1999

Field testing the accuracy and generality of selected wildlife-habitat models

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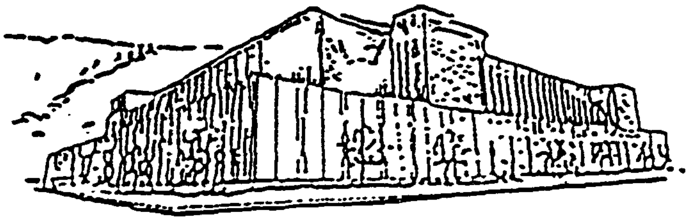

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FIELD-TESTING THE ACCURACY AND GENERALITY OF SELECTED WILDLIFE-HABITAT MODELS

by

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6-1-99

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UMI Number: 9935328

UMI Microform 9935328

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300 North Zeeb Road
Ann Arbor, MI 48103

Baumeister, Thomas R., Ph.D., May 1999 Forestry

Field-testing the accuracy and generality of selected wildlife-habitat models (135 pp.)

Co-chairs: Dr. Harold Salwasser, Dr. Jack Ward Thomas

Improving the objectivity of modeling wildlife-habitat relationships through more formal and verifiable approaches is time-consuming, expensive, and difficult. To justify these approaches, development and application costs need to be offset by greater accuracy. Yet, very little information exists to evaluate relative accuracy of alternative models. My research was designed to address various questions regarding accuracy, generality, and overall utility of selected wildlife-habitat models. First, I empirically determined the accuracy of a simple, expert-based habitat matrix for predicting bird species occurrence at the level of cover types (10^1-10^2 ha) and mosaics of cover types (10^3 ha). Matrix predictions were more accurate in predicting presence at the level of mosaics (62-83%) than at individual cover types (36-63%). The matrix overestimated bird presence—a result of either not detecting a species that was present or an incorrect matrix prediction. There was evidence to suggest that some undetected species were, indeed, absent. Second, I empirically compared the accuracy of different habitat suitability models developed with expert-opinion alone (EXPERT), expert opinion and field data (HSI, PATREC), or field data alone (LOGISTIC). Mean accuracy of classifying used and unused habitats was lowest for EXPERT at 58% and improved to 71% for LOGISTIC, to 73% for PATREC, and to 75% for HSI. Classification improvement over chance ranged from 16% for EXPERT to 50% for HSI. PATREC and LOGISTIC had 46% and 42% improvement over chance, respectively. The expert model was able to differentiate between used and unused habitats (based on prediction score) and described use versus availability similar to field-data models. Third, I empirically compared the accuracy of a locally developed, regression-based habitat suitability model among different places, times, and populations (generality). I found that a local model can accurately predict habitat suitability at different years and different places that are similar in climatic, topographical, and geological condition. Mean accuracy of correctly classifying used and unused habitats were statistically similar, ranging from 65% to 73%. Collectively, my research provides information on relative model accuracy that allows users of models to compare the advantages and disadvantages more effectively. Providing information on the degree to which model predictions are empirically correct generates confidence in model applications and helps define the utility of species-habitat matrices in decision-making.

PREFACE

Wildlife biologists and conservation biologists are involved in three major tasks: (1) to determine the location and suitability of species habitat, (2) to delineate and map species distribution, and (3) to assess the consequences of changes in habitat to species distribution. There is little doubt that long-term, intensive field studies of species populations provide the most reliable information to meet these tasks. Unfortunately, these field studies are time-consuming, expensive, and often difficult to design. As such, biologists seek alternatives requiring less time, money, and technical expertise. Wildlife-habitat modeling is one such alternative.

Wildlife-habitat models assign weights and rules to a database or map of environmental conditions. These weights and rules are assigned on the premise that biophysical characteristics, such as vegetation and topography, influence the provision of life requisites such as food and cover, and, hence, the occurrence of individuals. Formulating these relationships between habitat condition and species occurrences requires information on how individuals of a species use their environment. Sources of information include expert opinion, literature reviews, agency reports, field studies, or a combination of these.

The first generation of wildlife-habitat models, which were developed in the late 1970s, relied mostly on expert opinion and literature reviews. The second generation of models, which emerged in the mid-1980s, relied heavily on statistical modeling of field data on species habitat use. As of lately, a third generation of these statistical models emerged, which also incorporates spatial analysis and remotely sensed data such as satellite imagery, often within a GIS environment. In essence, over the last 20 years of habitat modeling, biologists have progressively moved from simple, inexpensive, and time-efficient professional judgements to more complex, expensive, and time-consuming statistical models, requiring considerable amounts of data inputs, expertise, and technology. The consequences of this shift for the quality of information in land use decisions affecting wildlife are largely unclear.

In applied wildlife-habitat modeling, the cost of building a model is justified on the basis of greater scientific rigor and implied improved accuracy. Yet, very little information exists to evaluate the relative accuracy of alternative models. As such, model users are asking: "How much are we gaining in predication accuracy from using more detailed and expensive statistical models versus using simple and less costly expert-opinion models?" What is the tradeoff between the cost of establishing more detailed and expensive models and the benefit of marginally better conservation decisions? My research was designed to address various aspects of these questions concerning accuracy, generality, and overall utility of wildlife-habitat models. Specifically, I addressed the following three research objectives.

(1) To empirically determine the accuracy of a simple, expert-based species-habitat matrix.

(2) To empirically compare the accuracy of different habitat suitability models developed with (1) expert-opinion alone, (2) expert opinion and field data, or (3) field data alone.

(3) To empirically compare the accuracy of a locally developed, statistical habitat suitability model among different places, times, and populations (generality).

An ideal model is one that is accurate, general, and practical. However, in reality, simultaneously maximizing accuracy, generality, and practicality is difficult. Tradeoffs are inescapable. My research provides an essential piece of information regarding relative model accuracy that allows users of models to compare the advantages and disadvantages more comprehensively. In essence, managers may now be able to more efficiently and effectively meet their conservation objectives for land, habitat, and wildlife.

The following dissertation is composed of three stand-alone chapters. In each, I address one of the three research objectives. Tables, figures, and appendices follow each chapter.

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ACKNOWLEDGMENTS

I owe a special debt of thanks to the Boone and Crockett Club for supporting my research financially and logistically through the Boone and Crockett Wildlife Conservation Program at The University of Montana and the Theodore Roosevelt Memorial Ranch. I feel honored to have had the opportunity to work with an organization as accomplished in the field of wildlife conservation as the Boone and Crockett Club. I am also grateful for the insight, inspiration, and encouragement that I received from my co-chairs Dr. Hal Salwasser and Dr. Jack Ward Thomas. Their relentless questions and deep insights into applied wildlife-habitat modeling have helped me understand the significance of my work for managers and planners of wildlife and habitat.

My committee, Dr. Scott Mills, Dr. Dan Pletscher, Dr. LLoyd Queen, and Dr. Roly Redmond, provided thoughtful suggestions, useful criticisms, and continued support throughout. Their office doors were always open to me. My special thanks goes to Bob and Kelly Peebles and their sons Chad, Matt, and Cole for their warm hospitality and strong sense of place at the Theodore Roosevelt Memorial Ranch. My "elk expert panel" included distinct and recognized individuals: Milo Burcham, Dr. Jack Lyon, Dr. Les Marcum, Dr. Jack Ward Thomas and Jim Williams—all who have contributed significantly to our body of knowledge on elk-habitat relationships. I would like to thank the many volunteers from The University of Montana especially Mark Robertson, Adam Quinn, and Bruin Herr for their dedication and spirit in conducting work under often miserable field conditions. In addition to a number of reviewers, I like to thank my friends and colleagues who have read draft manuscripts and made helpful suggestions, especially John Citta and Brendon Moynahan. I am grateful for the assistance I received

from the staff of the School of Forestry and the Wildlife Program, especially Jeannie Franz and Dave Wolverton.

And finally, I owe a special debt of thanks to Dayna, my wife, for her unrelenting encouragement, devoted commitment, and strong support in all phases of this project. Dayna put up with a difficult, preoccupied husband for months on end and then helped me with a critical mind and a sure hand in preparing this manuscript. She knows I could not have done it without her.

In conducting this research, I interacted with many resource professionals, landowners, and simply good folks. These wonderful individuals provided insights and helped shape my perspective on the need for comprehensive wildlife conservation in this spectacular landscape we call the Rocky Mountain Front.

CHAPTER 1: ACCURACY OF A SPECIES-HABITAT MATRIX FOR PREDICTING BIRD OCCURRENCE ON MONTANA'S ROCKY MOUNTAIN FRONT

INTRODUCTION

Conservation of species is enhanced by knowledge of how habitat changes due to natural processes or management affects distributions. Yet, the cost and time of conducting site-specific field studies to gather this knowledge, species by species, is not feasible for most conservation purposes (Flather et al. 1992, Block et al. 1998). Instead, efficient and effective means are needed for inventorying, managing, and monitoring suites of species (Marcot et al. 1994). One alternative is to develop a species-habitat matrix—a comprehensive synthesis of information on how habitat influences the distribution of individual and suites of species (Patton 1978, Thomas 1979, Salwasser et al. 1980, Scott et al. 1993).

A species-habitat matrix uses existing information to systematically link habitat (e.g., land cover type) with that of species' occurrence (Patton 1978, Thomas 1979, Verner and Boss 1980, Nelson and Salwasser 1982, Patton 1992). A matrix predicts species occurrence relative to how well a particular habitat can meet life requisites, such as reproduction, feeding, and resting (Table 1). These habitat ratings are made by experts familiar with the distribution and habitat requirements of a species in a particular region according to personal experience, scientific references, agency reports, and professional judgement (USDA Forest Service 1994, Stevens 1995). The ideal matrix is practical, comprehensive, spatially explicit, accurate, and compatible with planning and management inventories.

The desire for the coupling of operational simplicity with cost-efficiency has resulted in widespread application of species-habitat matrices in the Pacific Northwest (Thomas 1979), California (Verner and Boss 1980), western Montana (Prather and Burbridge 1985), and Colorado (Hoover and Wills 1984) as well as other regions (Koeln et al. 1991, Van Horne and Wiens 1991, Flather et al. 1992, Stevens 1995). Recently, species-habitat matrices have found application in landscape-scale analyses of species richness for land protection—e.g., GAP analysis (Scott et al. 1993, Machlis et al. 1994). These large-scale applications (minimum 1:100,000) are facilitated by remotely sensed data (satellite imagery), rapid analysis by Geographic Information Systems (GIS), and new paradigms such as landscape ecology and ecosystem management (Flather et al. 1992, Mellen et al. 1995, Edwards et al. 1996, Mack et al. 1997).

Applications of species-habitat matrices today are constrained by two major limitations. First, the quality and quantity of information vary widely among species (Verner 1983, Flather et al. 1992, Tamis and Van't Zelfde 1998). Available information is generally incomplete, uncertain, and inconsistent among species. Most field studies focus on charismatic fauna, such as game species, threatened and endangered species, and ecological indicator species. These studies often exclude many of the species that make up a community—including many amphibians and reptiles—which are often more difficult to inventory, but are also often more sensitive to changes in habitat (Block et al. 1998). In essence, there is too much information to process without a matrix design, but not enough to eliminate uncertainty when evaluating species occurrence. With the aid of GIS, limited data can easily be extrapolated to produce maps of habitat suitability and biological diversity, but they are of questionable thematic or spatial accuracy (Tamis and

Van't Zelfde 1998). Often predictions are kept general to avoid underestimating presence (Dedon et al. 1986).

Second, the information for building matrix relationships is generally only available at coarse resolutions (regional scale) and, thus, is often not suitable for predicting occurrence at the level of individual habitats (Mack et al. 1997, Tamis and Van't Zelfde 1998). Yet, regional species-habitat matrices are widely used in making habitat-specific predictions (e.g. HABSCAPES [Mellen et al. 1995], Wildlife Landscape Evaluation [USDA Forest Service 1994]). With limited knowledge of accuracy and the different resolutions of model development and application, the reliability of species-habitat matrices is questionable and validation is essential.

Many of the matrices in use today have not been field-validated, but there are some notable exceptions, particularly in California (Verner 1980, Dedon 1982, Dedon et al. 1986, Raphael and Marcot 1986). These validation studies give mixed results. For example, a species-habitat matrix for northwestern California accurately predicted presence/absence of terrestrial vertebrates at the scale of watersheds, but performed noticeably less well at the scale of individual forest stands (Raphael and Marcot 1986). In contrast, Edwards et al. (1996) found that GAP analysis for the entire state of Utah correctly predicted presence/absence of terrestrial vertebrates at the smaller scale of National Parks within the state. Yet, Block et al. (1994) found that both state and regional models for terrestrial vertebrates performed poorly when validated in three local areas of oak woodlands in California. These few validation studies make it difficult to judge matrix accuracy, especially when matrices are applied at finer resolutions than for which the knowledge base is available.

Lack of validation is a major limitation in defining the utility of species-habitat matrices for conservation purposes at different levels of spatial resolution (Morrison et al. 1998). The paucity of validation is largely due to the cost and time involved in field-testing models. However, no efficient and effective alternative to species richness modeling exists. For most conservation and management decisions, the large number of species to be considered makes direct inventory of individual species too costly and time-consuming. As such, relating species to habitat continues to appeal to land managers and efforts to validate must coincide with matrix development.

OBJECTIVE

My objective was to field-test the accuracy of a regional species-habitat matrix to predict bird species occurrence in land cover types (e.g., prairie grassland) along Montana's Rocky Mountain Front (Front) (Figure 1). I tested a matrix developed for the Northern Region of the USDA Forest Service which includes portions of Montana, Idaho, and the Dakotas, hereafter referred to as "Northern Region matrix" (Prather and Burbridge 1985). From the matrix, I extracted information on predicted bird species presence and absence and demonstrated explicitly, under field-testing conditions, the completeness and accuracy of these data in predicting bird species presence at two resolutions of: (1) a mosaic of land cover types (10^3 ha) and (2) individual land cover types (10^1-10^2 ha). Completeness was defined by the proportion of species observed that were predicted to be present. Accuracy was defined as the proportion of matrix predictions that were empirically correct when compared to field inventories on species presence. I chose the Front for this study because of the availability of (1) the Northern Region matrix, (2) independent bird species lists for mosaics of cover types, and (3) GIS map availability of cover types (Boone and Crockett 1994).

