kill sites). I generated KDEs in R (version 2.10.0, www.cran.r-project.org) using least-squares cross-validation, which provides robust bandwidth estimates particularly when there are no repeat locations (Gitzen and Millspaugh 2003, Gitzen et al. 2006, Steury et al. 2010). I used ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA) to represent each KDE as a 30 m resolution raster, which depicted the probability of a moose being wolf-killed at 1% intervals. The central concentration of carcasses occurred near the 1st KDE percentile with less-concentrated carcass distribution towards the 95th KDE percentile.

Table 8. Spatial autocorrelation of the environmental covariates associated with carcass locations for combined pathologic and non-pathologic moose and separately for pathologic moose and non-pathologic moose killed by wolves in winter on Isle Royale National Park, Lake Superior, USA, 2000-2008.

Variable	**Dataset**	**Moran's index**	**Expected index**	***var***	**z**	***P***
Canopy cover	Combined	0.250	-0.005	0.262	0.497	0.619
	Non-pathologic	0.158	-0.010	0.008	1.923	0.054
	Pathologic	0.016	-0.009	0.004	0.385	0.700
Conifer	Combined	1.004	-0.005	0.265	1.957	0.050
	Non-pathologic	0.056	-0.010	0.008	0.074	0.458
	Pathologic	-0.102	-0.009	0.005	-1.384	0.166
Elevation	Combined	2.092	-0.005	0.254	4.158	<.0001
	Non-pathologic	0.378	-0.010	0.007	4.515	<.0001
	Pathologic	0.153	-0.010	0.004	2.548	0.011
Slope	Combined	0.009	-0.005	0.239	0.030	0.976
	Non-pathologic	0.061	-0.01	0.008	0.813	0.416
	Pathologic	-0.063	-0.009	0.003	-0.912	0.362
Lake Superior	Combined	0.924	-0.005	0.264	1.809	0.070
	Non-pathologic	0.450	-0.010	0.008	5.245	<.0001
	Pathologic	0.531	-0.009	0.004	8.101	<.0001
Inland lakes	Combined	0.332	-0.005	0.261	0.659	0.510
	Non-pathologic	0.570	-0.010	0.008	6.670	<.0001
	Pathologic	0.365	-0.009	0.004	5.647	<.0001

Hunting patterns of predators are known to be inherently variable (Roth and Lima 2007). Additionally, wolves are opportunistic predators (Mech and Peterson 2003) hence locations of kills can appear random and be potentially influenced by outliers. Consequently, I used a Bayesian framework and Monte Carlo simulation tests (iterated 10,000 times) to identify the percentile that best represented the core area boundary of each kill zone (Wilson et al. 2010). This Bayesian framework utilizes functions within several R libraries including MASS, spatstat, splancs, and MCMCpack (Rowlingson and Diggle 1993, Venables and Ripley 2002, Baddeley and Turner 2005, Martin and Quinn 2006), and is based on comparing the distribution of locations to a completely spatial random distribution (Ripley 1976).

Regression Models

I assessed the landscape covariates at two spatial scales. First, I compared a pair of regression models that characterize the landscape covariates of kill zones for pathological and non-pathologic moose (kill zone models). I also compared regression models that characterize the landscape covariates of individual kill sites within each kill zone for pathologic and non-pathologic moose (kill site models). The purpose of these models was to examine variation in landscape covariates associated with predation events at scales that roughly correspond to the scale at which moose disperse or select their home ranges (kill zone models) and a scale the reflects within home range selections (kill site models). To facilitate these comparisons, I standardized the landscape covariates before building each regression model. None of the landscape covariates in the analysis were collinear (i.e., $R > 0.70$).

Kill Zone Models

I built a pair of multiple linear survey regression models based on a random sample of locations drawn from the pathologic and non-pathologic kill zones. I selected a sample size (n)

that would yield a desired level of precision (in the regression coefficients) given the observed variability in the landscape covariates. To determine n, I used this equation (Thompson 2002): $n = [(d^2/z^2\sigma^2) + (1/N)]^{-1}$, where d is desired margin of error, z is the standard z-score based on an α equal to 0.01, N is the total population of cells within the kill zone, and σ is the standard deviation for each landscape covariates. I estimated σ for each landscape covariate from a sample of 10,000 random locations across Isle Royale. Because the calculated sample varied among the six landscape covariates, I set the sample size equal to the largest of these random samples.

After generating the random sample I built a multiple linear survey regression model for pathologic and non-pathologic moose kill zones, using PROC SURVEYREG in SAS (version 9.2, Cary, NC) which accounts for the random sample (n) in relation to the total population (N). This model took the form: $Y_i = X\beta_i + \varepsilon$ where Y_i is the percentile of the KDE at the ith sample, $X\beta_i$ are the regression coefficients at the ith sample, and ε is the random error term. The residuals were homoscedastic and approximated the normal distribution.

Kill Site Models

` The kill site models were based on the landscape covariates in the direct vicinity of the sites where wolves killed moose within the kill zones. Specifically, I considered an area with a 50 m radius (0.79 ha) surrounding each wolf-killed moose. This area corresponds approximately to the spatial extent of daily moose movements, which are on the order of 10’s to 100’s of m (Phillips et al. 1973) and to the distances that wolves chase moose before killing them, which are on average < 100 m (Wikenros et al. 2009). Thus, this area likely reflects each moose’s’ habitat selection shortly before it was killed by wolves. I then calculated the mean of the landscape covariates and response variable (i.e., percentile of the KDE) that intersected the 50 m radius surrounding each kill site. I used SAS PROC MIXED to model these data as a spatial linear regression model: $Y_i = x_i'\beta + Z_i$, where Y_i is the percentile of the KDE at the ith kill site, x_i' represents the vectors of the landscape covariates at the ith kill site, β is the vector of fixed effects coefficients, and Z_i is the spatially autocorrelated random error term. Once again, the residuals were homoscedastic and approximated the normal distribution. Finally, I evaluated differences in landscape covariates associated with pathologic and non-pathologic moose kill zones and kill sites by comparing the regression coefficients produced from the respective models. I also produced models with non-influential coefficients (those with standard errors (se) overlapping 0) removed to illustrate that the parameter estimates (se) in less parameterized models varied only slightly in relation to the full model (see Figure B1 in Appendix B).

RESULTS

My sample included only wolf-killed moose whose skeletal remains were sufficient to permit being categorized as pathologic (n=109) or non-pathologic (n=106). For the entire sample, carcasses were not distributed randomly with respect to elevation ($P < 0.01$), but they were randomly distributed with respect to the other five covariates (Table 8). However, when the pathologic and non-pathologic moose were considered separately, their spatial distribution was significantly associated (i.e., $P < 0.01$) with three landscape covariates (elevation, distance to Lake Superior, and distance to inland lakes) (Table 8). This spatial patterning enabled us to examine landscape covariates for pathologic and non-pathologic moose separately at the two spatial scales of the analysis.

Bayesian analysis of the KDE indicated that the core areas of kill zones for pathologic moose correspond to the 30th KDE percentile, where the percentile (ranging from 1 to 30) is inversely equivalent to the likelihood of being killed by wolves in that area of the kill zone. Hereafter, I refer to smaller percentiles of a kill zone as being equivalent to more intense portions of the kill zone. For comparative purposes, I also identified the 30th percentile for non-pathologic moose. The extent and location of the kill zones differed between the pathologic and non-pathologic moose. The core kill zone for pathologic moose was a single contiguous polygon of 102 km2 whereas the core kill zone for non-pathologic was thirteen disjoint polygons covering a total of 84 km2 (Figure 15). The two kill zones overlapped by approximately one third (32 km2) (Figure 15). While these zones represent 29% of Isle Royale's winter area, 48% of the pathologic and non-pathologic moose died within their respective core kill zones. Furthermore, the core kill zone for pathologic moose covered just 16% of Isle Royale, yet contained 42% of all pathologic moose in the study.

Differences in the distribution and extent of kill zones for pathologic and non-pathologic moose are likely attributable to variation in the landscape covariates associated with each kill zone (Figure 16a). The most important difference between pathologic and non-pathologic moose kill-zones involved elevation. Specifically, the intensity of a kill zone increased greatly at higher elevations for pathologic moose ($P < 0.0001$), but decreased with elevation for non-pathologic moose ($P < 0.0001$) (Figure 16a). Another difference is that the intensity of a kill zone increased with greater distances from inland lakes for pathologic moose ($P < 0.0001$), but decreased for non-pathologic moose ($P < 0.0001$) (Figure 16a). Also, the intensity of a kill zone increased greatly at closer distances to Lake Superior for non-pathologic moose ($P < 0.0001$), but gradually increased for pathologic moose ($P = 0.001$) (Figure 16a). The distribution of conifer varied little between kill zones for pathologic and non-pathologic moose (Figure 16a). Finally, the likelihood of being wolf-killed decreased with canopy cover for pathologic moose (*P* <0.0001), but was non-influential for non-pathologic moose (*P* = 0.85) (Figure 16a).