STUDY AREA

The Rocky Mountain Front, in northcentral Montana, is geographically delineated by the Continental Divide to the west and south, US Highways 200, 89, and 287 to the east, and US Highway 2 to the north (Figure 1). The Front, as the ecotone between the northern Great Plains and the central Rocky Mountains (Barker and Whitman 1988, Demarchi and Lea 1992), is characterized by long, cold winters and short, warm summers. Mean annual temperatures vary considerably within the area and can range from -30° to 37° C (Aune and Kasworm 1989, Peebles pers. commun. 1997). Annual precipitation ranges from 150-200 cm in the high alpine zone to 30-40 cm along the foothills, with the greatest amount of precipitation occurring between April and July (Moeckel 1997). Winters and summers are both drought-prone periods.

The Front is an ecologically diverse region characterized by prairie grasslands interspersed with coniferous forest, aspen groves, and riparian corridors. Fescue (*Festuca* spp.) grasslands, irrigated hay meadows, and alfalfa fields vegetate the bottomlands and grade into limber pine (*Pinus flexilis*) savanna and Douglas-fir (*Pseudotsuga menziesii*) forests along ridges and plateaus (Mueggler and Stewart 1980, Offerdahl 1989, Ayers 1996). Cottonwood (*Populus* spp.) and willow (*Salix* spp.) dominate riparian areas (Hurlburt 1996). Fires on the fescue prairie occurred historically at intervals of 5 to 10 years (Arno 1980). The absence of fire over the last century has allowed coniferous trees to establish in grasslands, resulting in a temperate savanna landscape (Ayers 1996).

Field surveys were conducted at the 1,681 ha Theodore Roosevelt Memorial Ranch, owned by the Boone and Crockett Club, the 2,165 ha Blackleaf Wildlife Management Area, administered by Montana Fish, Wildlife, and Parks, and the 1,575 ha Scoffin Butte, a privately-owned ranch complex (Figure 1). Hereafter, these areas are collectively referred to as FIELD. Existing bird lists were obtained from two conservation areas: the 8,180 ha Pine Butte Swamp Preserve (PINE), which is owned by The Nature Conservancy and the 5,450 ha Freezeout Lake Wildlife Management Area (FREEZE), which is administered by Montana Fish, Wildlife, and Parks. Collectively, FIELD, PINE, and FREEZE are representative of the foothill habitats of the Front.

Prior to this study, a GIS database was established with information on (1) biophysical attributes (slope, aspect, land cover type), (2) human land use (including roads, buildings, administrative boundaries), and (3) spatial measures (size, shape, proximity of cover type patches) (Boone and Crockett 1994). Aerial photography (1:24,000) was used to map cover types. Classification keys for photo interpretation were developed at Theodore Roosevelt Memorial Ranch (Offerdahl 1989). Data on slope and aspect were derived from a 7.5-minute Digital Elevation Model (DEM) (U.S. Geological Survey). The database was mapped at a resolution of 30-m pixels.

METHODS

Bird-Habitat Matrix

From the Northern Region matrix, I extracted data on presence and absence of bird species in six land cover types during spring/summer (i.e., breeding season) (*see* Appendix A for description and code of matrix cover types). The Northern Region matrix includes three suitability ratings for how well a cover type meets the life requisites of a species. Because I compared predictions to presence/absence data, this required coding the suitability ratings into a binary variable. I considered a species to be present in a cover type if the type was rated to be of importance in meeting reproductive and/or feeding requirements (in Table 1 denoted as 1-3, R or F). As such, I included both optimal and marginal habitats. Conversely, a species was predicted absent if a type was rated as not important in meeting either one of these requirements (in Table 1 denoted by no entry).

Species List

Evaluating the accuracy of a species-habitat matrix requires a reference against which predictions can be compared. An ideal reference would be a database of species distribution referenced by habitat (Flather et al. 1992). I built such a database by combining existing occurrence information with personal field observations.

First, I reviewed range maps in field guides (Peterson 1990, Johnsgard 1992) and The Checklist of North American Birds (American Ornithologists' Union 1983) to compile a list of species whose ranges include the Front. I identified 203 species, which included 86% of the species known to breed in Montana (Hays et al. 1984). Based on the same sources, I classified each bird species by its seasonal occurrence: winter-resident (n=5), summer-resident (n=145), or yearlong-resident (n=53). I eliminated winter-residents since my focus was on spring/summer occurrence.

I then cross-referenced the resulting list with documented species occurrence on the Front according to the Montana Natural Heritage database (Montana Natural Heritage Program 1996) (*see* Appendix B). The database contains records of species observations referenced by season and location using 40 by 55 km quarter latitude-longitudes (see Montana Natural Heritage Program [1996] for more details). I selected records from the seven quarter latitude-longitudes comprising the Front (Figure 1). Only two of the 198 species in my first list, the Brown Creeper (*Certhia americana*) and the Williamson's Sapsucker (*Sphyrapicus thryroideus*), had not been recorded on the Front and were, subsequently, deleted from my database. For comparing matrix predictions to field observations, I only tested for these 196 species, all of which were included in the Northern Region matrix.

Species Survey

In spring (May-June) of 1995-97, I conducted field surveys to detect bird species in land cover types: grassland, riparian, aspen, limber pine, Douglas-fir, and water. My objective was to build a species list for each cover type. Within a cover type, I surveyed multiple sites to account for variation in species occurrence caused by microclimates and special habitat components, such as nest sites (Wiens 1987, Block and Morrison 1991). Cover types were diverse in topography and vegetation characteristics (Offerdahl 1989, Boone and Crockett 1994).

I surveyed for three years, 1995-97, to account for temporal variation in occurrence caused by stochastic variations (e.g., weather, delayed spring migration, and green-up) (Block and Morrison 1991). I selected two months as a sampling frame to account for changes in detection probability during the breeding season (Block and Morrison 1991). I conducted surveys in May and June when birds were more easily detected while establishing breeding territories and while green-up was only moderate. Daily surveys were conducted during the high activity periods of early morning (0600-1000 hours) and late afternoon (1600-1800 hours).

The time and cost involved in surveying for many species dictated the choice of an efficient survey method. I chose a one-visit survey method over a multiple-visit method. Although the latter method tends to result in greater certainty of species absence, it reduces overall sample size and increases the variability in detections within cover types (Block and Morrison 1991, Bolger et al. 1997). Conversely, the one-visit method may have resulted in a failure to detect the presence of some cryptic species, but at the benefit of greater certainty of detecting the presence of many of the more conspicuous species in more cover types.

I attempted to improve my chances of detecting less conspicuous species by using two survey methods: 5 minute point-counts (following a 2 minute waiting period after arrival) and 200 m line-transects. Specifically, the line-transect method was employed to increase my probability of visually detecting non-vocal and cryptic species, such as sharp-tailed grouse (*Tympanuchus phasianellus*).

In choosing survey sites, I superimposed in GIS a 150 m grid on all three areas comprising FIELD. I first identified those grid cells contained fully within cover type patches of $\geq$3 ha. I selected this minimum patch size to ensure correct association of a species with a particular cover type (Morrison et al. 1998). However, this may have resulted in a failure to detect edge species. Locations for point-counts were randomly selected within the remaining grid cells using the GIS. Within a cover type, I ensured that points were $\geq$200 m apart and $\geq$30 m from edge. This spacing was chosen to avoid counting birds twice while minimizing travel time between survey sites. I used the GIS to generate coordinates for point locations and a Global Positioning System (GPS) to locate these in the field.

I conducted variable-distance point counts to account for different detection probabilities in cover types (e.g. aspen versus prairie). The outer boundary was adjusted depending on visibility (vegetation density) and distance to edge. I identified bird species either by song or sight with the objective of detecting all species that were present. Once an individual of a species was detected, additional individuals of the same species were not registered to avoid diverting attention from detecting less abundant or vocal species. For each species, I recorded presence as one observation and considered a species undetected if no observations were made. I considered a species undetected instead of absent because my failure to detect a species did not provide evidence for its actual absence (Atwood et al. 1990). I did not survey during rain or strong winds (>30 m/s). Three hundred different point-counts were conducted annually in 1995-97; point locations were unique in each year.

Line-transect surveys were conducted annually (1995, *n*=277, 1996, *n*=777, and 1997, *n*=777). Line transects were located by systematically choosing cells in a checkerboard pattern from a 150 m grid superimposed over a map of land cover types in GIS. For each selected grid cell, I slowly walked the length of a 200 m transect placed diagonally from southwest to northeast (225° to 45° magnetic azimuth). I recorded all bird species seen or heard and the associated cover type. Collectively, both survey methods yielded 2731 unique cover type samples which were distributed in proportion to cover type availability at FIELD (Table 2).

Species Occurrence by Cover Type

I evaluated matrix accuracy for correctly predicting presence and absence of bird species in six cover types at FIELD. I cross-referenced cover types between the matrix and FIELD to compile a list of species predicted to be present and absent (Table 3). This species list was compared to the cover type-specific list established for FIELD.

Species Occurrence by Conservation Area

Next, I evaluated matrix accuracy for predicting presence and absence of bird species in mosaics of cover types at three conservation areas: Freezeout Wildlife Management Area (FREEZE), Pine Butte Swamp Preserve (PINE), and FIELD. Species lists for FREEZE (Schwitters 1994) and PINE (Waldt 1992) were based on incidental observations by area managers and ornithologists, as well as systematic inventories. Species lists included yearlong and summer residents. For each conservation area, I compiled a list of species predicted to be present and absent by cross-referencing available cover types with matrix entries (Table 3). For each area, presence and absence predictions were compared to observed presence (i.e., species list).

Comparison of Predicted to Observed Species Occurrence

Making inferences on matrix accuracy based on rates of under- and over-estimating presence requires detecting all species present in a cover type (Hodgson et al. 1988). This assumes a detection probability of one. If the detection probability is less than one, a proportion of species is undetected and matrix accuracy is underestimated. Though I attempted to devise a sampling scheme that would result in detection probabilities as close to one as possible (surveying many sites/cover type and using point-counts and line-transects), I report only on rates of correctly predicting presence and incorrectly predicting absence (Stefan et al. 1995). That is, true absence could not conclusively be separated from those instances in which a species was present but not detected (Hodgson et al. 1988, Buckland and Elston 1993). Even though this procedure resulted in loss of some information, it avoids making errors in causal inferences when underlying assumptions are likely violated. However, I present characteristics (rarity, habitat use, activity pattern) of those species predicted to be present, but failed to be detected, in an attempt to distinguish between a sampling error and a matrix error.

RESULTS

Species Survey

Using point-counts, I recorded 4,164 observations for 125 bird species in six cover types at FIELD (Table 4). Using the line-transect method, 2,043 additional observations were recorded for 82 species in six cover types.

The line-transect method yielded seven species which had not been detected using the point-count method: cordilleran flycatcher (*Empidonax occidentalis*), golden-crowned kinglet (*Regulus satrapa*), gray partridge (*Perdix perdix*), horned grebe (*Podiceps auritus*), lark sparrow (*Chondistes grammacus*), sharp-shinned hawk (*Accipiter striatus*), and violet-green swallow (*Tachycineta thalassina*). For 115 species, the detection rate (# of species observations/# of cover type sampled) was greater for point-counts than for line-transects (*see* Appendix C for detection rates). I pooled point-count and line-transect data to result in a cover type-referenced species list.

Combined, I observed 132 (67%) of the 196 "detectable" species as defined by previously established species list. I detected 99 (69%) of the 143 summer-residents and 33 (62%) of the 53 yearlong-residents. I detected more of the widespread species than those more rare in distribution. My list included 54% of species recorded in ≤3 quarter latitude-longitudes and 97% of those recorded in ≥5 quarter latitude-longitudes (Montana Natural Heritage Program 1996). Of the 64 species that remained undetected, 32 (50%) had never been recorded in the quarter latitude-longitude in which FIELD was located.

Species Occurrence by Cover Type

Forty-two percent of the 132 detected species were detected in one cover type, while 58% were recorded in two or more cover types (24% in two, 29% in three, and 5%

in four cover types). The cover types GRASS and RIPRN yielded the greatest number of observations (42% and 21% of observation total, respectively) and greatest number of species (54% and 60% of species total, respectively) (Table 4).

I evaluated the matrix for correctly predicting presence and incorrectly predicting absence of bird species in cover types at FIELD. The accuracy of correctly predicting presence in all cover types averaged 51% (S.E.=4%) (Figure 2). The relative accuracy was greatest for cover type WATER (62%, *n*=42) and lowest for DFIR (36%, *n*=87). The rate of incorrectly predicting absence averaged 19% (S.E.=7%). The relative error was greatest for the cover type RIPRN (42%, *n*=52) and lowest for DFIR (3%, *n*=68). Overall, the cover type WATER ranked highest and RIPRN ranked lowest in terms of a relatively high rate of correctly predicted presence and a relatively low rate of incorrectly predicted absence.

Species Occurrence by Conservation Area

I also evaluated the matrix for correctly predicting presence and incorrectly predicting absence of bird species at conservation areas (mosaics of cover types). The accuracy of correctly predicting species presence ranged from 62% at FREEZE (*n*=172) to 83% at PINE (*n*=189) (Table 5). The rate of incorrectly predicted absence varied widely ranging from 0% at FIELD (*n*=21) to 17% at FREEZE (*n*=24) to 57% at PINE (*n*=7). For FREEZE, the species detected that were predicted to be absent included the violet-green swallow, sharp-shinned hawk, mountain bluebird (*Sialia currucoides*), and Northern oriole (*Icterus galbula*). For PINE, these species included the Northern oriole, rock dove (*Columba livia*), veery (*Hylocichla fuscescens*), and Vaux's swift (*Chaetura vauxi*).

Forty-three species predicted to be present at FIELD were not detected. These species may have been present, if so, I failed to detect them. However, forty of these species were considered unlikely to be detected with my sampling protocol (Table 5). Twenty-four species had no preexisting occurrence record in the quarter latitude-longitude (Montana Natural Heritage Program 1996) in which FIELD was located (*see* Appendix B). Twelve species were considered associated with special habitat components not well represented at FIELD such as waterfalls, snags, and rock outcroppings. Furthermore, four species were primarily nocturnal in their activity patterns, which included the owls.

DISCUSSION

Species-habitat matrices are systematic approaches of structuring existing information in the form of scientific knowledge and professional experience for decision-makers in land and resource management. Knowing the expected accuracy of species-habitat matrices allows users of modeling technology to incorporate output uncertainty into the decision-making process when evaluating alternatives for land management and protection (Salwasser 1986, Flather et al. 1992). Providing information on the degree that model predictions are empirically correct generates confidence in model applications and helps define the utility of species-habitat matrices in decision-making.

The Northern Region matrix (Prather and Burbridge 1985) generated accurate predictions (62-83%) on bird species presence for mosaics of cover types (10^3 ha) in the foothill along Montana's Rocky Mountain Front. At the resolution of individual cover types (10^1-10^2 ha), accuracy for presence predictions was considerably lower (36-63%). Raphael and Marcot (1986) also reported lower and more variable prediction accuracy in seral stages then for watersheds for a species-habitat matrix tested in NW California.

The matrix "overestimated" presence when compared to field data—a result of either not detecting a species that was present or an incorrect matrix prediction. However, differentiating among these alternatives is difficult (Raphael and Marcot 1986, Buckland and Elston 1993). Possible explanations include that (a) a habitat was suitable but unoccupied, (b) a species was present, but I failed to detect it, and (c) coding suitability ratings into presence/absence may have resulted in overrated suitability.

A species may be absent from a cover type for reasons other than the type being unsuitable habitat; biotic interactions (competition, predation), abiotic factors (weather), historical events, and individual choice may determine the absence of a species. A species may also shift use of a habitat in response to different needs during the breeding season (e.g., courtship versus nesting) and changing resource availability (e.g., insect availability). Similarly, a species may inhabit a large home range relative to the sampling resolution (e.g., peregrine falcon). Thus, the lack of presence does not necessarily indicate a lack of habitat suitability (Van Horne 1983, Block and Brennan 1993).

Given experienced birders as well as suitable weather conditions, the detectability of a bird species is primarily a function of its inherent nature (e.g., size, coloration, behavior) and the characteristics of its habitat (e.g., cover type structure and composition). Some species are easily detected. For example, a species may be conspicuous because of its foraging behavior (e.g., Clark's Nutcracker (*Nucifraga columbiana*) collecting seeds from terminal branches of limber pine), frequently emitted and clearly audible songs (e.g. western meadowlark (*Sturnella neglecta*), plumage coloration (e.g., red-winged blackbird (*Agelaius phoeniceus*)), limited fear of observers (e.g., hooting blue grouse (*Dendragapus obscurus*), aerial courtship display (e.g., common snipe (*Gallinago gallinago*)), and other salient behavioral characteristics (e.g., drumming by ruffed grouse (*Bonasa umbellus*)).

Nevertheless, the real problem in making inferences about the accuracy of a matrix is the difficulty of differentiating whether a non-detected species is truly absent from a cover type or only undetectable relative to the sampling method being used. Without additional data on individual species' detectability, it is difficult to explain the presence of undetectable species. For those species at FIELD, I examined their distribution and habitat use. Based on distribution data (Montana Natural Heritage Program 1996), the majority of these species seemed to be either rare in the area or associated with unique habitat elements. Thus, there is some evidence to suggest that some of these undetected species may have not been present at FIELD in which case the matrix overestimated presence.

If these undetected species were, in fact, present, the likelihood of failing to detect them seemed small. I used 2,731 samples to inventory species presence. Given the sampling intensity of 1 sample/2 ha, the departure of equal species detectability may be of little consequence. By chance alone, I should have detected many of these species. As such, pooling samples across cover types, sampling techniques and years should have resulted in differences of detectability to be reduced. I compared my species list to a list compiled for Theodore Roosevelt Memorial Ranch in summer of 1985 by a group of birders from The University of Montana (Metzgar 1985); this list contained no species I didn't detect. Furthermore, during my stays at Theodore Roosevelt Memorial Ranch from 1995-99, I did not detect any additional species incidental to non-sampling activities.

Some error may have occurred from initially overrating cover type suitability when coding the suitability rating into presence/absence. Initially, I considered a species predicted present if a cover type was rated to be of "least important " status in meeting a species' requirement for reproduction and/or feeding (in Table 1 denoted as 3 R or F). Alternatively, I excluded this importance level and considered a species predicted present if a cover type was rated as either moderate or most important in meeting a requirement (in Table 1 denoted as 1 and 2 R or F). The prediction accuracy changed little. Overall, the accuracy of predicting presence for cover type mosaics increased, on average, by 0.3% (S.E.=0.1%). For individual cover types, accuracy increased, on average, by 3.3% (S.E.=1.0%). The rate of incorrectly predicting absence remained unchanged for mosaics and individual cover types.

Examining accuracy by itself is informative, although limited, in establishing overall utility of a species-habitat matrix (Block et al. 1998). For most applications, accuracy needs to be compared against the costs of conducting alternative approaches for evaluating species richness. The alternative to modeling is to conduct field studies. Field studies can be very thorough, but may not necessarily be more accurate than a species-habitat matrix. The field survey at FIELD illustrates the effort and time involved in establishing a species list versus that of using a species-habitat matrix.

Establishing the species list required 1728 person-hours of time, or 13 person-hours/species, similar to efforts of detecting birds in a Douglas-fir forest in northwestern California (Marcot et al. 1983). However, my estimate does not reflect the incremental cost of detecting new species since the effort necessary to detect additional species with the same sampling methods increases exponentially (Verner 1983).

Using the same techniques, I believe that placing additional samples would result in few new species detections (<10 species). Instead, alternative sampling techniques may be considered tailored to specific characteristics of species (multiple site visits for cryptic species, sampling of large areas for species with large home ranges) (Block and Morrison 1991). However, this adds to the cost and time of conducting a field study. On the other hand, compiling, synthesizing, and structuring existing information into a species-habitat matrix costs time and energy as well, although generally less than conducting field studies.

Expenses of building a species-habitat matrix tend to be one-time, whereas the costs of conducting field studies are recurring (Verner 1983, Edwards et al. 1996). From this, it may appear that a matrix is more cost-efficient than field surveys, while yielding similar results. In my study, the Northern Region matrix predicted the presence of 175 species at FIELD with accuracy of 75%. The field survey resulted in the detection of a comparable 67% of 196 "detectable" species. As such, a species-habitat matrix is an efficient and consistent means of presenting information for a suite of species, particularly for those that are more difficult to detect with standard survey techniques. This has implications for land and species management.

Independent of cost, a manager has to decide on which side to err: (1) overestimating presence by using a matrix, or (2) underestimating presence by using a field survey. The choice depends on the question of interest. For example, if land use is curtailed to protect a portion of FIELD for a specific species then a field survey may produce more reliable information on actual presence. On the other hand, if the purpose is to compare relative species richness of FIELD to FREEZE then a species-habitat matrix may be more appropriate.

There are limitations to predicting presence at the level of individual cover types, including not detecting species associated with edge habitat and/or spatial habitat arrangements (Mellen et al. 1995, Bolger et al. 1997). The accuracy of predicting presence at the level of cover types should not be expected to be very high since species respond to a complex of habitat elements, environmental conditions, and biotic interactions when selecting habitat. Consequently, simple information on the type of land cover may not capture the conditions necessary for species presence (Dedon et al. 1986, Raphael and Marcot 1986, Young 1996). Depending on the purpose, a regional species-habitat matrix may be more useful in predicting species presence for mosaics than for individual cover types. For most applications of matrices in species richness evaluations, erring on the side of overestimating presence is generally more desirable to ensure that all existing species in an area are, in fact, accounted for, while still reasonably predicting species absence (Dedon et al. 1986, Edwards et al. 1996). The balance between overestimation and making an incorrect management decision needs to be evaluated relative to the cost of making a wrong decisions.

The greatest accuracy of a species-habitat matrix can be expected to occur within the region for which it was originally developed and the area within which experts acquired knowledge on species and their habitats. However, it is important to note here that patterns of presence/absence, as presented in species-habitat matrices, are a simplistic view of the reality of species distributions. Species are not uniformly distributed throughout their geographic range or habitats. As such, a validated species-habitat matrix is not designed to provide for an analysis of factors responsible for the distribution of species. Rather, a species-habitat matrix is intended to be an effective and efficient tool for inventorying species richness independent of how well a particular habitat provides for the life requisites that ultimately determine survival and reproductive success of a species.

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TABLES

Table 1. Hypothetical species-habitat matrix for bird species; land cover types are rated qualitatively for their importance in meeting requirements for reproduction (R) and feeding (F). A cover type is of most important status (1) if used the majority of time, is selected for when available, or is obviously selected when available, or used in much greater proportion than its occurrence; is of moderate important status (2) if used less than half the time, or is apparently selected for when available, or is used approximately in proportion to availability; and is of least important status, (3) if used occasionally, or as a last resort, or is used in much lower proportion than its occurrence (Prather and Burbridge 1985).

	Land cover type			
Bird species	Prairie grassland	Agricultural land	Wetland	Limber pine
Canada goose	2R	2R	1R, 2F	-
Blue grouse	-	-	-	1F, 1R
Green-winged teal	-	-	1F,1R	-
American goldfinch	1F,1R	1F,1R	-	3F

Table 2. Availability (%) of cover types and survey method for species detection at FIELD, 1995-97.

		Survey method	
Cover type [a]	Availability (%)[b]	Line-transect (% of n=1,831)	Point-count (% of n=900)
GRASS	68.3	1,279 (69.9)	477 (53.0)
RIPRN	11.7	118 (6.4)	171 (19.0)
ASPEN	3.3	19 (1.0)	18 (2.0)
LIMB	12.7	360 (19.7)	108 (12.0)
DFIR	2.1	15 (0.8)	18 (2.0)
WATER	1.9	40 (2.2)	108 (12.0)

[a] *See* Appendix A for description and code of cover types.

[b] Boone and Crockett GIS (1994)

Table 3. The availability of matrix cover types (Prather and Burbridge 1985) (*see* Appendix A for description of cover type and code) at Freezeout Wildlife Management Area (FREEZE), Pine Butte Swamp Preserve (PINE) and FIELD.

	Conservation area		
Cover type [a]	FREEZE	PINE	FIELD
GRASS	X	X	X
DFIR		X	X
LIMB		X	X
RIPRN	X	X	X
ASPEN		X	X
WATER	X	X	X

[a] *See* Appendix A for description and code of cover types.

Table 4. Number of bird species observations and number of species detections by cover type and survey method at FIELD, 1995-97.

	# of species observations (# of species)			
Cover type [a]	Point-count	Line-transect	Total	% of total # of species observations (% of total # of species)
GRASS	1,612 (65)	1016 (57)	2,628 (71)	42.3 (53.8)
RIPRN	1,085 (76)	198 (38)	1,283 (79)	20.7 (59.8)
ASPEN	113 (24)	24 (15)	137 (30)	2.2 (22.7)
LIMB	419 (37)	606 (36)	1,025 (52)	16.5 (39.4)
DFIR	507 (39)	28 (14)	535 (33)	8.6 (25.0)
WATER	428 (32)	171 (16)	599 (30)	9.7 (22.7)
Total	4,164 (125)	2,043 (82)	6,207 (132)	

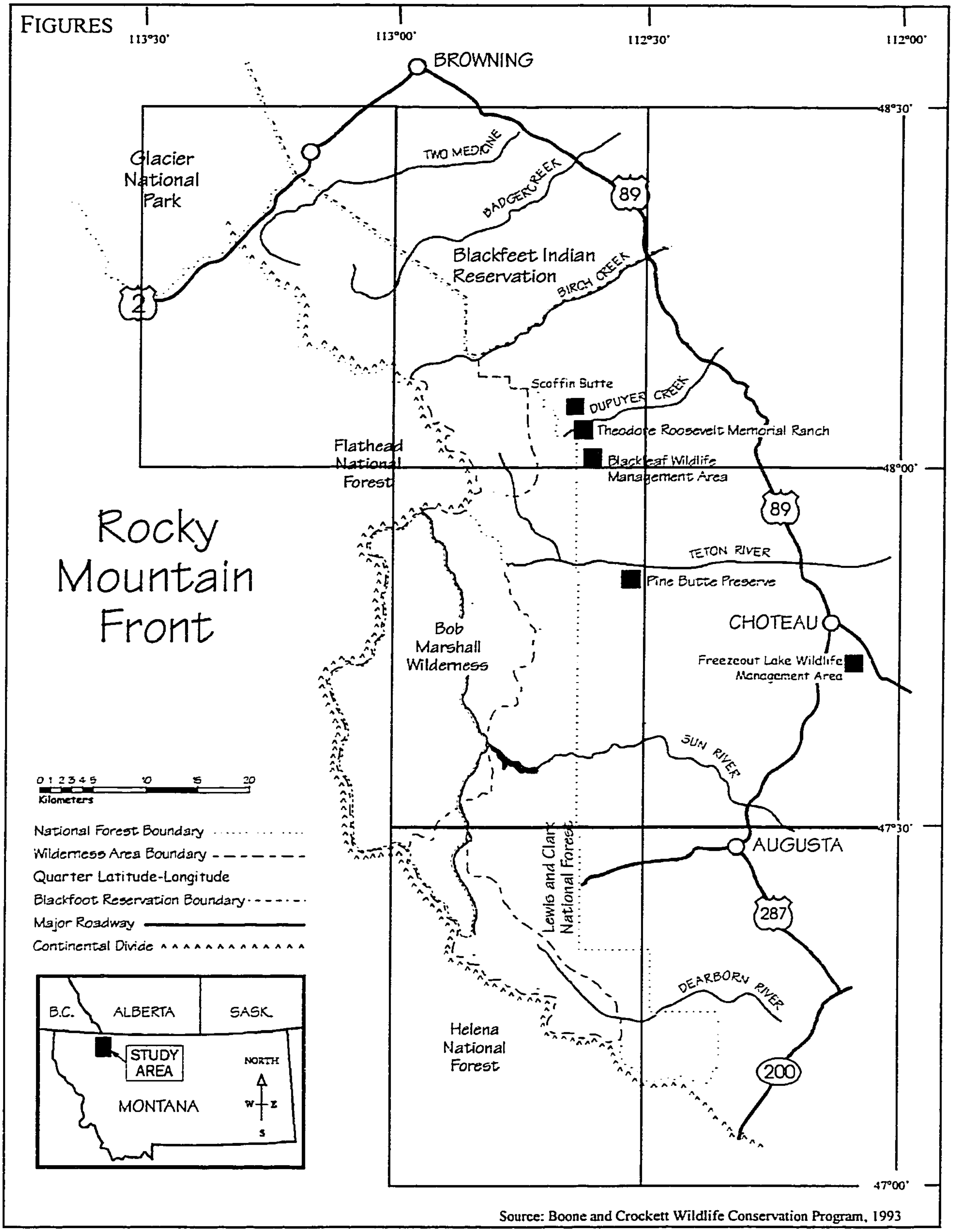
[a] *See* Appendix A for description and code of cover types.