The kill zone models, described above, correspond to an approximate spatial scale at which moose select home ranges or distances at which they disperse (i.e., 10's of km2). Kill site models, on the other hand, focus on spatial scales corresponding to within home range selections by moose. This distinction is important because, while kill site models revealed differences in landscape covariates between pathologic and non-pathologic moose, they were not always the same differences revealed by the kill zone models (cf., Figure 16a and 16b). For example, the intensity of a kill zone at sites where pathologic moose were killed tended to decrease with canopy cover (*P* = 0.28) and increase with conifer cover (*P* = 0.11); however, the opposite was true for non-pathologic moose for canopy cover (*P* = 0.05) and for conifer cover (*P* = 0.06; Figure 16b). Another difference between kill zone and kill site models involved distance to shorelines. In particular, the influence of distance to Lake Superior and to inland lakes differed between pathologic and non-pathologic moose for the kill zone models (Figure 16a), but not for the kill site models (Figure 16b). The kill zone and kill site models were similar with respect to the influence of elevation on pathologic and non-pathologic moose. The intensity of a kill site increased greatly with increasing elevation for pathologic moose (*P* = 0.001), but not for non-pathologic moose (*P* = 0.45).

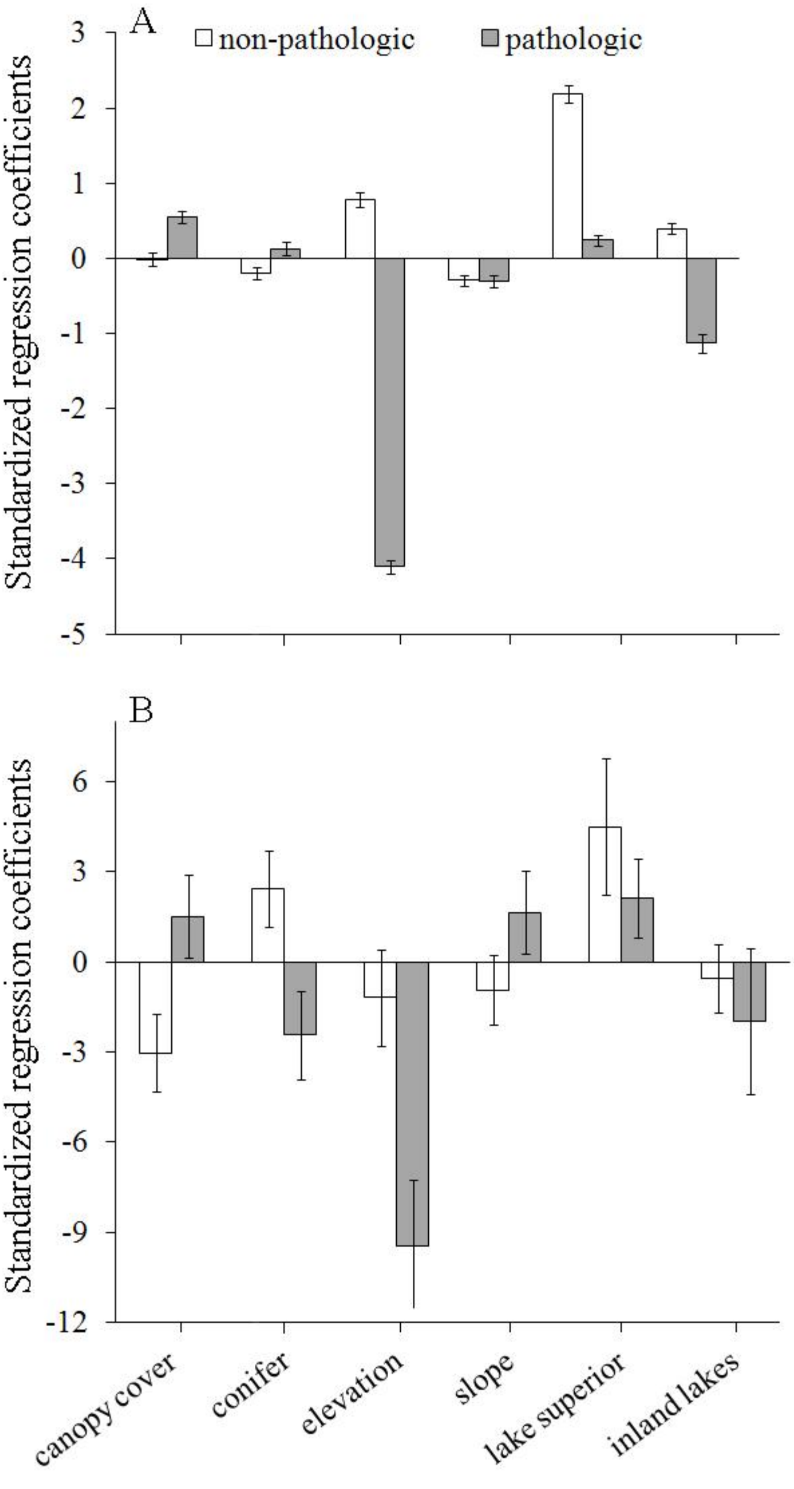


Figure 16. Standardized regression coefficients with standard error bars for all environmental covariates from A) the kill-zone model (multiple linear survey regression) and B) the kill-site model (spatial mixed linear regression).

Based on examinations of the area associated with the upper quartile (> 75% of the distribution) of both moose and wolf densities I identified that regions of high moose density (Figure 14a) correspond to regions of high wolf density (Figure 14b; $\chi^2 = 11.53$, $P < 0.001$). Furthermore, regions of high moose density (Figure 14a) correspond to the spatial position of the pathologic moose kill zone (Figure 15; $\chi^2 = 33.51$, $P < 0.001$) and the non-pathologic moose kill zones (Figure 15; $\chi^2 = 4.39$, $P = 0.04$).

DISCUSSION

My analysis demonstrates that wolves killed moose with senescent-associated pathology in areas that were geographically distinct and functionally different in the composition of landscape covariates from areas where non-pathologic moose were wolf-killed. I observed these spatial patterns of predation at two spatial scales suggesting that moose habitat selection, and the corresponding likelihood of being preyed upon by wolves, operated hierarchically (Johnson 1980, McLoughlin et al. 2002). These patterns were not evident when examining all moose carcasses together, regardless of individual body condition. However, significant spatial patterning (i.e., $P < 0.01$) became evident when I analyzed landscape covariates associated with moose carcass locations separately by moose condition (i.e., senescent-associated pathology or not).

Examining the spatial patterns of predation at the larger spatial scale (i.e., kill zones) revealed that moose, by individual condition, broadly died in different regions of the island. Moose with senescent-associated pathology died in one contiguous area on the east end of the island while non-pathologic moose died in 13 different kill zones covering the full extent of the island. The two kill zones did overlap by approximately one third illustrating that most predation occurred on the east end of the island (Figure 15). I attribute this spatial pattern in predation to the spatial pattern of resources. The Isle Royale system has three trophic levels including balsam fir (*Abies balsamea*), moose, and wolves (Wilmers et al. 2006). The east end of Isle Royale has more balsam fir, a preferred winter forage of moose (Vucetich and Peterson 2005), and correspondingly higher moose densities (Figure 14a). Given that there are higher moose densities on this end of the island I would expect there to be higher wolf densities because wolf hunting corresponds to prey habitat selection (Jedrzejewski et al. 2001, Bergman et al. 2006). Figure 14b illustrates that this is the exact relationship that I observed across the study period. Conversely, the west end of the island likely presents moose with a source of refugia from predation because of lower moose densities (Vucetich and Peterson 2004b) and lower wolf densities (Fig 1b) that I suggest derives from habitat heterogeneity (i.e., fewer balsam fir stands). This result indicates that habitat heterogeneity can create prey refugia (Lewis and Eby 2002, Brown 2003, Briggs and Hoopes 2004). Theory suggests refugia can have a stabilizing effect on predator-prey interactions (Fryxell et al. 1988, Ellner et al. 2001, Kauffman et al. 2007). Isle Royale should be expected to be relatively unstable given that it is a single predator/single prey system (Peterson and Page 1988). We know that ratio-dependent kill rates represent one stabilizing mechanism on the island (Vucetich et al. 2002) and this analysis highlights that spatial variation in predation may represent another stabilizing mechanism.

At the finer spatial scale (i.e., kill sites within kill zones), I find that moose die in fundamentally different areas by individual body condition (senescent-associated pathology or not). This result corresponds to the theoretical idea that spatial patterns in predation can arise from intrinsic properties of predators or prey (i.e., not only from exogenic processes, like spatial variation in resource abundance) (McNamara and Houstson 1987, Heithaus et al. 2007). In this case, the spatial patterning likely rises from the fact that moose (a long-lived prey species that senesces) have different states of their life history (just like fish or insects; McCoy et al. 2009) and within those different states habitat selection varies. My analysis suggests that those variations in habitat selection can result in landscape level patterns in predation (e.g., Figure 15). For instance, I discovered that 42% of moose with senescent-associated pathology selected habitat within an area covering just 16% of the Isle Royale landscape before being predated upon by wolves. Within that area moose with senescent-associated pathology selected for higher elevations, greater percent conifer, and lower canopy cover. The selection of areas at higher elevations and with more complex vegetation structure (i.e., conifer cover) can be interpreted as anti-predator strategies. Many ungulates will select habitat at higher elevations or with more conifer cover when vulnerable to predation (Bergerud et al. 1984, Adams et al. 1995, Fortin et al. 2005, Barnowe-Meyer et al. 2010).

Wolves influence the deposition of prey carcasses (Wilmers et al. 2003, Wilmers and Getz 2004) which can have important fertilizer effects on the environment (Bump et al. 2009). Bump et al. (2009) discovered variation in spatial patterning of moose carcasses in Isle Royale National Park across space and time which were attributed, at least in part, to the behavior of wolves. My research suggests that both habitat heterogeneity and the individual body condition of moose could also be causal mechanisms contributing to these patterns. Though my observations do not represent a full assessment of the causes and consequences of the spatial patterns of predation on Isle Royale, they do suggest that; i) spatial patterns in predation-related phenomena can be found in large, terrestrial mammals; (ii) these patterns can occur at relatively small spatial scales (i.e., hundreds of square kilometers, not only at continental scales); and (iii) these spatial patterns can arise from subtle changes in landscape structure and subtle changes in life history. These findings should inspire empirical ecologists to look for similarly subtle, but potentially important patterns in other terrestrial systems; and theoreticians to develop models that involve hierarchical and subtle sources of variation like what I observed here, so that I can better understand the consequences of spatial patterns of predation.

CONCLUSION

It is doubtful that the pre-20th century naturalists who painstakingly recorded organism-habitat associations through visual observation could have possibly conceived of the technological advances that currently inform habitat selection research. Researchers have moved from hours spent every day in the field collecting data to mere seconds at the computer engaged in the same activity. The quest to comprehend animal ecology, however, remains the same. The prospect of elucidating the ecology of an individual animal which might characterize a population or even the species itself has proved completely absorbing. Researchers have made important technological advances and have developed new and interesting models to describe habitat selection. These collective innovations have led to a vast progression of the discipline of habitat selection research.

The relationship between organisms and their habitat is considered integral to species survivability and the inferences garnered from habitat selection research inform management and policy decisions. This information is particularly useful in the dynamic 21st century where threats to environmental change are ubiquitous and persistent. There is no doubt that further technological and quantitative innovations will be an integral part of the continued development of habitat selection research.

The models that I developed in Chapters 1 and 2 revealed that despite the continued advances of the technology associated with habitat selection research, efforts to ensure that sound research methodologies are employed remain fundamental to the discipline. None of the techniques used to incorporate telemetry error, typical of VHF systems, into habitat selection models were reliably accurate. This accuracy was particularly poor across categorical covariates demonstrating that telemetry error interacts with patch size to influence the accuracy of these models. The results of Chapter 2 demonstrated that ignoring telemetry error, even for highly resolute telemetry systems, can only be done when the consequences of such actions are rectified with the experimental design. I also showed that the effects of telemetry error can be magnified given the resolution of the categorical covariates used to describe habitat features. For instance, to attain accuracies >90% the researcher needs small telemetry errors (<10 m) across habitat with relatively large patch sizes (20−200 ha). These results articulate that habitat selection research may need to move away from point-based estimation and I make recommendations to consider alternative methodologies which include state-space models and utilization distributions. Both of these methodologies are relatively impervious to the effects of telemetry error and have proved to be powerful means for estimating of animal-habitat associations.

Chapters 4 and 5 further illustrate the power of modeling habitat selection through examination of predator-killed animals. This is a particularly important method because carcass locations, where individual body conditions can be readily documented, can be used to assess the relative influence of life history state on animal decision-making. My research demonstrated how interactions between individual body conditions and the biotic world (namely winter severity) can alter habitat selection. It also provided evidence to support the theory that large mammals, like other fish and insects, may utilize fundamentally different landscapes in various states of their life history. Not only will moose adjust their habitat selection in response to their condition but there are specific landscape-level patterns of predation that result from these selections. This result became evident when evaluating the three trophic level system of Isle Royale National Park. Moose prefer to forage on balsam fir in winter and where there is more balsam fir there are more moose and correspondingly more wolves. Therefore, my work provides evidence that habitat heterogeneity can create prey refugia and that moose rely on specific landscape covariates given their state (pathologic or not). This research is novel in that comparable results have not yet been demonstrated in large mammals, as they have in other animal communities. This illustrates that mammals have complex life histories that are greatly dependent on their state (whether that be senescent-aged or prime-aged, pathologic or non-pathologic). Furthermore, my research also showed that moose will adjust their decision-making in response to predation risk in the preceding year. This highlights the potential for lingering residual effects of predation risk. My research demonstrates that future research should consider examining predation risk in both year t and $t-1$.

APPENDIX

APPENDIX A

SUPPLEMENTARY FIGURES FOR CHAPTER 4

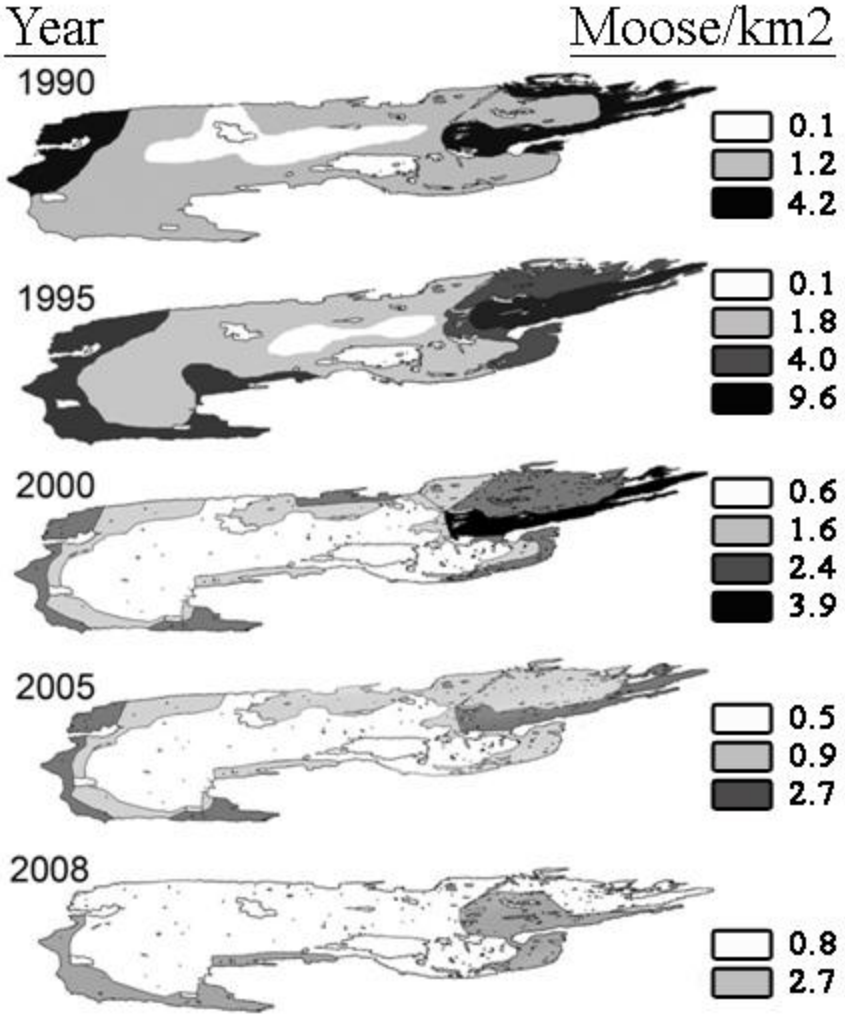


Figure A.1. During each year of the study period moose abundance was estimated across Isle Royale using aerial survey methods and random stratified sampling. More specifically, the number of moose was counted on 91 permanent plots (each 1 km2 in size). The plots represent 18% of Isle Royale's land area. Mean estimated sightability is 75% (Peterson and Page 1993). Other details of the aerial survey techniques are described in Peterson and Page (1993). Stratification was based on methods described in Gasaway et al. (1986) (see also Gasaway et al. 1992). Using the negative binomial distribution to describe the distribution of plot counts, statistical parsimony (i.e., AIC) was used to judge whether two strata should be combined for a single estimate of density or kept separate with different estimates of density.