Table 5. Comparison of predicted to observed bird species at FIELD, at Pine Butte Swamp Preserve (PINE), and Freezeout Wildlife Management Area (FREEZE) using the Northern Region matrix (Prather and Burbridge 1985).

	Conservation area		
	FIELD	PINE	FREEZE
No. of species predicted to be present	175	189	172
No. of species detected which were predicted to be present (% of total # of species predicted to be present)	132 (75.4)	157 (83.1)	107 (62.2)
No. of undetected species of those predicted to be present that were considered unlikely to be detected because:	40 (22.9)	27 (14.3)	39 (22.7)
1. no preexisting occurrence records in the particular quarter latitude longitude of the site, or	24	23	31
2. with preexisting occurrence records but associate with special habitat components (e.g., waterfalls)*	12	1	3
3. primarily nocturnal (i.e., owls)	4	3	5
No. of species predicted to be absent	21	7	24
No. of species detected which were predicted absent	0	4	4

* *See* Appendix B for list of species.

FIGURES



Source: Boone and Crockett Wildlife Conservation Program, 1993

Figure 1. Conservation areas and location of quarter latitude-longitude (Montana Natural Heritage Program 1996) on Montana's Rocky Mountain Front.

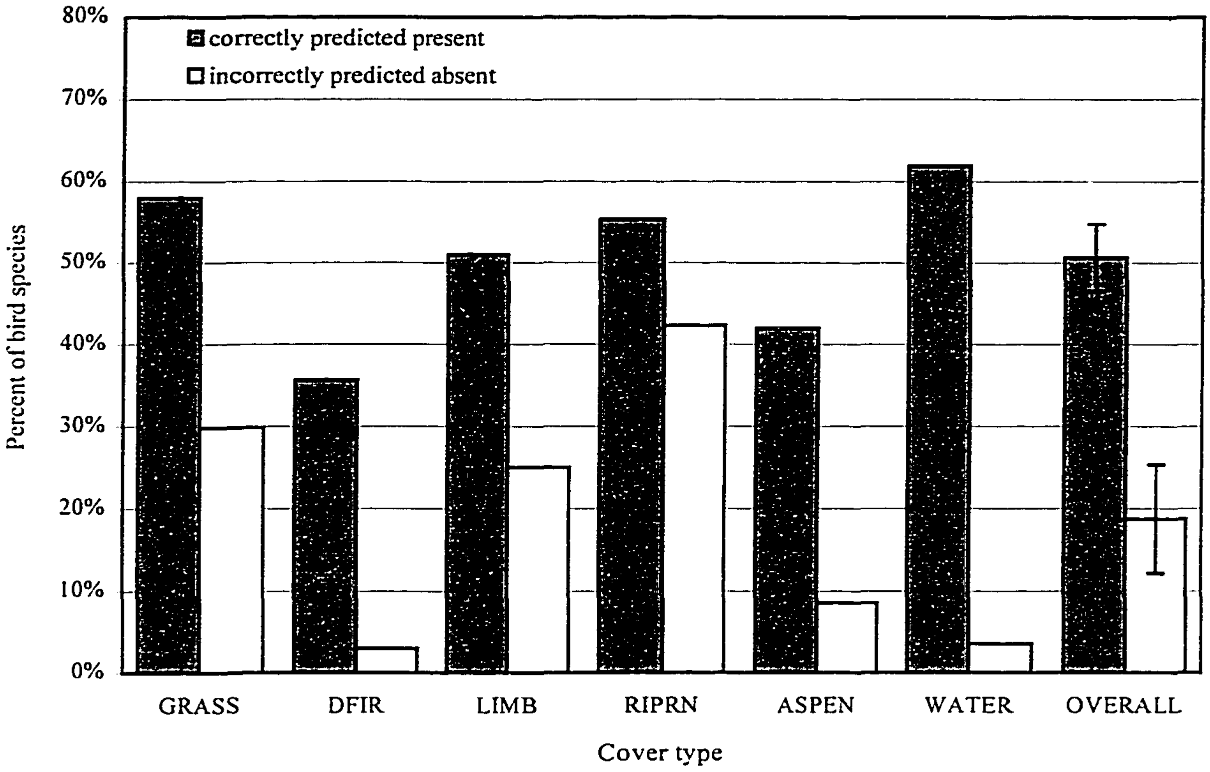


Figure 2. Comparison of predicted to detected bird species in cover types at FIELD using the Northern Region matrix, 1995-97. Percent correctly predicted present and % incorrectly predicted absent are based on the following sample sizes: GRASS (predicted present=102, predicted absent=94), DFIR (predicted present =105, predicted absent =91), LIMB (predicted present =54, predicted absent =142), RIPRN (predicted present =121, predicted absent =75), ASPEN (predicted present =53, predicted absent =143), WATER (predicted present =62, predicted absent =134). OVERALL is the mean accuracy of correctly predicting presence and incorrectly predicting absence (± S.E.) across all cover types. (*See* Appendix A for description and code of cover types).

APPENDICES

Appendix A. Description and code of Northern Region matrix cover types (Prather and Burbridge 1985).

Cover type	CODE	Description
Douglas-fir	DFIR	Coniferous forest with Douglas-fir dominated overstory
Quaking aspen	ASPEN	Deciduous forest with quaking aspen dominated overstory
Limber pine	LIMB	Coniferous forest with limber pine dominated overstory
Foothill grassland	GRASS	Grassland dominated by bunchgrasses and shrubby cinquefoil
Riparian	RIPRN	Vegetation associated with rivers, streams, marshes, creeks, and bogs
Open water	WATER	Permanent lakes and ponds

Appendix B. Seasonal distribution of bird species along Front as indexed by occurrence in seven quarter latitude-longitudes (Montana Natural Heritage Program 1996) and likelihood of species detection at FREEZE, PINE, and FIELD. The classification of a species as "unlikely to be detected" is based on: (1) nocturnal activity pattern for FIELD only, and/or (2) primary use of a cover type not present at a survey site.

				Occurrence in quarter latilongs								Unlikely to be detected at:			
Common Name	Scientific Name	Family	Season	1	2	3	4	5	6	7	total	FREEZE	PINE	FIELD	Primary use or activity (after Johnsgard 1986)
American Avocet	Recurvirostra americana	Avocets, Stilts	summer	X	X	X	X	X	X	X	7				
American Bittern	Botaurus lentiginosus	Herons, Bitterns	summer	X	X		X	X			4				
American Coot	Fulica americana	Rails	summer	X	X		X	X	X	X	6				
American Crow	Corvus brachyrrhynchos	Crows, Jays	yearlong	X	X		X	X		X	5				
American Dipper	Cinclus mexicanus	Dippers	yearlong	X	X		X		X		4	X		X	Rapidly flowing mountain streams and waterfalls.
American Goldfinch	Carduelis tristis	Finches	summer	X	X		X	X	X	X	6				
American Kestrel	Falco sparverius	Falcons	summer		X	X	X	X	X	X	6				
American Pipit	Anthus rubescens	Wagtails	summer	X	X			X			3			X	Alpine meadows.
American Redstart	Setophaga ruticilla	Wood Warblers	summer	X	X	X	X	X		X	6				
American Robin	Turdus migratorius	Kinglets, Gnatcatchers	summer	X	X		X	X	X	X	6				
American Tree Sparrow	Spizella arborea	Wood Warblers	yearlong	X				X		X	3				
American White Pelican	Pelecanus erythrorhynchos	Pelicans	summer			X	X	X	X	X	5				
American Wigeon	Anas americana	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Baird's Sparrow	Ammodramus bairdii	Wood Warblers	summer		X					X	2				
Bald Eagle	Haliaeetus leucocephalus	Hawks	yearlong	X	X			X		X	4				
Bank Swallow	Riparia riparia	Swallows	summer	X	X		X	X		X	5				
Barn Swallow	Hirundo rustica	Swallows	summer	X	X		X	X	X	X	6				
Barrow's Goldeneye	Bucephala islandica	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Belted Kingfisher	Ceryle alcyon	Kingfishers	yearlong	X	X		X	X	X	X	6				
Black Swift	Cypseloides niger	Swifts	summer	X							1				
Black Tern	Chlidonias niger	Gulls, Terns	summer	X		X	X				3			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Black-backed Woodpecker	Picoides arcticus	Woodpeckers	yearlong	X							1	X	X	X	Burned coniferous forests.
Black-billed Magpie	Pica pica	Crows, Jays	yearlong	X	X		X	X	X	X	6				
Black-capped Chickadee	Parus atricapillus	Chickadees, Titmice	yearlong	X	X		X	X		X	5				
Black-crowned Night Heron	Nycticorax nycticorax	Herons, Bitterns	summer					X			1			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Black-headed Grosbeak	Pheucticus melanocephalus	Wood Warblers	summer	X	X		X	X		X	5				
Blue Grouse	Dendragapus obscurus	Pheasants, Grouse, Partridges	yearlong	X	X		X		X		4				
Blue-winged Teal	Anas discors	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Bobolink	Dolichonyx oryzivorus	Wood Warblers	summer	X			X	X	X	X	5				
Brewer's Blackbird	Euphagus cyanocephalus	Wood Warblers	summer	X	X	X	X	X	X	X	7				
Brewer's Sparrow	Spizella breweri	Wood Warblers	summer				X			X	2				
Brown Thrasher	Toxostoma rufum	Mockingbirds, Thrashers	summer	X				X			2				
Brown-headed Cowbird	Molothrus ater	Wood Warblers	summer	X	X		X	X		X	5				
Bufflehead	Bucephala albeola	Swans, Geese, Ducks	summer	X	X			X	X		4			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Burrowing Owl	Speotyto cunicularia	Owls	summer					X			1				
California Gull	Larus californicus	Gulls, Terns	summer	X	X		X	X	X	X	6				
Calliope Hummingbird	Stellula calliope	Hummingbirds	summer	X			X				2	X			Coniferous forests.
Canada Goose	Branta canadensis	Swans, Geese, Ducks	yearlong	X	X		X	X	X	X	6				
Canvasback	Aythya valisineria	Swans, Geese, Ducks	summer	X	X			X	X	X	5				
Cassin's Finch	Carpodacus cassinii	Finches	yearlong	X			X				2				
Cedar Waxwing	Bombycilla cedrorum	Waxwings	summer	X	X	X	X	X		X	6				

				Occurrence in quarter latilongs								Unlikely to be detected at:			
Common Name	Scientific Name	Family	Season	1	2	3	4	5	6	7	total	FREEZE	PINE	FIELD	Primary use or activity (after Johnsgard 1986)
Chestnut-backed Chickadee	Parus rufescens	Chickadees, Titmice	yearlong	X							1				
Chestnut-collared Longspur	Calcarius ornatus	Wood Warblers	summer				X	X			2				
Chipping Sparrow	Spizella passerina	Wood Warblers	summer	X	X		X	X	X		5				
Cinnamon Teal	Anas cyanoptera	Swans, Geese, Ducks	summer	X	X		X	X		X	5				
Clark's Grebe	Aechmophorus clarkii	Grebes	summer					X			1			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Clark's Nutcracker	Nucifraga columbiana	Crows, Jays	yearlong	X	X		X	X	X		5				
Clay-colored Sparrow	Spizella pallida	Wood Warblers	summer	X	X		X	X		X	5				
Cliff Swallow	Hirundo pyrrhonota	Swallows	summer	X	X	X	X	X	X	X	7				
Common Goldeneye	Bucephala clangula	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Common Grackle	Quiscalus quiscula	Wood Warblers	summer	X	X		X	X		X	5				
Common Loon	Gavia immer	Loons	summer	X				X		X	3		X	X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Common Merganser	Mergus merganser	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Common Nighthawk	Chordeiles minor	Goatsuckers	summer	X	X		X	X	X	X	6				
Common Raven	Corvus corax	Crows, Jays	yearlong	X	X		X	X	X	X	6				
Common Snipe	Gallinago gallinago	Sandpipers	summer	X	X		X	X	X	X	6				
Common Tern	Sterna hirundo	Gulls, Terns	summer					X			1		X	X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Common Yellowthroat	Geothlypis trichas	Wood Warblers	summer	X	X		X	X	X	X	6				
Cooper's Hawk	Accipiter cooperii	Hawks	summer	X	X						2				
Cordilleran Flycatcher	Empidonax occidentalis	Flycatchers	summer				X			X	2				
Dark-eyed Junco	Junco hyemalis	Wood Warblers	yearlong	X	X		X	X	X		5				
Double-crested Cormorant	Phalacrocorax auritus	Cormorants	summer	X	X	X		X	X	X	6				
Downy Woodpecker	Picoides pubescens	Woodpeckers	yearlong	X	X		X			X	4				
Dusky Flycatcher	Empidonax oberholseri	Flycatchers	summer	X			X	X	X		4				
Eared Grebe	Podiceps nigricollis	Grebes	summer	X	X			X			3			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Eastern Kingbird	Tyrannus tyrannus	Flycatchers	summer	X	X	X	X	X	X	X	7				
European Starling	Sturnus vulgaris	Starlings	yearlong	X	X		X	X	X	X	6				
Evening Grosbeak	Coccothraustes vespertinus	Finches	yearlong	X	X		X			X	4				
Ferruginous Hawk	Buteo regalis	Hawks	summer		X			X		X	3				
Forster's Tern	Sterna forsteri	Gulls, Terns	summer					X			1			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Fox Sparrow	Passerella iliaca	Wood Warblers	summer	X			X				2				
Franklin's Gull	Larus pipixcan	Gulls, Terns	summer	X	X		X	X			4			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Gadwall	Anas strepera	Swans, Geese, Ducks	summer	X	X			X	X	X	5				
Golden Eagle	Aquila chrysaetos	Hawks	yearlong	X	X		X	X	X	X	6				
Golden-crowned Kinglet	Regulus satrapa	Kinglets, Gnatcatchers	yearlong	X			X				2	X			Coniferous forests.
Grasshopper Sparrow	Ammodramus savannarum	Wood Warblers	summer					X			1				
Gray Catbird	Dumetella carolinensis	Mockingbirds, Thrashers	summer	X	X		X	X		X	5				
Gray Jay	Perisoreus canadensis	Crows, Jays	yearlong	X			X		X		3	X			Coniferous forests.
Gray Partridge	Perdix perdix	Pheasants, Grouse, Partridges	yearlong	X	X	X	X	X		X	6				
Great Blue Heron	Ardea herodias	Herons, Bitterns	summer	X	X		X	X	X	X	6				
Great Gray Owl	Strix nebulosa	Owls	yearlong	X			X				2				
Great Horned Owl	Bubo virginianus	Owls	yearlong	X	X	X	X	X	X		6			X	Nocturnal
Green-winged Teal	Anas crecca	Swans, Geese, Ducks	summer	X	X			X	X	X	5				
Hairy Woodpecker	Picoides villosus	Woodpeckers	yearlong	X	X		X			X	4				
Hammond's Flycatcher	Empidonax hammondii	Flycatchers	summer	X			X		X		3	X		X	Coniferous forests.
Harlequin Duck	Histrionicus histrionicus	Swans, Geese, Ducks	summer	X	X		X		X		4	X			Rapidly flowing mountain streams and waterfalls.
Hermit Thrush	Catharus guttatus	Kinglets, Gnatcatchers	summer	X			X				2	X		X	Coniferous forests.
Hooded Merganser	Lophodytes cucullatus	Swans, Geese, Ducks	summer		X		X	X			3				