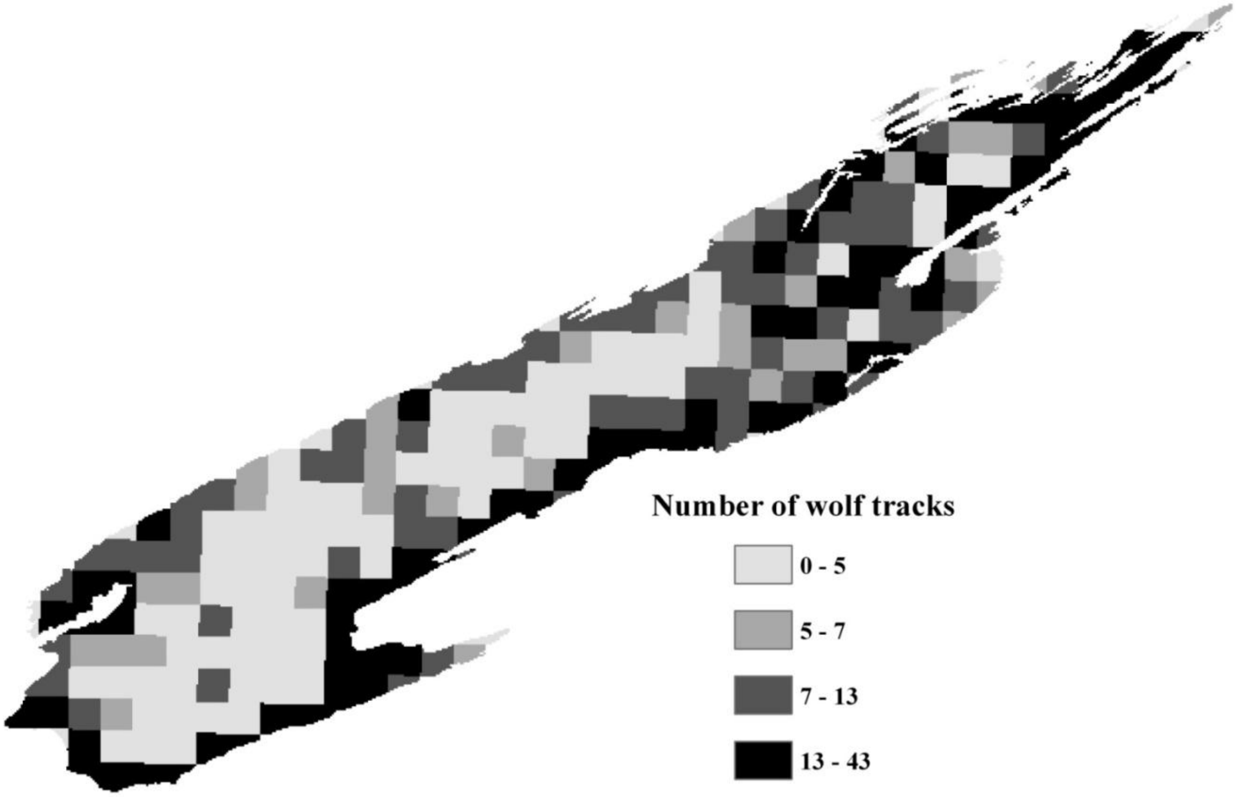


Figure A.2. During each 7-week field season in midwinter locations and travel routes (tracks through the snow) of wolves on Isle Royale were recorded from aerial surveys using fixed-wing aircraft. Locations and routes were recorded in the process of estimating kill rate, and represent a complete record of travel and routes for approximately 44 days each winter (median = 44, interquartile range = [38, 47]. Travel routes were recorded on 1:274,560 maps that depict each 1 square mile sections on Isle Royale. I compiled the travel routes from seven years of observation (1980, 1985, 1990, 1995, 2000, 2005, and 2010) by recording the number of times that wolves traveled through each section.

APPENDIX B

SUPPLEMENTARY FIGURE FOR CHAPTER 5

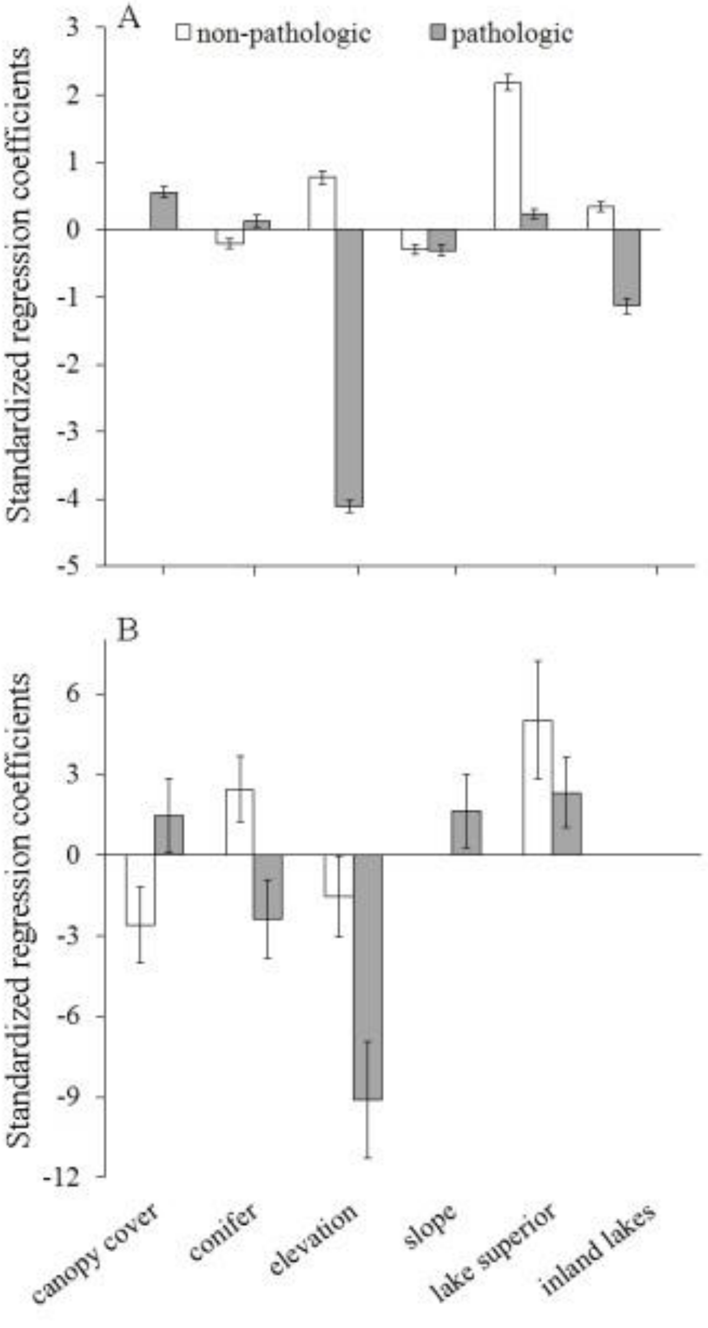


Figure B1. Standardized regression coefficients with standard error bars for influential environmental covariates from A) the kill-zone model (multiple linear survey regression) and B) the kill-site model (spatial mixed linear regression).

LITERATURE CITED

LITERATURE CITED

Adams L.G., F.J. Singer, and B.W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584-594.

Adams, J. R., L. M. Vucetich, P. W. Hedrick, R. O. Peterson, and J. A. Vucetich. 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. Proceedings of the Royal Society B-Biological Sciences 278:3336-3344.

Aebischer, N. J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and season movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076-1088.

Alldredge, J. R., and J. Griswold. 2006. Design and analysis of resource selection studies for categorical resource variables. Journal of Wildlife Management 70:337-346.

Alldredge, J. R., and N. Dasgupta. 2003. Multiple comparisons in resource selection using logistic regression. Journal of Agricultural, Biological, and Environmental Statistics 8:356-366.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-267.

Anderson, D. P., M.G. Turner, J.D. Forester, J.U.N. Zhu, M.S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management 69:298-310.

Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk by the American marten. Ecology 89:2273-2280.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. Journal of Wildlife Management 73:876-884.

Baddeley, A., and R. Turner. 2005. Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12:1–42.

Baker, J.D. and T.C. Johanos. 2004. Abundance of the Hawaiian monk seal in the main Hawaiian Islands. Biological Conservation 116:103-110.

Barnowe-Meyer K.K., P.J. White, T.L. Davis, D.W. Smith, R.L. Crabtree, and J.A. Byers. 2010. Influences of wolves and high-elevation dispersion on reproductive success of prognhorn (Antilocapra americana). Journal of Mammalogy 91:712-721.

Barron, D. G., J.D. Brawn, and P.J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods in Ecology and Evolution 1:180-187.

Benson, E. 2010. Wired wilderness: technologies of tracking and the making of modern wildlife. Johns Hopkins University Press, Baltimore, MD. USA.

Berger-Tal, O., S. Mukherjee, B.P. Kotler, and J.S. Brown. 2010. Complex state-dependent games between owls and gerbils. Ecology Letters 13:302-310.

Bergerud A.T., H.E. Butler, and D.R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62:1566-1575.

Bergman E.J., R.A. Garrott, S. Creel, J.J. Borkowski, R. Jaffe, and F.G.R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16:273-284.

Beyer, E., Jr., and J.B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. Journal of Wildlife Management 58:178-180.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. at: <http://www.spatialecology.com/htools>. Accessed 2 Dec 2009.

Beyer, H. L., D.T. Haydon, J.M. Morales, J.L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2245-2254.

Birkhofer, K., S. Stefan, and T. Wiegand. 2010. Assessing spatiotemporal predator-prey patterns in heterogeneous habitats. Basic and Applied Ecology 11:486-494.

Birkhofer, K., V. Wolters, and T. Diekötter. 2011. Density-dependent and -independent effects on the joint use of space by predators and prey in terrestrial arthropod food-webs. Oikos 120:1705-1711.

Blunt, W. 2004. Linnaeus: The compleat naturalist. William Collins, Sons & Company Ltd. London, England. UK.

Bonter, D.N., S.A. Gauthreaux, Jr., and T.M. Donovan. 2008. Characteristics of important stopover locations for migrating birds: remote sensing with radar in the Great Lakes basin. Conservation Biology 23:440-448.

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

Boyce, M. S., J. Pitt, J.M. Northrup, A.T. Morehouse, K.H. Knopff, B. Cristescu, and G.B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2213-2219.

Boyce, M.S., J.S. Mao, E.H. Merrill, D. Fortin, M.G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421-431.

Briggs C.J. and M.F. Hoopes. 2004. Stabilizing effects in spatial parasitoid-host and predator-prey models: a review. Theoretical Population Biology 65:299-315.

Brook, B.W., N.S. Sodhi, and P.K.L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424:420-426.

Brown B.L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. Ecology Letters 6:316-325.

Browne, J. 2010. Charles Darwin: Voyaging. Random House, London, England. UK.

Bubenik, A. 1997. Evolution, Taxonomy and Morphophysiology. Ecology and Management of the North American Moose (eds. C. C. Schwartz and A. W. Franzmann), pp. 77-124. Smithsonian Books, Washington, D.C. USA.

Bump J.K., R.O. Peterson, and J.A. Vucetich. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90:3159-3167.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, NY. USA.

Buskirk, S. W. and J.J. Millspaugh. 2006. Metrics for studies of resource selection. Journal of Wildlife Management 70:358-366.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2157-2162.

Carbyn, L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. Journal of Wildlife Management 47:963-976.

Cargnelutti, B., A. Coulon, A.J.M. Hewison, M. Goulard, J.-M. Angibault, and N. Morellet. 2007. Testing global positioning system performance for wildlife monitoring using mobile collars and known reference points. Journal of Wildlife Management 71:1380-1387.

Carpenter, S. R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639.

Carrel, W. K., R. A. Ockenfels, J. A. Wennerlund, and J. C. Devos, Jr. 1997. Topographic mapping, LORAN-C, and GPS accuracy for aerial telemetry locations. Journal of Wildlife Management 61:1406-1412.

Chetkiewicz, C.-L. B., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036-1047.

Christ, A., J.M. Ver Hoef, and D. Zimmerman. 2008. An animal movement model incorporating home range and habitat selection. Environmental and Ecological Statistics 15:27-38.

Christianson, D. A., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. Journal of Wildlife Management 71:164-176.

Chu, D. S., B. A. Hoover, M. R. Fuller, and P. H. Geissler. 1989. Telemetry location error in a forested habitat. Pages 188-194 in C. J. Amlaner, editor. Proceedings of the Tenth International Symposium on Biotelemetry, University of Arkansas Press, Baltimore, MD. USA.

Conner, L. M., M. D. Smith, and L. W. Burger. 2003. A comparison of distance-based and classification-base analyses of habitat use. Ecology 84:526-531.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80:566-575.

Copeland, J. P., J. M. Peek, C. R. Groves, W. E. Melquist, K. S. McKelvey, G. W. McDaniel, C. D. Long, and C. E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. Journal of Wildlife Management 71:2201-2212.

Coulombe, M.-L., A. Massé, and S. D. Côté. 2006. Quantification and accuracy of activity data measured with VHF and GPS telemetry. Wildlife Society Bulletin 34:81-92.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T.H. Clutton-Brock, M.J. Crawley, and B.T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292, 1528–1531.

Cox, J. J., D. S. Maehr, and J. L. Larkin. 2006. Florida panther habitat use: New approach to an old problem. Journal of Wildlife Management 70:1778-1785.

Craighead, F. C., and J. J. Craighead. 1970. Radiotracking of grizzly bears in Yellowstone Park, Wyoming, 1965. National Geographic Society Research Reports, 1965 Projects, p.35-43.

Creel, S., and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: Implications for trophic cascades. Ecology 90:2454-2466.

Creel, S., and J. J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour 69:1181-1189.

Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Cressie, N., C. A. Calder, J. S. Clark, J. M. Ver Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. Ecological Applications 19:553-570.

Cutler, T. L., and D.E. Swann. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27:571-581.

Cypher, B. L., C.D. Bjurlin, and J.L. Nelson. 2009. Effects of roads on endangered San Joaquin kit foxes. Journal of Wildlife Management 73:885-893.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, England. UK.

D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430-439.

Devictor, V., R. Julliard, and F. Jiguet. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507-514.

Dickson, B.G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66:1235-1245.

Doherty, T.J. 2003. Invited Review: Aging and sarcopenia. Journal of Applied Physiology 95:1717-1727.

Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619-628.

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

Edge, W. D., C.L. Marcum, and S.L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51:844-851.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60:185-189.

Ellner S.P., E. McCauley, B.E. Kendall, C.J. Briggs, P.R. Hosseini, S.N. Wood, A. Janssen, M.W. Sabelis, P. Turchin, R.M. Nisbet, and W.W. Murdoch. 2001. Habitat structure and population persistence in an experimental community. Nature 412:538-543.

Ericsson, G., and K. Wallin. 2001. Age-specific moose (Alces alces) mortality in a predator-free environment: evidence for senescence in female. Ecoscience 8:157-163.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, Alces alces. Ecology 82:1613-1620.

Findholt, S. L., B. K. Johnson, L. D. Bryant, and J. W. Thomas. 1996. Corrections for position bias of a LORAN-C radio-telemetry system using DGPS. Northwest Science 70:273-280.

Findholt, S. L., B. K. Johnson, L. McDonald, J. W. Kern, A. A. Ager, R. J. Stussy, and L. D. Bryant. 2002. Adjusting for radiotelemetry error to improve estimates of habitat use. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-555, Portland, OR. USA.

Forester, J. D., H.K. Im, and P.J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554-3565.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (Cervus elaphus) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:273-287.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2187-2200.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ. USA.

Fretwell, S. D. and L.H. Lucas, Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Fryxell J.M., J. Greever, and A.R.E. Sinclair. 1988 Why are migratory ungulates so abundant? American Naturalist 131:781-798.

Fuller, T.K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. Canadian Journal of Zoology 69:283-287.

Gantz, G. F., L.C. Stoddart, and F.F. Knowlton. 2006. Accuracy of aerial telemetry locations in mountainous terrain. Journal of Wildlife Management 70:1809–1812.

Gardner, B., J.A. Royle, and M.T. Wegan. 2009. Hierarchical models for estimating density from DNA mark-recapture studies. Ecology 90:1106-1115.

Gardner, B., J.A. Royle, M.T. Wegan, R.E. Rainbolt, and P.D. Curtis. 2010. Estimating black bear density using DNA data from hair snares. Journal of Wildlife Management 74:318-325.

Garrett, K. L., G.R. Martin, and R.D. Dixon. 1996. White-headed woodpecker (Picoides albolarvatus). In Poole, A. (ed) The birds of North America online. Cornell Lab of Ornithology; Retrieved from the birds of North America online: http://bna.birds.cornell.edu/bna/species/252doi:10.2173/bna.252. Ithaca, NY. USA.

Garrott, R. A., G. C. White, R. M. Bartmann, and D. L. Weybright. 1986. Reflected signal bias in biotelemetry triangulation systems. Journal of Wildlife Management 50:747-752.

Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pages 16-42 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, New York, NY. USA.

Gasaway, W.C., R.D. Boertje, D.V. Grangaard, D.G. Kelleyhouse, R.O. Stephenson, and D.G. Larsen. 1992. The role of predation in limiting moose at low-densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:1-59.

Gasaway, W.C., S.D. Dubois, S.J. Harbo, and D.J. Reed. 1986. Estimating moose population parameters from aerial surveys. Biological Papers. University of Alaska. 22:108pp.

Geist, V. 1982. Adaptive behavioral strategies. Pages 389-434 in D.E. Toweill and J.W. Thomas (eds.). North American elk. Wildlife Management Institute.