				Occurrence in quarter latilongs								Unlikely to be detected at:			
Common Name	Scientific Name	Family	Season	1	2	3	4	5	6	7	total	FREEZE	PINE	FIELD	Primary use or activity (after Johnsgard 1986)
Horned Grebe	Podiceps auritus	Grebes	summer	X				X	X	X	4				
Horned Lark	Eremophila alpestris	Larks	yearlong	X	X	X	X	X		X	6				
House Sparrow	Passer domesticus	Finches	yearlong	X				X		X	3				
House Wren	Troglodytes aedon	Wrens	summer	X	X		X	X	X	X	6				
Killdeer	Charadrius vociferus	Plovers	summer	X	X		X	X	X	X	6				
Lark Bunting	Calamospiza melanocorys	Wood Warblers	summer	X			X	X		X	4				
Lark Sparrow	Chondestes grammacus	Wood Warblers	summer	X			X	X			3				
Lazuli Bunting	Passerina amoena	Wood Warblers	summer	X	X		X	X			4				
Least Flycatcher	Empidonax minimus	Flycatchers	summer	X	X		X	X		X	5				
Lesser Scaup	Aythya affinis	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Lewis's Woodpecker	Melanerpes lewis	Woodpeckers	summer					X			1				
Loggerhead Shrike	Lanius ludovicianus	Gulls, Terns	summer	X		X		X			3				
Long-billed Curlew	Numenius americanus	Sandpipers	yearlong	X	X		X	X	X	X	6				
Long-eared Owl	Asio otus	Owls	yearlong					X			1			X	Nocturnal
MacGillivray's Warbler	Oporornis tolmiei	Wood Warblers	summer	X	X	X	X	X	X		6				
Mallard	Anas platyrhynchos	Swans, Geese, Ducks	yearlong	X	X		X	X	X	X	6				
Marbled Godwit	Limosa fedoa	Sandpipers	summer	X	X		X	X		X	5				
Marsh Wren	Cistothorus palustris	Wrens	summer					X			1			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
McCown's Longspur	Calcarius mccownii	Wood Warblers	summer				X	X		X	3				
Merlin	Falco columbarius	Falcons	summer	X	X		X				3				
Mountain Bluebird	Sialia currucoides	Kinglets, Gnatcatchers	summer	X	X		X	X	X		5				
Mountain Chickadee	Parus gambeli	Chickadees, Titmice	yearlong	X	X		X		X		4	X			Coniferous forests.
Mourning Dove	Zenaida macroura	Pigeons, Doves	summer	X	X		X	X		X	5				
Nashville Warbler	Vermivora ruficapilla	Wood Warblers	summer	X							1				
Northern Flicker	Colaptes auratus	Woodpeckers	yearlong	X	X		X	X	X	X	6				
Northern Goshawk	Accipiter gentilis	Hawks	yearlong	X	X		X	X	X		5				
Northern Harrier	Circus cyaneus	Hawks	summer	X	X		X	X	X	X	6				
Northern Oriole	Icterus galbula	Wood Warblers	summer		X		X	X		X	4				
Northern Pintail	Anas acuta	Swans, Geese, Ducks	summer	X	X		X	X		X	5				
Northern Pygmy Owl	Glaucidium gnoma	Owls	yearlong	X			X				2				
Northern Rough-winged Swallow	Stelgidopteryx serripennis	Swallows	summer	X	X		X	X	X	X	6				
Northern Saw-whet Owl	Aegolius acadicus	Owls	yearlong	X			X	X			3			X	Nocturnal
Northern Shoveler	Anas clypeata	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Northern Waterthrush	Seiurus noveboracensis	Wood Warblers	summer	X	X	X	X	X	X	X	7				
Olive-sided Flycatcher	Contopus borealis	Flycatchers	summer	X			X		X		3				
Orange-crowned Warbler	Vermivora celata	Wood Warblers	summer	X			X				2				
Osprey	Pandion haliaetus	Hawks	summer	X	X		X	X	X		5				
Peregrine Falcon	Falco peregrinus	Falcons	summer	X	X		X				3				
Pied-billed Grebe	Podilymbus podiceps	Grebes	summer	X	X		X	X	X	X	6			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Pileated Woodpecker	Dryocopus pileatus	Woodpeckers	yearlong	X							1	X		X	Coniferous forests.
Pine Grosbeak	Pinicola enucleator	Finches	yearlong	X							1				
Pine Siskin	Carduelis pinus	Finches	yearlong	X			X	X	X		4				
Prairie Falcon	Falco mexicanus	Falcons	summer	X	X		X	X	X		5				
Red Crossbill	Loxia curvirostra	Finches	yearlong	X	X		X				3	X			Coniferous forests.
Red-breasted Nuthatch	Sitta canadensis	Nuthatches	yearlong	X	X		X	X	X		5	X			Coniferous forests.
Red-eyed Vireo	Vireo olivaceus	Vireos	summer	X	X		X	X			4				
Redhead	Aythya americanus	Swans, Geese, Ducks	summer	X	X			X	X	X	5			X	Wetlands, ponds, marshes, or lakes (>1ha in size).

				Occurrence in quarter latilongs								Unlikely to be detected at:			
Common Name	Scientific Name	Family	Season	1	2	3	4	5	6	7	total	FREEZE	PINE	FIELD	Primary use or activity (after Johnsgard 1986)
Red-naped Sapsucker	Sphyrapicus nuchalis	Woodpeckers	summer	X	X		X				3				
Red-necked Grebe	Podiceps grisegena	Grebes	summer	X	X		X	X	X	X	6				
Red-tailed Hawk	Buteo jamaicensis	Hawks	yearlong	X	X		X	X	X	X	6				
Red-winged Blackbird	Agelaius phoeniceus	Wood Warblers	summer	X	X		X	X	X	X	6				
Ring-billed Gull	Larus delawarensis	Gulls, Terns	summer	X	X		X	X	X	X	6			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Ring-necked Duck	Aythya collaris	Swans, Geese, Ducks	summer	X	X		X	X	X	X	6				
Ring-necked Pheasant	Phasianus colchicus	Pheasants, Grouse, Partridges	yearlong		X	X	X	X		X	5				
Rock Dove	Columba livia	Pigeons, Doves	yearlong	X	X	X		X			4				
Rock Wren	Salpinctes obsoletus	Wrens	summer	X	X		X	X		X	5				
Ruby-crowned Kinglet	Regulus calendula	Kinglets, Gnatcatchers	summer	X			X	X	X		4	X			Coniferous forests.
Ruddy Duck	Oxyura jamaicensis	Swans, Geese, Ducks	summer	X	X			X		X	4				
Ruffed Grouse	Bonasa umbellus	Pheasants, Grouse, Partridges	yearlong	X	X		X	X	X		5	X			Coniferous forests.
Rufous-sided Towhee	Pipilo erythrophthalmus	Wood Warblers	summer	X	X						2				
Sandhill Crane	Grus canadensis	Cranes	summer	X	X		X	X		X	5				
Savannah Sparrow	Passerculus sandwichensis	Wood Warblers	yearlong	X	X		X	X		X	5				
Say's Phoebe	Sayornis saya	Flycatchers	summer	X			X	X			3				
Sharp-shinned Hawk	Accipiter striatus	Hawks	summer	X	X		X				3				
Sharp-tailed Grouse	Tympanuchus phasianellus	Pheasants, Grouse, Partridges	yearlong	X	X		X	X	X		5				
Short-eared Owl	Asio flammeus	Owls	summer					X			1				
Solitary Vireo	Vireo solitarius	Vireos	summer	X		X	X				3				
Song Sparrow	Melospiza melodia	Wood Warblers	summer	X	X		X	X	X	X	6				
Sora	Porzana carolina	Rails	summer	X	X		X	X	X	X	6			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Spotted Sandpiper	Actitis macularia	Sandpipers	summer	X	X		X	X	X	X	6				
Sprague's Pipit	Anthus spragueii	Wagtails	summer	X	X		X	X		X	5				
Spruce Grouse	Dendragapus canadensis	Pheasants, Grouse, Partridges	yearlong	X	X						2			X	Mature, high-altitude coniferous forest.
Steller's Jay	Cyanocitta stelleri	Crows, Jays	yearlong	X					X		2				
Swainson's Hawk	Buteo swainsoni	Hawks	summer		X		X	X		X	4				
Swainson's Thrush	Catharus ustulatus	Kinglets, Gnatcatchers	summer	X	X		X	X	X		5				
Three-toed Woodpecker	Picoides tridactylus	Woodpeckers	yearlong	X			X				2		X		Burned coniferous forests
Townsend's Solitaire	Myadestes townsendi	Kinglets, Gnatcatchers	yearlong	X	X		X		X		4				
Townsend's Warbler	Dendroica townsendi	Wood Warblers	summer	X			X				2			X	Mature, high-altitude coniferous forest.
Tree Swallow	Tachycineta bicolor	Swallows	summer	X	X		X	X	X	X	6				
Trumpeter Swan	Cygnus buccinator	Swans, Geese, Ducks	yearlong	X	X			X	X	X	5		X	X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Turkey Vulture	Cathartes aura	American Vultures	summer	X	X			X			3				
Upland Sandpiper	Bartramia longicauda	Sandpipers	summer	X	X		X	X		X	5				
Varied Thrush	Ixoreus naevius	Kinglets, Gnatcatchers	summer	X							1	X			Coniferous forests.
Vaux's Swift	Chaetura vauxi	Swifts	summer					X			1				
Veery	Catharus fuscescens	Kinglets, Gnatcatchers	summer	X	X		X	X	X	X	6				
Vesper Sparrow	Pooecetes gramineus	Wood Warblers	summer	X	X	X	X	X	X	X	7				
Violet-green Swallow	Tachycineta thalassina	Swallows	summer	X	X		X	X		X	5				
Warbling Vireo	Vireo gilvus	Vireos	summer	X	X		X	X	X	X	6				
Western Bluebird	Sialia mexicana	Kinglets, Gnatcatchers	summer	X			X			X	3				
Western Grebe	Aechmophorus occidentalis	Grebes	summer	X				X			2		X	X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Western Kingbird	Tyrannus verticalis	Flycatchers	summer		X		X	X		X	4				
Western Meadowlark	Sturnella neglecta	Wood Warblers	summer	X	X	X	X	X	X	X	7				
Western Screech-owl	Otus kennicottii	Owls	summer				X				1			X	Nocturnal
Western Tanager	Piranga ludoviciana	Wood Warblers	summer	X	X		X	X	X		5				

				Occurrence in quarter latilongs								Unlikely to be detected at:			
Common Name	Scientific Name	Family	Season	1	2	3	4	5	6	7	total	FREEZE	PINE	FIELD	Primary use or activity (after Johnsgard 1986)
Western Wood-pewee	Contopus sordiculus	Flycatchers	summer	X	X		X	X	X	X	6				
White-breasted Nuthatch	Sitta carolinensis	Nuthatches	yearlong	X							1				
White-crowned Sparrow	Zonotrichia leucophrys	Wood Warblers	summer	X	X		X	X	X		5				
White-faced Ibis	Plegadis chihi	Ibises	summer					X			1			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
White-throated Swift	Aeronautes saxatalis	Swifts	summer				X				1	X			Coniferous forests.
Willet	Cataptrophorus semipalmatus	Sandpipers	summer	X	X		X	X	X	X	6				
Willow Flycatcher	Empidonax traillii	Flycatchers	summer	X	X		X		X	X	5				
Wilson's Phalarope	Phalaropus tricolor	Sandpipers	summer	X	X		X	X	X	X	6				
Wilson's Warbler	Wilsonia pusilla	Wood Warblers	summer	X			X	X	X		4				
Winter Wren	Troglodytes troglodytes	Wrens	summer	X			X				2				
Wood Duck	Aix sponsa	Swans, Geese, Ducks	summer	X	X			X			3			X	Wetlands, ponds, marshes, or lakes (>1ha in size).
Yellow Warbler	Dendroica petechia	Wood Warblers	summer	X	X		X	X	X	X	6				
Yellow-headed Blackbird	Xanthocephalus xanthocephalus	Wood Warblers	summer	X			X	X	X	X	5				
Yellow-rumped Warbler	Dendroica coronata	Wood Warblers	summer	X	X		X	X	X		5				

Appendix C. Detection rate of bird species (# of species observations/# cover type samples) by survey method (line transect, point count) and cover type at FIELD, 1995-97.