Gitzen, R. A., and J. J. Millspaugh. 2003. Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. Wildlife Society Bulletin 31:823-831.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth Selection for Fixed-Kernel Analysis of Animal Utilization Distributions. Journal of Wildlife Management 70:1334-1344.

Goodchild, M. F. 2003. Geographic information science and systems for environmental management. Annual Review of Environment and Resources 28:493-519.

Gregory, C. J., R.R. Carthy, and L.G. Pearlstine. 2006. Survey and monitoring of species at risk at Camp Blanding training site, northeastern Florida. Southeastern Naturalist 5:473-498.

Grinnell, J. 1917. The niche-relationships of the California thrasher. Auk 34:427-433.

Gutzwiller, K.J., R.T. Wiedenmann, K.L. Clements, and S.H. Anderson. 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. Auk 111:28-37.

Hallett, T.B., T. Coulson, J.G. Pilkington, T.H. Clutton-Brock, J.M. Pemberton, and B. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430: 71-75.

Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2303-2312.

Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377-387.

Hebblewhite, M., M. Percy, and E. H. Merrill. 2007. Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. Journal of Wildlife Management 71:2026-2033.

Hebblewhite, M., D.H. Pletscher, and P.C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80:789-799.

Heezen, K. L., and J. R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. Journal of Wildlife Management 31:124-141.

Heithaus M.R., A. Frid, A.J. Wirsing, L.M. Dill, J.W. Fourqurean, D. Burkholder, J. Thomson. and L. Bejder. 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. Journal of Animal Ecology 76:837-844.

Hirzel, A. H. and G. Le Lay. 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology 45:1372-1381.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199:142-152.

Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J. N. VanDriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. Photogrammetric Engineering & Remote Sensing 73:337-341.

Hooten, M.B., D. S. Johnson, E. M. Hanks, and J. H. Lowry. 2010. Agent-based inference for animal movement and selection. Journal of Agricultural, Biological, and Environmental Statistics 15:523-538.

Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution 25:119-128.

Hoskinson, R. L. 1976. The effect of different pilots on aerial telemetry error. Journal of Wildlife Management 40:137-139.

Houle, M., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2010. Cumulative effects of forestry on habitat use by gray wolf (Canis lupus) in the boreal forest. Landscape Ecology 25:419-433.

Howeth, J. G., and M. A. Leibold. 2010. Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities. Journal of Animal Ecology 79:1000-1011.

Huggard, D.J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management 57:382-388.

Hupp, J. W., and J. T. Ratti. 1983. A test of radio telemetry triangulation accuracy in heterogeneous environments. International Conference on Wildlife Biotelemetry 4:31-46.

Hurrell, J. W. 1995. NAO index data, climate analysis section, NCAR. Boulder, CO. USA. URL: www.cgd.ucar.edu/cas/jhurrell/indices.html. [Accessed Sep 2011].

Jędrzejewski W., K. Schmidt, J. Theuerkauf, B. Jędrzejewska, and H. Okarma. (2001) Daily movements and territory use by radio-collared wolves (Canis lupus) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology 79:1993-2004.

Jerde, C. L., and D. R. Visscher. 2005. GPS measurement error influences on movement model parameterization. Ecological Applications 15:806-810.

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

Johnson, C. J., and M. P. Gillingham. 2008. Sensitivity of species-distribution models to error, bias, and model design: An application to resource selection functions for woodland caribou. Ecological Modelling 213:143-155.

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

Johnson, D. S., D. L. Thomas, J. M. Ver Hoef, and A. Christ. 2008a. A general framework for the analysis of animal resource selection from telemetry data. Biometrics 64:968-976.

Johnson, D. S., J.M. London, M.-A. Lea, and J. W. Durban. 2008b. Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215.

Johnson, N.L., S. Kotz, and N. Balakrishnan. 1994. Continuous univariate distributions, Second Edition. John Wiley and Sons, Inc., New York, NY. USA.

Jordan P.A., B.E. McLaren, and S.M. Sell. 2000. A summary of research on moose and related ecological topics at Isle Royale, U.S.A. Alces 36:233-267.

Jurzenski, J. and W.W. Hoback. 2011. Opossums and leopard frogs consume the federally endangered American burying beetle (Coleoptera: Silphidae). Coleopterists Bulletin 65:88-90.

Kalof L. 2007. Looking at animals in human history. Reaktion Books, Ltd. London, England. UK.

Kauffman M.J., N. Varley, D.W. Smith, D.R. Stahler, D.R. MacNulty, and M.S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters 10:690-700.

Keating, K. A. and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774-789.

Kenow, K. P., R. G. Wright, M. D. Samuel, and P. W. Rasmussen. 2001. Integrating SAS and GIS software to improve habitat-use estimates from radiotelemetry data. Wildlife Society Bulletin 29:1006-1009.

Kenward, R. E. 1987. Wildlife radio tagging: Equipment field techniques and data analysis. Academic Press, New York, NY. USA.

Kenward, R. E. 2001. A manual for wildlife radio tagging. Academic Press, New York, NY. USA.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 126-166 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, CA. USA.

Kingsland, S. 1995. Modeling nature: Episodes in the history of population ecology. University of Chicago Press, Chicago, IL. USA.

Koehler, G. M., and M. G. Hornocker. 1989. Influences of seasons on bobcats in Idaho. Journal of Wildlife Management 53:197-202.

Kotler, B.P., J. Brown, S. Mukherjee, O. Berger-Tal, and A. Bouskila. 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. Proceedings of the Royal Society B: Biological Sciences 277:1469-1474.

Krefting, L.W. 1974. The ecology of the Isle Royale moose. University of Minnesota Agricultural Experiment Station, Technical Bulletin 297, Forestry Series 15.

Land, E. D., D. B. Shindle, R. J. Kawula, J. F. Benson, M. A. Lotz, and D. P. Onorato. 2008. Florida panther habitat selection analysis of concurrent GPS and VHF telemetry data. Journal of Wildlife Management 72:633-639.

Lee, J. E., G. C. White, R. A. Garrott, R. M. Bartmann, and A. W. Alldredge. 1985. Accessing accuracy of a radiotelemetry system for estimating animal locations. Journal of Wildlife Management 49:658-663.

Lewis D.B. and L.A. Eby. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. Oikos 96:119-129.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

London, J. and E. Richmond. 2010. National Marine Mammal Laboratory researchers census harbor seals along coastal Alaska. Alaska Fisheries Science Center Quarterly Research Report, NOAA Fisheries, Seattle, WA. USA.

Long, R. A., J. D. Muir, J. L. Rachlow, and J. G. Kie. 2009. A comparison of two modeling approaches for evaluating wildlife-habitat relationships. Journal of Wildlife Management 73:294-302.

Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology 13:367-377.

Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains Montana. Journal of Applied Ecology 33:1395-1404.

MacKenzie, D. I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, J.E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, New York, NY. USA.

MacKenzie, D.I. 2005. What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management 69:849-860.

Mangel, M. 2008. Environment, damage and senescence: modelling the life-history consequences of variable stress and caloric intake. Functional Ecology 22:422-430.

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

Mann, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15:102-122.

Marcström, V., R.E. Kenward, and M. Karlbom. 1989. Survival of ring-necked pheasants with backpacks, necklaces, and leg bands. Journal of Wildlife Management 53:808-810.

Martin, A. D., and K. M. Quinn. 2006. Applied Bayesian inference in R using MCMCpack. R News 6:2–7.

Marzluff, J. M., J.J. Millspaugh, P. Hurvitz, and M.S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411-1427.

McCoy M.W., M. Barfield, and R.D. Holt. 2009. Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems. Oikos 118:87-100.

McKelvey, K. S., and B. R. Noon. 2001. Incorporating uncertainties in animal location and map classification into habitat relationships modeling. Pages 72-90 in C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case, editors. Spatial uncertainty in ecology: Implications for remote sensing and GIS applications. Springer, New York, NY. USA.

McKenzie, H., C. Jerde, D. Visscher, E. Merrill, and M. Lewis. 2009. Inferring linear feature use in the presence of GPS measurement error. Environmental and Ecological Statistics 16:531-546.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555-1558.

McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society B: Biological Sciences 273:1449-1454.

McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia 132:102-108.

McNamara J.M., and A.I. Houston. 1986. The common currency for behavioral decisions. American Naturalist 127:358-378.

McNamara J.M. and A.I. Houston. 1987. Starvation and predation as factors limiting population size. Ecology 68:1515-1519.

Mech, L. D. 1967. Telemetry as a technique in the study of predation. Journal of Wildlife Management 31:492-496.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, MN. USA.

Mech, L.D and R.O. Peterson. 2003. Wolf prey relations. In Wolves: behaviour, ecology and conservation. Eds. Mech L.D, L. Boitani. pp. 131–160. The University of Chicago Press. Chicago, IL. USA.

Merrill, E., H. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2279-2288.