	Line-transect (n)								Point count (n)							
Common Name	species observations	GRASS (1,279)	RIPRN (118)	ASPEN (19)	LIMB (360)	DFIR (15)	WATER (40)	Overall (1,831)	species observations	GRASS (477)	RIPRN (177)	ASPEN (18)	LIMB (108)	DFIR (18)	WATER (108)	Overall (900)
American Avocet									13						0.120	0.014
American Bittern																
American Crow	51	0.018	0.025		0.069			0.028	136	0.157	0.023	0.167	0.167	1.000		0.151
American Goldfinch	10	0.003	0.017		0.011			0.005	145	0.055	0.237		0.435	1.000		0.161
American Kestrel	13	0.005	0.008	0.053	0.014			0.007	33	0.046			0.102			0.037
American Redstart									9		0.011	0.278	0.019			0.010
American Robin	62	0.014	0.076	0.105	0.091			0.034	161	0.050	0.322	1.000	0.259	1.000		0.179
American Tree Sparrow	15				0.042			0.008	8		0.045					0.009
American Wigeon	14						0.350	0.008	31	0.010	0.017				0.213	0.034
Baird's Sparrow																
Bald Eagle																
Bank Swallow									21	0.006	0.011				0.148	0.023
Barn Swallow	1						0.025	0.001	27	0.008	0.045				0.139	0.030
Barrow's Goldeneye	4						0.100	0.002	1						0.009	0.001
Belted Kingfisher	2		0.008		0.003			0.001	7		0.040					0.008
Black-billed Magpie	32	0.016	0.017	0.158	0.019			0.017	75	0.075	0.062	0.222	0.130	1.000		0.083
Black-capped Chickadee	8	0.001	0.017		0.014			0.004	55		0.023	0.111	0.176	1.000		0.061
Black-headed Grosbeak									1		0.006					0.001
Blue Grouse	55	0.003	0.008		0.139			0.030	28	0.004	0.006		0.139	0.556		0.031
Blue-winged Teal	1						0.025	0.001	5						0.046	0.006
Bobolink									5	0.010						0.006
Brewer's Blackbird	201	0.106	0.356		0.064			0.110	353	0.478	0.593		0.093	1.000		0.392
Brewer's Sparrow																
Brown Thrasher									2	0.002	0.006					0.002
Brown-headed Cowbird	2	0.002						0.001	30		0.169					0.033
Bufflehead																
California Gull	54	0.002	0.008				1.000	0.029	262	0.478	0.034				0.259	0.291
Calliope Hummingbird																
Canada Goose	36	0.012	0.076				0.300	0.020	160	0.176	0.040				0.639	0.178
Canvasback									5						0.046	0.006
Cassin's Finch									2		0.006	0.056				0.002
Cedar Waxwing									27		0.107			0.556		0.030
Chestnut-backed Chickadee																
Chestnut-collared Longspur																
Chipping Sparrow	328	0.072	0.085	0.053	0.568	2.222		0.179	89	0.004	0.034		0.472	1.000		0.099
Cinnamon Teal									15						0.139	0.017

	Line-transect (n)								Point count (n)							
Common Name	species observations	GRASS (1,279)	RIPRN (118)	ASPEN (19)	LIMB (360)	DFIR (15)	WATER (40)	Overall (1,831)	species observations	GRASS (477)	RIPRN (177)	ASPEN (18)	LIMB (108)	DFIR (18)	WATER (108)	Overall (900)
Clark's Grebe																
Clark's Nutcracker	49	0.002			0.122	0.222		0.027	15				0.074	0.667		0.017
Clay-colored Sparrow	72	0.050	0.025	0.105	0.008			0.039	52	0.059	0.113	0.056	0.028			0.058
Cliff Swallow									12	0.004	0.056					0.013
Common Goldeneye	3						0.075	0.002	2						0.019	0.002
Common Grackle									1				0.009			0.001
Common Merganser	6						0.150	0.003	11		0.023				0.065	0.012
Common Nighthawk									2		0.006	0.056				0.002
Common Raven	16	0.009		0.053	0.006	0.167		0.009	77	0.059		0.167	0.139	1.000	0.009	0.086
Common Snipe	46	0.023	0.110	0.053	0.006			0.025	66	0.065	0.181		0.009		0.019	0.073
Common Yellowthroat	3	0.001	0.017					0.002	32		0.181					0.036
Cooper's Hawk									2	0.004						0.002
Cordilleran Flycatcher	2		0.017					0.001								
Dark-eyed Junco	17		0.008	0.053	0.039	0.167		0.009	105	0.042	0.153	0.222	0.222	1.000		0.117
Downy Woodpecker	1		0.008					0.001	8		0.028	0.111	0.009			0.009
Dusky Flycatcher	1			0.053				0.001	65		0.113		0.139	1.000		0.072
Eastern Kingbird	1	0.001						0.001	49	0.059	0.102	0.111	0.009			0.054
European Starling	1			0.053				0.001	104	0.071	0.395					0.116
Ferruginous Hawk																
Fox Sparrow	1		0.008					0.001	4		0.023					0.004
Gadwall	4						0.100	0.002	17						0.157	0.019
Golden Eagle	12	0.008			0.006			0.007	13	0.008	0.006		0.056	0.222		0.014
Golden-crowned Kinglet	1				0.003			0.001								
Grasshopper Sparrow																
Gray Catbird									4		0.023					0.004
Gray Partridge	2	0.002						0.001								
Great Blue Heron	3	0.001	0.017					0.002	7	0.006	0.023					0.008
Green-winged Teal									1						0.009	0.001
Hairy Woodpecker	1				0.003			0.001	18	0.002	0.068	0.278				0.020
Harlequin Duck																
Hooded Merganser									2						0.019	0.002
Horned Grebe	4						0.100	0.002								
Horned Lark	3	0.002						0.002	15	0.031						0.017
House Sparrow									3	0.002	0.011					0.003
House Wren									28	0.004	0.056	0.833	0.009			0.031
Killdeer	13	0.010						0.007	55	0.111					0.019	0.061
Lark Bunting									75	0.157						0.083
Lark Sparrow	14	0.011						0.008								
Lazuli Bunting																
Least Flycatcher									2		0.011					0.002

	Line-transect (n)								Point count (n)							
Common Name	species observations	GRASS (1,279)	RIPRN (118)	ASPEN (19)	LIMB (360)	DFIR (15)	WATER (40)	Overall (1,831)	species observations	GRASS (477)	RIPRN (177)	ASPEN (18)	LIMB (108)	DFIR (18)	WATER (108)	Overall (900)
Lesser Scaup									26						0.241	0.029
Lewis's Woodpecker																
Loggerhead Shrike																
Long-billed Curlew	44	0.034						0.024	55	0.111	0.006	0.056				0.061
MacGillivary's Warbler									6				0.009	0.556		0.007
Mallard	54	0.004					1.000	0.029	96	0.029	0.068				0.648	0.107
Marbled Godwit	8	0.006						0.004	41	0.071					0.065	0.046
McCown's Longspur																
Merlin	11	0.003			0.019			0.006	8	0.010	0.006		0.019			0.009
Mountain Bluebird	20	0.007	0.025	0.105	0.014	0.167		0.011	33	0.019	0.051	0.278	0.093			0.037
Mountain Chickadee	37	0.001	0.034	0.053	0.083	0.111		0.020	35		0.011		0.093	1.000		0.039
Mourning Dove	7				0.019			0.004	66	0.092	0.124					0.073
Nashville Warbler									1					0.111		0.001
Northern Flicker	22	0.002	0.051		0.033	0.167		0.012	74	0.004	0.141	0.500	0.167	1.000		0.082
Northern Goshawk																
Northern Harrier	26	0.016	0.025		0.008			0.014	50	0.088	0.017		0.046			0.056
Northern Oriole									2		0.011					0.002
Northern Pintail	2						0.050	0.001	5	0.004					0.028	0.006
Northern Rough-winged Swallow	14	0.007	0.042					0.008	8		0.045					0.009
Northern Shoveler	2						0.050	0.001	16						0.148	0.018
Northern Waterthrush									1		0.006					0.001
Olive-sided Flycatcher									1	0.002						0.001
Orange-crowned Warbler									5		0.028					0.006
Osprey									1	0.002						0.001
Peregrine Falcon																
Pied-billed Grebe																
Pine Siskin									31	0.002	0.085			1.000		0.034
Prairie Falcon									1				0.009			0.001
Red Crossbill									15					1.000		0.017
Red-breasted Nuthatch									30				0.093	1.000		0.033
Red-eyed Vireo									5		0.011	0.056	0.019			0.006
Red-naped Sapsucker	1		0.008					0.001	9		0.051					0.010
Red-tailed Hawk	10	0.003	0.034		0.006			0.005	28	0.025	0.073		0.028			0.031
Red-winged Blackbird									105	0.052	0.367				0.139	0.117
Ring-necked Duck	2						0.050	0.001	7						0.065	0.008
Ring-necked Pheasant	2	0.002						0.001	17	0.027	0.011		0.019			0.019
Rock Dove	10	0.008						0.005	7	0.008	0.017					0.008
Rock Wren																
Ruby-crowned Kinglet	18	0.008	0.034		0.011			0.010	32		0.051		0.028	1.000		0.036

	Line-transect (n)								Point count (n)							
Common Name	species observations	GRASS (1,279)	RIPRN (118)	ASPEN (19)	LIMB (360)	DFIR (15)	WATER (40)	Overall (1,831)	species observations	GRASS (477)	RIPRN (177)	ASPEN (18)	LIMB (108)	DFIR (18)	WATER (108)	Overall (900)
Ruddy Duck																
Ruffed Grouse	9	0.001	0.034	0.211				0.005	20	0.004	0.062	0.056	0.037	0.222		0.022
Rufous-sided Towhee									4		0.023					0.004
Sandhill Crane	3	0.002						0.002	16	0.017	0.045					0.018
Savannah Sparrow	150	0.111	0.068					0.082	45	0.080	0.040					0.050
Say's Phoebe									1				0.009			0.001
Sharp-shinned Hawk	1	0.001						0.001								
Sharp-tailed Grouse	46	0.029	0.034		0.014			0.025	39	0.048	0.040		0.056	0.333		0.043
Solitary Vireo									5					0.444		0.006
Song Sparrow	46	0.031	0.034		0.006			0.025	44	0.015	0.203		0.009			0.049
Spotted Sandpiper									24		0.062				0.120	0.027
Sprague's Pipit	5	0.004						0.003	1	0.002						0.001
Steller's Jay																
Swainson's Hawk	3	0.002						0.002	16	0.019	0.017		0.037			0.018
Swainson's Thrush									12		0.034		0.009	0.556		0.013
Townsend's Solitaire	18	0.002			0.044			0.010	10				0.046	0.444		0.011
Tree Swallow	9		0.076					0.005	68	0.006	0.288				0.130	0.076
Turkey Vulture																
Upland Sandpiper	7	0.005						0.004	3	0.006						0.003
Vaux's Swift																
Veery	1				0.003			0.001	6		0.034					0.007
Vesper Sparrow	29	0.019	0.025		0.006			0.016	68	0.109			0.148			0.076
Violet-green Swallow	4		0.034					0.002								
Warbling Vireo									30			0.833		1.000		0.033
Western Bluebird	1	0.001						0.001	2				0.019			0.002
Western Grebe																
Western Kingbird									3	0.006						0.003
Western Meadowlark	114	0.088			0.006			0.062	90	0.184	0.011					0.100
Western Tanager									6	0.002				0.333		0.007
Western Wood-pewee	4	0.003						0.002	11		0.006	0.278		0.333		0.012
White-breasted Nuthatch																
White-crowned Sparrow	41	0.015	0.093	0.105	0.022	0.111		0.022	123	0.061	0.237	0.111	0.176	1.000		0.137
Willet	2	0.002						0.001	3	0.002					0.019	0.003
Willow Flycatcher									15		0.085					0.017
Wilson's Phalarope	17						0.425	0.009	31						0.287	0.034
Wilson's Warbler									2		0.011					0.002
Wood Duck																
Yellow Warbler	4		0.017	0.053	0.003			0.002	33		0.181	0.056				0.037
Yellow-headed Blackbird									8	0.017						0.009
Yellow-rumped Warbler	74	0.005	0.093		0.158			0.040	55	0.002	0.164	0.167	0.019	1.000		0.061

CHAPTER 2: PREDICTING ELK OCCURRENCE ON A WINTER RANGE IN MONTANA: A COMPARISON OF FOUR HABITAT SUITABILITY MODELS

INTRODUCTION

Knowing the distribution of a species is essential for its conservation. Because of the difficulty, time, and cost of acquiring reliable field-estimates of distribution, habitat suitability mapping is a commonly used alternative (Flather et al. 1992, Block et al. 1994, Morrison et al. 1998). Habitat suitability mapping evaluates the quality and quantity of habitat for a species based on species-habitat associations (U.S. Fish and Wildlife Service 1981). Suitability is defined in terms of how well a habitat provides life requisites, such as food and shelter, which contribute to individual fitness and population persistence (Van Horne 1983, Block and Brennan 1993).

Habitat suitability mapping involves assigning weights and rules to a database or a map of environmental conditions within a species range (Wisdom et al. 1986, Pereira and Itami 1991, Duncan et al. 1995). These weights and rules are assigned on the premise that biophysical characteristics, such as topography, vegetation, and human land use, influence species occurrence (Lancia et al. 1982, Irwin and Cook 1985, Thomasma et al. 1991). The premise in the classification is that the resulting map is similar to how individuals of a species occupy habitat. Two sources of information are used in formulating species-habitat associations: expert opinion and empirical studies.

The first generation of suitability models relied primarily on professional judgement for identifying species-habitat associations, e.g. Habitat Suitability Index (HSI) models (U.S. Fish and Wildlife Service 1981). Experts familiar with the autecology of a particular species often know its habitat associations (Thomas et al. 1979). However, expert-based models tend to be general and should be refined, as more information becomes available. Recently, expert opinions have been supplemented with information from literature and field studies, e.g. GAP analysis (Scott et al. 1993). In GAP analysis, suitability models map the regional distribution of terrestrial vertebrate species by assigning weights to an environmental database based on expert opinion, peer-reviewed literature, and agency reports (Scott et al. 1993, Machlis et al. 1994, Edwards et al. 1996).

In the second generation of suitability models, species-habitat associations were described more objectively based on analysis of field data (Lancia et al. 1982, Brennan et al. 1986). In the mid-1980s, inductive statistical analyses, such as linear regression (Maurer 1986), logistic regression (Capen et al. 1986), and pattern recognition (Grubb 1988), gained popularity for minimizing biases in developing models (*see* Verner et al. (1986) for additional examples). These approaches involve analyzing field data for habitat use patterns and selecting and ranking from a set of field measurements attributes explaining variation in species occurrence (James and McCullough 1990). Sorting through these measurements required computers and statistical packages. As these tools became user-friendlier, multivariate statistical analyses eventually replaced the first generation of expert-based models (Brennan 1991).