Millspaugh, J. J., G. C. Brundige, J. A. Jenks, C. L. Tyner, and D. R. Hustead. 1995. Immobilization of Rocky Mountain elk with Telazol and xylazine hydrochloride, and antagonism by yohimbine hydrochloride. Journal Wildlife Diseases 31:259-262.

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

Mladenoff, D.J., M.K. Clayton, S.D. Pratt, T.A. Sickley, and A.P. Wydeven. 2009. Changes in occupied wolf habitat in the Northern Great Lakes Region. In Wydeven, A.P., Van Deelen, T.R., and Heske, E.J. (eds) Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. pp. 119-138. Springer, New York, NY. USA.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favourable gray wolf habitat in the Northern Great Lakes region. Conservation Biology 9:279-294.

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

Moen, R., J. Pastor, and Y. Cohen. 2001. Effects of animal activity on GPS telemetry location attempts. Alces 37:207-216.

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

Montgomery, G. 2005. Place, practice and primatology: Clarence Ray Carpenter, primate communication and the development of field methodology, 1931-1945. Journal of the History of Biology. 38:495-533.

Montgomery, R. A., G.J. Roloff, and J.M. Ver Hoef, and J.J. Millspaugh. 2010. Can we accurately characterize wildlife resource use when telemetry data are imprecise? Journal of Wildlife Management 74:1917-1925.

Montgomery, R. A., G.J. Roloff, and J.M. Ver Hoef. 2011. Implications of ignoring telemetry error on inference in wildlife resource use models. Journal of Wildlife Management 75:702-708.

Morales, J. M., P.R. Moorcroft, J. Matthiopoulos, J.L. Frair, J.G. Kie, R.A. Powell, E.H. Merrill, and D.T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2289-2301.

Morris, D.W., and J.T. MacEachern 2010. Active density-dependent habitat selection in a controlled population of small mammals. Ecology 91:3131-3137.

Morrison, M. L., B.G. Marcot, and R.W. Mannan. 2006. Wildlife-habitat relationships: concepts and applications (3rd edition). The University of Wisconsin Press, Madison, WI. USA.

Moser, B. W., and E. O. Garton. 2007. Effects of telemetry location error on space-use estimates using a fixed-kernel density estimator. Journal of Wildlife Management 71:2421-2426.

Mosser, A., J.M. Fryxell, L.E. Eberly, and C. Packer. 2009. Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. Ecology Letters 12:1050-1060.

Müller, J., and R. Brandl. 2009. Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. Journal of Applied Ecology 46:897-905.

Mysterud, A., and E. Østbye. 2006. Effect of climate and density on individual and population growth of roe deer Capreolus capreolus at northern latitude: the Lier valley, Norway. Wildlife Biology 12:321-329.

Nams, V. 1989. Effects of radiotelemetry error on sample size and bias when testing for habitat selection. Canadian Journal of Zoology 67:1631-1636.

Nams, V. O., and S. Boutin. 1991. What is wrong with error polygons? Journal of Wildlife Management 55:172-176.

Nams, V.O. 1989. Effects of radiotelemetry error on sample size and bias when testing for habitat selection. Canadian Journal of Zoology 67:1631-1636.

Nelson, M.E. and L.D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-474.

Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J. M. Gaillard. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Functional Ecology 22:393-406.

O'Brien, R.M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality and Quantity 41:673-690.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, and N. C. Stenseth. 2001. Ecological effects of the north Atlantic oscillation. Oecologia 128:1-14.

Otto, C. and G.J. Roloff. 2011. Using multiple methods to assess detection probabilities of forest-floor wildlife. Journal of Wildlife Management 75:423-431.

Pace, R. M. 2001. Estimating and visualizing movement paths from radio-tracking data. Pages 190-206 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. New York, NY. USA.

Patterson, B. R., and V. A. Power. 2002. Contributions of Forage Competition, Harvest, and Climate Fluctuation to Changes in Population Growth of Northern White-Tailed Deer. Oecologia 130:62-71.

Pellet, J., and B.R. Schmidt. 2005. Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. Biological Conservation 123:27-35.

Perfecto, I., and J. Vandermeer. 2008. Spatial pattern and ecological process in the coffee agroforestry system. Ecology 89:915-920.

Peterson, R.O., and R.E. Page. 1988. The rise and fall of Isle Royale wolves, 1975-1986. Journal of Mammalogy 69:89-99.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Department of Interior National Park Service Scientific Monograph Series, No. 11. Washington, D.C. USA.

Peterson, R. O., and R. E. Page. 1988. The rise and fall of Isle Royale wolves, 1975-1986. Journal of Mammalogy 69:89-99.

Peterson, R. O., J. A. Vucetich, G. Fenton, T. D. Drummer, and C. S. Larsen. 2010. Ecology of arthritis. Ecology Letters 13:1124-1128.

Peterson, R.O. and R.E. Page. 1993. Detection of moose in midwinter from fixed-wing aircraft over dense forest cover. Wildlife Society Bulletin 21:80-86.

Petren, K. 2001. Habitat and niche, a concept of. Pages 303-315 in S.A. Levin, editor. Encyclopedia of Biodiversity Academic Press, San Diego, CA. USA.

Phillips, R. L., W. E. Berg, and D. B. Siniff. 1973. Moose movement patterns and range use in northwestern Minnesota. Journal of Wildlife Management 37:266-278.

Pimm, S. L., and M. L. Rosenzweig. 1981. Competitors and habitat use. Oikos 37:1-6.

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

Post, E., R.O. Peterson, N.C. Stenseth, and B.E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature 401:905-907.

Puttock G.D., P. Shakotko, and J.G. Rasaputra. 1996. An empirical habitat model for moose, Alces alces, in Algonquin Park, Ontario. Forest Ecology and Management, 81, 169-178.

Quinn, T. 1995. Using public sighting information to investigate coyote use of urban habitat. Journal of Wildlife Management 59:238-245.

Ralph, C. J., G.R. Geupel, P. Pyle, T.E. Martin, and D.F. DeSante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-149. Pacific Southwest Research Station, Albany, CA. USA.

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

Rettie, W. J., and P. D. McLoughlin. 1999. Overcoming radiotelemetry bias in habitat-selection studies. Canadian Journal of Zoology 77:1175-1184.

Ripley, B. D. 1976. The second-order analysis of stationary point processes. Journal of Applied Probability 13:255-266.

Ripple, W. J., and R.L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138:514-519.

Rittenhouse, C. D., F. R. Thompson, W. D. Dijak, J. J. Millspaugh, and R. L. Clawson. 2010. Evaluation of habitat suitability models for forest passerines using demographic data. Journal of Wildlife Management 74:411-422.

Rittenhouse, C. D., J. J. Millspaugh, A. B. Cooper, M. W. Hubbard, S. L. Sheriff, and R. A. Gitzen. 2008. Modeling resource selection using polytomous logistic regression and kernel density estimates. Environmental and Ecological Statistics 15:39-47.

Robel, R. J., J. N. Briggs, J. J. Cebula, N. J. Silvy, C. E. Viers, and P. G. Watt. 1970. Greater prairie chicken ranges, movements, and habitat usage in Kansas. Journal of Wildlife Management 34:286-306.

Rodewald, A. D. 2002. Nest predation in forested regions: landscape and edge effects. Journal of Wildlife Management 66:634-640.

Roloff, G. J., and J.B. Haufler. 2002. Modeling habitat-based viability from organism to population. In Scott, J. M., Heglund, P. J., Morrison, M. L., Haufler, J. B., Raphael, M. G., Wall, W. A., and Samson, F. B., (eds) Predicting species occurrences: issues of scale and accuracy. Pages 673-685. Island Press, Washington, DC. USA.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. Journal of Wildlife Management 65:899-914.

Roloff, G. J., M. L. Donovan, D. W. Linden, and M. L. Strong. 2009. Lessons learned from using GIS to model landscape-level wildlife habitat. Pages 287-320 in J. J. Millspaugh and F. R. Thompson, III, editors. Models for Planning Wildlife Conservation in Large Landscapes. Elsevier Science, Amsterdam. NED.

Roth, T. C., and S. L. Lima. 2007. Use of prey hotspots by an avian predator: purposeful unpredictability? American Naturalist 169:264-273.

Rowlingson, B. S., and P. J. Diggle. 1993. SPLANCS: spatial point pattern analysis code in S-Plus. Computers and Geosciences 19:627–655.

Saltz, D. 1994. Reporting error measures in radio location by triangulation: A review. Journal of Wildlife Management 58:181-184.

Saltz, D., and P. U. Alkon. 1985. A simple computer-aided method for estimating radio-location error. Journal of Wildlife Management 49:664-668.

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

Samuel, M. D., and M. R. Fuller. 1994. Wildlife radiotelemetry: Equipment and data analysis. Pages 370-418 in T. Bookhout, editor. Wildlife Management Techniques Manual, 5th Edition. The Wildlife Society, Bethesda, MD. USA.

Schick, R. S., S.R. Loarie, F. Colchero, B.D. Best, A. Boustany, D.A. Conde, P.N. Halpin, L.N. Joppa, C.M. McClellan, and J.S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338-1350.