Recently, mapping habitat suitability has been enhanced by the availability of remotely sensed data and Geographic Information Systems (GIS), leading to a third generation of models for mapping habitat suitability over large geographic areas. Spatially-referenced models are developed by laying a grid over an area and computing habitat suitability based on the association of species occurrence with cell attributes (Pereira and Itami 1991, Osborne and Tigar 1992, Augustin et al. 1996). For example, Austin et al. (1996) used land cover types classified from satellite imagery to model in

GIS the spatial distribution of nest sites for a buzzard (*Buteo buteo*) across portions of Scotland.

Within all these generations of habitat suitability models, there is no doubt that intensive and long-term studies provide the most reliable information for mapping habitat suitability (Wiens et al. 1987, Fielding and Haworth 1995). However for most conservation purposes, the cost of conducting these field studies is prohibitive (Flather et al. 1992). Furthermore, since conservation often requires timely decisions, the time required for collecting field data with sufficient power may be too long. If insufficient data are collected and statistical assumptions are violated (e.g., independence, randomization), the reliability of resulting statistical models is questionable as spurious species-habitat associations are generated (James and McCullough 1990).

Generally, the costs of building a statistical model are justified on the basis that improved accuracy and greater scientific rigor in meeting its purpose outweigh the costs (Mack et al. 1997). This requires cost-effective and accurate means of evaluating habitat suitability (Block et al. 1994). Yet, very little information exists to evaluate the relative accuracy of alternative models, including expert-opinion based models. As such, model users are asking, "How much are we gaining in prediction accuracy from using more detailed and expensive statistical models versus using simple and less costly expert-opinion models?" (Salwasser pers. commun. 1995). What is the tradeoff between the cost of establishing more detailed and expensive models and the benefit of marginally better information for conservation decisions?

To address these questions, I modeled habitat suitability for elk (*Cervus elaphus nelsoni*), a common and highly valued species. In Montana, evaluations of habitat suitability for elk often focus on providing adequate winter habitat, particularly in regions where development pressures compete with elk for most productive habitats. Mitigating these effects requires an understanding of how elk use an area. Typically, this involves differentiating between used and unused habitats, comparing use of a habitat relative to its availability, and identifying use of habitats over time. Establishing this understanding by collecting field data for the many winter ranges, one by one, is not feasible. Instead, models of habitat suitability are an essential tool.

Determining which models will provide the greatest accuracy relative to the cost and time for development and application is difficult. There needs to be some form of comparison to inform users of the applicability of different models for mapping habitat suitability. I provided this information by comparing the accuracy of models using a set of environmental descriptors for mapping suitability.

OBJECTIVE

My objective was to field-test the accuracy of four different modeling technologies to predict habitat suitability for wintering elk. Models included (1) expert opinion (EXPERT), (2) habitat suitability index (HSI), (3) pattern recognition (PATREC), and (4) logistic regression (LOGISTIC). Models were tested by comparing observed elk use in 1995-97 with simulated habitat suitability on the Theodore Roosevelt Memorial Ranch (TRMR), a winter range located on Montana's Rocky Mountain Front (Figure 1).

The winter range was mapped as a grid of cells. For each cell, suitability was predicted based on cell attributes (e.g., vegetation, topography, human use, spatial arrangement) and compared to actual use by elk. Use of a particular cell was defined by the presence of elk. I tested the following hypotheses:

Mean Suitability Score: For each model, I tested the null hypothesis that there was no difference in the mean suitability score between used and unused cells. The alternative hypothesis was that there was a difference in the mean suitability score between used and unused cells.

Use versus Availability: If use depends on habitat suitability, use of suitability classes should differ from their availability. For each model, I tested the null hypothesis that use of suitability classes was not different from their availability on the winter range in 1995. The alternative hypothesis was that use differed from availability.

Frequency of Use: Similarly, if habitat suitability influences use, habitats with higher suitability should be used more often than those of lower suitability. For each model, I tested the null hypothesis that there was no difference in the mean suitability score for cells used in one, two, and three years in 1995-97. The alternative hypothesis was that there was a difference in the mean suitability score among years.

Yet, comparing mean suitability scores between used and unused cells as described above does not reveal how well a model can classify used and unused cells. A more useful descriptor is the classification accuracy, which reveals a model's ability to correctly classify reference data (Lillesand and Kiefer 1994). If accuracy varies among modeling technologies then the rate of correctly predicting used and unused habitats should differ. To address accuracy differences among modeling technologies, I compared the rate of correctly classifying used and unused cells among models in 1995-97.

STUDY AREA

I compared predicted habitat suitability to observed habitat use by elk on the Theodore Roosevelt Memorial Ranch (TRMR) which is located in the center of the geographic distribution of the wintering Teton River elk herd along Montana's Rocky Mountain Front (Olson 1981, Olson et al. 1994) (Figure 1). Elk are present at TRMR year-round, though most elk move to summer range at higher elevations in May and return by early December after the hunting season and/or snowfall at higher altitudes (Olson et al. 1994). Up to 400 elk use TRMR from December to May (Olson pers. commun. 1998).

On the Front, elk winter in low-elevation habitats (<1,500 m) comprised of bunchgrass prairie interspersed with patches (<10 ha) of coniferous and aspen (*Populus tremuloides*) forests (Picton 1960, Knight 1970, Olson 1981, Olson et al. 1994). TRMR winter range typifies this habitat. Elk encounter abundant forage, comprised mainly of palatable, digestible, and nutritious fescue grasses (*Festuca* spp.) (Mueggler and Steward 1980, Offerdahl 1989, Jourdonnais and Bedunah 1991). Bottomlands are comprised of bunchgrass prairie, irrigated hay meadows, and alfalfa fields which grade into limber pine (*Pinus flexilis*) forest on western exposures, ridges, and plateaus (Mueggler and Stewart 1980, Offerdahl 1989, Ayers 1996). Cottonwood (*Populus* spp.) and willow (*Salix* spp.) communities flank small waterways. Forested cover on TRMR is sparse, totaling 437 ha, comprised of limber pine (36%), cottonwood/willow (40%), and aspen (24%) communities. Cover patches average 6.8 ha in size (Offerdahl 1989). The range also provides wintering habitat for mule deer (*Odocoileous hemionus*), white-tailed deer (*O. virginianus*), wolf (*Canis lupus*), mountain lion (*Felis concolor*), and golden eagle (*Aquila hrysaetos*), among others.

Climate is characterized by long, cold winters and short, warm summers. Temperatures vary considerably, ranging from -30° to 37° C annually (Aune and Kasworm 1989, R. Peebles, pers. commun. 1995). Annual precipitation ranges from 30-40 cm, with the greatest amount of precipitation occurring between April and July (Moeckel 1997). Warm winter winds, Chinooks, often raise the temperature dramatically in a matter of a few hours, melting snow and leaving ground free of snow through most of winter.

The 1680 ha range is privately owned by the Boone and Crockett Club and has been managed for dual objectives of wildlife habitat and cattle grazing. TRMR is designated as a "conservation area" with restricted use during winter (e.g., human access, cattle grazing). Cattle grazing occurs from March to October, with greatest use during early spring and early autumn. Annual grazing intensity includes that of 120-150 cow-calf pairs (Peebles pers. commun. 1997). Cattle are used as a management tool to promote productive and healthy fescue grasses that produce quality forage for wintering elk (Baumeister et al. 1996, Peebles pers. commun. 1997). Irrigated meadows and alfalfa fields produce feed for cattle during winter in a small, easily accessible pasture. The remaining ranch is closed off to human use during winter, except for a graveled county road bordering the eastern portion of the ranch.

Prior to this study, a GIS database was established with information on (1) biophysical attributes (slope, aspect, land cover type), (2) human land use (roads, buildings, administrative boundaries), and (3) spatial measures (size, shape, proximity of cover type patches) (Boone and Crockett 1994). Interpreted aerial photography (1:24,000) was used to map cover types. Classification keys for photo interpretations were developed at TRMR (Offerdahl 1989). Using an algorithm in GIS, data on slope and aspect were derived from a 7.5-minute Digital Elevation Model (DEM) (U.S. Geological Survey). The database was mapped at a resolution of 30-m pixels.

METHODS

Pellet-group Count

I used pellet-group counts to index habitat use. Such counts are inexpensive, easily interpreted, and widely applied for evaluating habitat use by ungulates (Perry and Overly 1977, Leopold et al. 1984, Loft and Kie 1988). Lyon (1983), for example, used pellet-group counts to quantify distribution of elk relative to roads in western Montana. Based on these data, he developed a model describing habitat suitability as influenced by road density, which has been incorporated into a series of elk HSI models (Wisdom et al. 1986, Thomas et al. 1988, Burcham and Jellison 1993).

I counted pellet-groups along rectangular, 0.01 ha belt transects (50 m long and 2 m wide) (Neff 1968, Freddy and Bowden 1983). Pellets were counted as one group if ≥ 5 pellets of the same general size, shape, and color were present within 0.5 m^2 (Bowden et al. 1969). Elk pellets were distinguished from deer pellets based on size and shape differences. "Winter" pellets were separated from "non-winter" pellets by color, vegetative overgrowth, and signs of deterioration (Loft and Kie 1988).

Sampling took place over a variety of bunchgrass communities and adjacent habitats over a 30-day period. Transects were read in spring after elk left the range (after May 15th) and prior to "green-up" (approximately June 15th). Using the GIS, diagonals were superimposed over TRMR at 200 m intervals except for patches >5 ha of riparian vegetation which were seldom used by elk in winter (Picton 1960, Knight 1970, Olson et al. 1994). I avoided backtracking and, thereby, increased sampling efficiency by systematically placing transects along parallel diagonals oriented from southwest (225°) to northeast (45°) (Figure 2). Starting coordinates for each transect were located using a Global Positioning System and generated using GIS (Boone and Crockett 1994). I personally read all transects, thereby eliminating inter-observer bias.

Pellet-group Calibration

I did not assume that pellet-group counts reflected amounts of time spent in a habitat, biological need, population densities, or that pellet-groups indicated use of a habitat for a particular function such as resting or grazing. Pellet-group counts simply determined whether or not elk were present in a habitat. Nevertheless, the primary problem with using pellet-group counts for indexing habitat use is the lack of calibration with true use (Leopold et al. 1984).

Pellet deposition rates likely vary among different habitats or are deposited while traveling between habitats (Collins and Urness 1982, Rowland et al. 1984). Using pellet-group counts under those circumstances biases habitat use estimates. I calibrated pellet-group counts using radio-telemetry data as an additional estimate of habitat use. I tested whether habitat use described by pellet-group counts differed from that of radio-telemetry locations (Loft and Kie 1988). Radio-telemetry yields estimates of point locations within an error polygon (Morrison et al. 1998). My hypothesis was that relative use of habitats as measured by these two methods was not significantly different. That is, a ranking of habitats from least to greatest use would be identical for both methods. Unfortunately, during my study there were no elk radio-collared. Therefore, I relied on previously collected data by Olson et al. (1994), understanding that the time difference may introduce error into the calibration as elk may have shifted their pattern of habitat use.

Olson et al. (1994) used elk telemetry locations (n=41) to compare use to availability for three cover types (rough fescue prairie, non-rough fescue prairie, and shrubland/forest) on TRMR winter range using a chi-square analysis (Neu et al. 1974, Byers et al. 1984). I compared the distribution of pellet-group counts ($\geq$ 1 pellet-group/transect = use) to that of telemetry locations (1 location/habitat = use) relative to these three cover types. If I failed to reject my hypothesis of no difference in rank of cover type use, then I concluded that pellet-group counts can yield similar results to use measured by telemetry locations for TRMR winter range.

Spatial Resolution

Comparison of predicted habitat suitability to observed habitat use required matching the grid cell size to variation in pellet-group counts (Block and Morrison 1991). To determine if the pattern of use as described by pellet-group counts was scale-dependent (Hutto 1985, Porter and Church 1987, Morrison et al. 1998), I tested different spatial resolution to identify where variation was greatest. I reviewed literature on elk-habitat relationships and factors influencing habitat selection (e.g., morphology, physiology, and behavior) (Picton 1960, Knight 1970, Thomas 1979, Thomas and Toweill 1982, Olson et al. 1994) and found that elk select habitat at several spatial scales ranging from large-scale (geographic range) to small scale (sites within a home range). This selection is akin to the hierarchical model of progressively finer and inclusive scales of selection, down to the level of individual feeding and bedding sites (Johnson 1980). This suggests that there is a spatial resolution at which variation in pellet-group counts would be greatest.

However, selecting this level of resolution *a priori* would be subjective since the scales at which habitat selection occurs likely form a continuum or a hierarchy (Wiens et al. 1987). No obvious structure or composition within bunchgrass communities appeared that might automatically and conclusively be considered important or correlated with important factors on selection patterns. Instead, I tested the null hypothesis that there is no variation in the number of pellet-groups for a series of inclusive resolutions using a nested analysis of variance (nested ANOVA). A nested ANOVA is a suitable statistical technique to test for significant differences in the variation of pellet-group numbers between two nested spatial resolutions (Sokal and Rohlf 1995). For each resolution, nested ANOVA computed the amount of explained variation (Underwood 1997).

Using 1995 data, I aggregated individual transect readings, which were placed in GIS as a diagonal through a 35 m cell, into progressively larger cells in GIS. While there may be a finer resolution operative in habitat use by elk than that of transect-level counts, I considered this to be the finest resolution at which to model habitat use given the resolution of the existing GIS habitat database (30 m pixel). I used the mid-way point to spatially reference each transect in GIS. The GIS pixel within which the mid-way point was located provided the habitat attributes for a particular transect. A shorter transect (<50 m) would have resulted in identical habitat information. Also, moving to a shorter transect would have increased the chance of adjacent transects sharing the same GIS pixels (Pereira and Itami 1991).

For the nested ANOVA, I selected three transects at TRMR as starting locations within three bunchgrass communities $\geq$2 km apart. At each starting transect, I aggregated transects into larger blocks of 150 m x 150 m, 450 m x 450 m, and 1350 m x 1350 m, resulting in four adjacent transects/150 m square, nine, 150 m squares/450 m square, and nine, 450 m squares/1350 m square (Figure 2). Within each of the three resulting 1350 m squares, I randomly chose four of the nine (44%), 450 m blocks for the nested ANOVA.