Schmitz, O.J., D. Hawlena, and G.C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. Ecology Letters 13:1199-1209.

Schmutz, J. A., and G. C. White. 1990. Error in telemetry studies: effects of animal movement on triangulation. Journal of Wildlife Management 54:506-510.

Seavy, N. E., J.H. Viers, and J.K. Wood. 2009. Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height. Ecological Applications 19:1848-1857.

Servheen, G. and L.J. Lyon. 1989. Habitat use by woodland caribou in the Selkirk Mountains. Journal of Wildlife Management 53:230-237.

Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology 76:882-891.

Singh, N., N. Yoccoz, Y. Bhatnagar, and J. Fox. 2009. Using habitat suitability models to sample rare species in high-altitude ecosystems: a case study with Tibetan argali. Biodiversity and Conservation 18:2893-2908.

Soisalo, M.K. and S.M.C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture- recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129:487–496.

Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. Journal of Wildlife Management 43:926-935.

Stehman, S. V., J. D. Wickham, J. H. Smith, and L. Yang. 2003. Thematic accuracy of the 1993 National land-cover data for the eastern United States: statistical methodology and regional results. Remote Sensing of Environment 86:500-516.

Stenseth, N. C., A. Shabbar, K.-S. Chan, S. Boutin, E. K. Rueness, D. Ehrich, J. W. Hurrell, O. C. Lingjærde, and K. S. Jakobsen. 2004. Snow conditions may create an invisible barrier for lynx. Proceedings of the National Academy of Sciences of the United States of America 101:10632-10634.

Stenseth, N. C., W. Falck, K.-S. Chan, O. N. Bjørnstad, M. O'Donoghue, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, and N. G. Yoccoz. 1998. From patterns to processes: Phase and density dependencies in the Canadian lynx cycle. Proceedings of the National Academy of Sciences 95:15430-15435.

Stenseth, N.C., A. Mysterud, G. Ottersen, J.W. Hurrell, K.S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1295.

Steury, T. D., J. E. McCarthy, T. C. Roth II, S. L. Lima, and D. L. Murray. 2010. Evaluation of root-n bandwidth selector for kernel density estimation. Journal of Wildlife Management 74:539-548.

Strum, S.C. and L.M. Fedigan. 2000. Changing views of primate society: a situated North American perspective. In Strum, S.C. and Fedigan, L.M. (eds) Primate encounters:

models of science, gender, and society. Pages 3-56. The University of Chicago Press, Chicago, IL. USA.

Sundell, J., O. Huitu, H. Henttonen, A. Kaikusalo, E. Korpimäki, H. Pietiäinen, P. Saurola, and I. Hanski. 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. Journal of Animal Ecology 73:167-178.

Swenson, J. E., K. Wallin, G. Ericsson, G. Cederlund, and F. Sandegren. 1999. Effects of ear-tagging with radiotransmitters on survival of moose calves. Journal of Wildlife Management 63:354-358.

Swihart, R.K., and N.A. Slade. 1985a. Influence of sampling interval on estimates of home range size. Journal of Wildlife Management 49:1019-1025.

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

Telesco, D. J., and F. T. Van Manen. 2006. Do black bears respond to military weapons training? Journal of Wildlife Management 70:222-230.

Telesco, D. J., and F. T. Van Manen. 2006. Do black bears respond to military weapons training? Journal of Wildlife Management 70:222-230.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M.C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79-92.

Thompson, S. K. 2002. Sampling. Second edition edition. John Wiley & Sons, Inc., New York, NY. USA.

Thorn, M., D.M. Scott, M. Green, P.W. Bateman, and E.Z. Cameron. 2009. Estimating brown hyaena occupancy using baited camera traps. South African Journal of Wildlife Research 39:1-10.

Tuljapurkar, S., U. K. Steiner, and S. H. Orzack. 2009. Dynamic heterogeneity in life histories. Ecology Letters 12:93-106.

Turner, M. G., R.H. Gardner, and R.V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer Verlag, New York, NY. USA.

Turner, M. G., W.H. Romme, R.A. Reed, and G.A. Tuskan. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landscape Ecology 18:127-140.

Urbano, F., F. Cagnacci, C. Calenge, H. Dettki, A. Cameron, and M. Neteler. 2010. Wildlife tracking data management: a new vision. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2177-2185.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York, NY. USA.

Ver Hoef, J. M., N. Cressie, R.N. Fisher, and T.J. Case. 2001. Uncertainty and spatial linear models for ecological data. In C.T. Hunsaker, M.F. Goodchild, M.A. Friedl, and T.J. Case, (eds) Spatial uncertainty in ecology. Pages 214-237. Springer-Verlag, New York, NY. USA.

Visscher, D. R. 2006. GPS measurement error and resource selection functions in a fragmented landscape. Ecography 29:458-464.

Vucetich J.A., L.M. Vucetich, and R.O. Peterson. 2012. The causes and consequences of partial prey consumption by wolves preying on moose. Behavioral Ecology and Sociobiology 66:295-303.

Vucetich J.A., R.O. Peterson, and C.L. Schaefer. 2002. The effect of prey and predator densities on wolf predation. Ecology 83:3003-3013.

Vucetich, J. A., and R. O. Peterson. 2004a. The influence of top-down, bottom-up and abiotic factors on the moose (Alces alces) population of Isle Royale. Proceedings of the Royal Society B: Biological Sciences 271:183-189.

Vucetich, J. A., and R. O. Peterson. 2004b. Grey wolves—Isle Royale. Pages 281–292 in D. W. Macdonald and C. Sillero- Zubiri. The biology and conservation of wild canids. Oxford University Press, London. UK.

Vucetich, J. A., and R. O. Peterson. 2005. Ecological studies of wolves on Isle Royale. Annual report 2004-2005, Michigan Technological University, Houghton, MI. USA.

Vucetich, J. A., and R. O. Peterson. 2011. Ecological studies of wolves on Isle Royale. Annual report 2010-2011, Michigan Technological University, Houghton, MI. USA.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator–prey ratios in three wolf-ungulate systems. Journal of Animal Ecology 80:1236-1245.

Vucetich, J. A., R. O. Peterson, and C. L. Schaefer. 2002. The effect of prey and predator densities on wolf predation. Ecology 83:3003-3013.

Vucetich, J.A., M. Hebblewhite, D.W. Smith, and R.O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate, and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology 80:1236-1245.

Wallace, A. R. 1876. The geographical distribution of animals. MacMillan and Co., London, England. UK.

Wallestad, R. O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. Journal of Wildlife Management 35:129-136.

Wells, D. E., N. Beck, D. Delikaraoglou, A. Kleusberg, E. J. Krakiwsky, G. Lachapelle, R. B. Langley, M. Nakiboglu, K. P. Schwarz, J. M. Tranquilla, and P. Vanicek. 1986. Guide to GPS positioning. Department of Geodesy and Geomatics Engineering Lecture Note No. 58, University of New Brunswick, Fredericton, CAN.

White, G. C. 1985. Optimal locations of towers for triangulation studies using biotelemetry. Journal of Wildlife Management 49:190-196.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. Journal of Wildlife Management 50:509-513.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, CA. USA.

White, G. C., and T. M. Shenk. 2001. Population estimation with radio-marked animals. Pages 329-350 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, New York, NY. USA.

Wickham, J. D., S. V. Stehman, J. A. Fry, J. H. Smith, and C. G. Homer. 2010. Thematic accuracy of the NLCD 2001 land cover for the conterminous United States. Remote sensing of environment 114:1286-1296.

Wikenros, C., H. Sand, P. Wabakken, O. Liberg, and H. C. Pedersen. 2009. Wolf predation on moose and roe deer: chase distances and outcome of encounters. Acta Theriologica 54:207-218.

Wilmers C.C. and W.M. Getz. 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. Ecological Modelling 177:193-208.

Wilmers C.C., D.R. Stahler, R.L. Crabtree, D.W. Smith, and W.M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6:996-1003.

Wilmers C.C., E. Post, R.O. Peterson, and J.A.Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. Ecology Letters 9:383-389.

Wilson, R. R., M. B. Hooten, B. N. Strobel, and J. A. Shivik. 2010. Accounting for individuals, uncertatinty, and multiscale clustering in core area estimation. Journal of Wildlife Management 74:1343-1352.

Winnie, J., and S. Creel. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behaviour 73:215-225.

Withey, J. C., T. D. Bloxton, and J. M. Marzluff. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. Pages 43-75 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio Tracking and Animal Populations. Academic Press, New York, NY. USA.

Withey, J. C., T. D. Bloxton, and J. M. Marzluff. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. Pages 43-75 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, New York, NY. USA.

Wright, G. J., R. O. Peterson, D. W. Smith, and T. O. Lemke. 2006. Selection of northern Yellowstone elk by gray wolves and hunters. Journal of Wildlife Management 70:1070-1078.