In each of these, I randomly chose three of the five sampled (60%), 150 m squares, each of which, in turn, was described by four replicate transects. Thus, each selected transect was described in terms of its nested location within progressively coarser resolutions.

I present the results of the nested ANOVA here, because the resolution chosen is essential for presenting the remaining methods (Table 1). Most (53.5%) of the variation in pellet-group counts was explained by the 150 m squares when compared to 20.8 % for transects, 7.9 % for 450 m squares, and 17.7 % for 1350 m squares. Based on these results, I chose the 150 m square as the resolution for describing habitat use by elk because it accounted for the largest amount of variation in pellet-group counts. These 150 m squares are hereafter referred to as "cells."

In GIS, I mapped TRMR winter range at the 150 m resolution. Resulting cells were described for elk use, habitat characteristics, and model predictions. Use of a cell by elk was quantified by summing pellet-group counts of four adjacent transects. Cells were described for habitat characteristics using the GIS database. Individual models were developed by analyzing the association of habitat characteristics and elk use at the cell-level resolution.

Univariate Analysis

I tested individual habitat variables for their ability to differentiate between used cells and unused cells. If elk used a cell based on a habitat characteristic (e.g., distance to cover), I expected to find differences in the mean values of habitat characteristics between used cells and unused cells (Pereira and Itami 1991). I selected variables similar to those used in elk HSI models of regions resembling the environmental conditions of the Front. These models were winter range HSI models for the Blue Mountains of Oregon (Thomas et al. 1988) and the Bighorn Mountains of Wyoming (Burcham and

Jellison 1993); none were available for Montana. From these models, I selected six variables: (1) distance to nearest road traveled by vehicles during winter, (2) distance from forage to nearest cover-forage edge, (3) distance from cover to nearest cover-forage edge, (4) cattle grazing intensity, (5) winter forage availability, and (6) slope.

I tested each variable for its ability to differentiate between used and unused cells. In GIS, I identified county and ranch roads with some vehicular traffic during winter. I computed the mean distance from each cell to the nearest road (ROADDIST). I classified a 150 cell as "cover" if >50% of the area (>12, 30 m pixels) in GIS was comprised of limber pine, aspen, and/or cottonwood/willow. Similarly, a cell was classified as "forage" if $\geq$50% ($\geq$12, 30 m pixels) was comprised of prairie grasslands and/or hayfields. Distance to cover (COVERDIST) and distance to forage (FORAGEDIST) were calculated as mean averages of 25 pixel values for each 150 m cell. For each forage cell, I also computed the total area comprised of rough fescue (*Festuca scabrella*) and Idaho fescue (*F. idahoensis*) (BUNCH). I quantified the intensity of cattle use by counting cow droppings on transects surveyed for pellet-groups (CATTLE). I averaged slope values for all pixels in each 150 m cell (SLOPE).

I randomly selected 50 used ($\geq$1 pellet-group) and 50 unused (0 pellet-groups) cells for the univariate analysis. Where appropriate, I compared group means using the Student's *t*-test and mean ranking using the Mann-Whitney *U*-test. I selected those variables for inclusion into a model that most differentiated between used and unused cells using the significance level p as a criterion. I set α=0.1 to reduce the likelihood of a Type II error by failing to include a potentially important predictor in the multivariate suitability model (Capen et al. 1986, James and McCullough 1990, Green et al. 1994).

This may have resulted in some Type I errors because I did not adjust α for multiple tests (Thomas and Taylor 1990, Mills pers. commun. 1999).

I attempted to build parsimonious models by including only three significant variables. As more variables are included in a model, the probability of a correlation between variables increases and the predictive power of individual variables decreases (Bunnell 1989, Van Horne and Wiens 1991). I reduced the set of variables using the Spearman rank correlation coefficient for bivariate combinations by removing variables most correlated with other variables. From a pair of correlated variables, I selected the one with greater between-group significance p (Block et al. 1998). The set of significant and only weakly correlated variables was used for building the set of multivariate suitability models.

Sensitivity Analysis

The variables in the models were selected based on a univariate analysis of mean rankings between used cells (≥ 1 pellet-groups/cell) and unused cells (0 pellet-groups/cell). As such, I assigned equal weight to cells with one or several pellet-groups. Conceivably, different use versus non-use cut-offs of pellet-group counts could have yielded a different set of variables. To test for this, I evaluated the sensitivity of univariate results relative to different cut-offs for coding pellet-group counts. I classified a cell as a used cell in increments of one pellet-group for the range of 0-8 pellet-groups. A classification of used cells as >8 pellet-groups was not considered because it resulted in too few samples classified as used (<20).

Spatial Autocorrelation

To test for sample independence, I examined whether the random sample of 50 used and 50 unused cells was spatially autocorrelated. Collectively, this sample constituted 16% of the cells comprising TRMR winter range (*n*=636). Surveying this many cells in a relatively small area, even if randomly selected, can result in a spatially autocorrelated sample since cells that are closer together are more likely to be similar in their measurement values than those farther apart (Swihart and Slade 1985, Legendre 1993). For elk, these "neighborhood effects" (Chou and Soret 1996) may result from social interactions as well as from similar responses to environmental conditions.

I tested for spatial autocorrelation by determining the degree of correlation between pellet-group counts of cells that were fixed distances apart from one another (Real and McElhany 1996). I randomly drew a sample of 25 cells from the sample of used and unused cells and paired each associated pellet-group count with one count that was randomly drawn from the four cell counts immediately adjoining in a checkerboard pattern (50% sampling intensity). I then repeated this process for cells that were separated by one cell (25% sampling intensity) and two cells (12.5% sampling intensity). A sample size of 20-30 is recommended for a correlation analysis to ensure adequate statistical power to detect a correlation if it exists while avoiding detecting a spurious correlation resulting from a large sample size (Hair et al. 1995).

I graphically examined the degree of correlation between paired cells by plotting the number of pellet-groups at location x against the number of pellet-groups at location x + a fixed distance h (e.g., one cell apart) using an h-scatterplot (Hair et al. 1995). If perfect correlation exists, the number of pellet-groups in a pair of cells are identical and the line of the *h*-scatterplot has a slope of 1. Any deviation from that pattern is defined by a scatter of points around the diagonal suggesting less than a perfect correlation.

Multivariate Models

Using an identical set of explanatory variables, I built four models for evaluating habitat suitability: EXPERT, HSI, PATREC, and LOGISTIC. For consistency with previous approaches of modeling habitat suitability (e.g., Wisdom et al. 1986, Stauffer and Best 1986, and Thomas et al. 1988), I coded each continuous variable into a categorical variable with 3-4 classes with ≥ 5 used cells for each class (Hair et al. 1995).

<u>EXPERT:</u> I developed a rule-based expert system to imitate an expert's reasoning process (McNay et al. 1987). EXPERT was built to predict the probability that a cell is used by elk given a set of cell characteristics. I developed the expert model based on five expert evaluations. Each expert had many years of experience studying elk-habitat relationships in Montana and/or other states in the Pacific Northwest. Experts were familiar with the environmental conditions on the Front, though none had intimate knowledge of elk-habitat relationships at TRMR. I presented each expert with the same written background information and instructions on the set of habitat characteristics to use for evaluating suitability (*see* Appendix A). No additional information was provided.

I asked experts to rate the suitability of a set of "habitats" for a Front winter range (TRMR winter range was not mentioned). A habitat was defined spatially as a 200 m long and 2 m wide transect. Each habitat constituted a unique combination of variable classes. The number of habitats to evaluate equaled the number of possible combinations for grouping variable classes. I asked experts to rate each habitat for the presence of ≥ 1 pellet-groups (i.e., use=1) following an average winter (December-

May). For each habitat, I averaged the five "expert" values of 0s and 1s to yield a probability of use rating. Using GIS, an EXPERT suitability score was then assigned to each respective cell according to its specific attribute values.

HSI: I built an HSI model to evaluate the suitability of habitats based on a set of habitat characteristics for each cell. The modeling approach was identical to HSIs for elk habitat built elsewhere (Wisdom et al. 1986, Thomas et al. 1988, Burcham and Jellison 1993) and was based on comparing use of a habitat to its availability.

For each variable class (e.g., ROADDIST 1000-1500 m), I first computed a preference index by dividing the proportion of used cells by the proportion of available cells (Morrison et al. 1998). Use was quantified based on cells surveyed in 1995 (n=274). Availability was quantified based on cells comprising TRMR (n=636). Preference indices (Hs) of individual variable classes were then used as diagnostics for evaluating suitability. For example, the preference index for ROADDIST 1000-1500 (m) might be 2.0 (the proportion of cells used is twice that of its availability) and, thus, a cell with a value of 1200 m for ROADDIST would be assigned a value of 2.0. This procedure was repeated for all variables. Individual scores for preference indices were aggregated into an overall score according to the geometric mean:

$$Hs_{overall} = (Hs_1 \text{ x } Hs_2 \text{ x } Hs_3)^{1/3}$$

where Hs_1 = suitability score for variable 1, Hs_2 = suitability score for variable 2, and Hs_3 = suitability score for variable 3. A resulting HSI suitability score was assigned to each respective cell.

PATREC: Pattern Recognition (PATREC) computes, in a simple mathematical form, the probability that a cell is used by elk given the probabilities that certain cell characteristics are present (Williams et al. 1977, Haithcoat 1987). Similar to HSI, I developed PATREC by first computing a preference index for each variable class. For each variable, I identified those classes with indices ≥ 1. These classes were considered "used in proportion equal or greater to availability." For example, ROADIST 1000-1500 m might have a preference index of 2.0. A sample of used cells is then evaluated for the proportion of cells that fall into the class ROADIST 1000-1500 m. Suppose 90% of the used cells have ROADIST 1000-1500 m. This proportion of 0.9 can now be used as a diagnostic for evaluating the probability that a cell is used given information on ROADDIST 1000-1500 m. Unused cells are evaluated in the same way by computing the proportion of unused cells with ROADIST 1000-1500 m.

Based on this approach, I developed each variable with its corresponding diagnostic for used and unused cells. When a particular attribute is present, the diagnostic value x is recorded. If the attribute is absent, $1-x$ is recorded. This process is repeated for all cell attributes resulting in three conditional probabilities for calculating the likelihood that a cell is used. For example, a cell with ROADDIST 1200 m would fall into the class of ROADIST 1000-1500 m and similarly might also fall into another "preference" class for a second variable, but not so for a third variable. In this particular example, the probability P that elk use a cell is then computed as $P = (P_{\text{ROADDIST}}) \times (P_{\text{V2}}) \times (1 - P_{\text{V3}})$, where $P_{\text{ROADDIST}} = 0.9$, P_{V2}= the proportion of used cells that fall into variable class 2, $P_{\text{V3}} = 1 -$ (the proportion of used cells that fall into variable class 3). The process is also repeated for the probability that a cell is unused. The overall probability that a cell is used by elk is computed according to Bayes' Theorem by taking into account the probability that a cell is unused (after Grubb 1988): $P(use) = \dfrac{0.5(P_{used})}{0.5(P_{used}) + 0.5(P_{unused})}$

For more detail on this methodology, see Williams et al. (1977), Grubb (1988), and Roseberry and Hao (1996). The resulting PATREC suitability score was assigned to each respective cell.

<u>LOGISTIC:</u> I built a logistic regression model to identify the contribution of variables to predict the probability that elk are present in a cell. Logistic is similar to linear regression except logistic regression predicts a binary dependent variable (used, unused). A model was built by entering (forcing) into the equation the set of variables selected from the univariate analysis. Forcing variables into the model was preferred over that of a stepwise process to ensure consistency in use of variables when comparing accuracy among models (Fielding and Haworth 1995).

Given inventory data for a cell, the probability P that ≥ 1 pellet-groups are present in a cell (P) was computed as: $P = \frac{1}{1 + e^{-\beta_0 - (\beta_1 * x_1) - (\beta_2 * x_2) - (\beta_3 * x_3)}}$

where x_n are the data values from a cell, β_o is the y-intercept, and β_n are the regression coefficients for each variable. Equation parameters were estimated using the maximum likelihood method (Hosmer and Lemeshow 1989). LOGISTIC suitability scores were assigned to each respective cell.

Model Validation

I tested each model to examine how well each modeling approach describes the actual pattern of cell use by elk on TRMR in 1995-1997. I tested the following null hypotheses:

<u>Mean Prediction Score:</u> For each model, I tested the null hypothesis that there was no difference in the mean suitability score between used and unused cells by using the 50 used and 50 unused cells used for model building that were randomly selected from

the cells surveyed in 1995 (n=274). Where appropriate, I compared means using the Student's t-test or mean ranking using the Mann-Whitney U-test.

Use versus Availability: For each model, I tested the null hypothesis that use of cells with different suitability classes was not different from their availability on TRMR winter range in 1995. For each model, I coded suitability scores into five equally spaced categories at 0.2 increments (e.g., 0-0.2). Using a chi-square test, I compared the observed number of used cells to that of the expected number of used cells based on availability at TRMR.

Frequency of Use: For each model, I tested the null hypothesis that there was no difference in the mean suitability for cells used in one, two, and three years. I randomly drew cells surveyed in 1995-97 to result in three samples (n=30 each) for cells used in only one year, used in two years, and used in all three years. For each model, group means of suitability scores were tested for significant differences using a one-way ANOVA. If the null hypothesis of equal means was rejected then *a posteriori* multiple comparisons were performed to test which means were different using the Student-Newman-Keuls procedure (Underwood 1997).

Classification Accuracy: The accuracy of each modeling approach was evaluated based on how well it predicted the actual pattern of cell use on TRMR in 1995-97. Perfect accuracy would occur if all of the used and unused cells were correctly predicted. I compared classification accuracy for used and unused cells among models. I conducted the test by defining used cells in one of two ways using 1995-97 survey data: (1) used only once in three years (a possible definition of marginally suitable habitat), and (2) used in all three years (a possible definition of suitable habitat). For each test design, I randomly chose 50 used and 50 unused cells.

Calculating accuracy involved constructing a cross-tabulation of predicted with observed cell use. This required converting the prediction score (scaled from 0 to 1) into a binary variable of predicted used (0) and unused (1) through specification of a cut-off value. Below this value, all cells are considered unused, while all above are considered used. Depending on the cut-off value selected, the classification accuracy can vary widely (Pereira and Itami 1991). I accounted for this sensitivity by presenting classification accuracy relative to all cut-offs at 0.1 increments.

I also calculated a chance-corrected measure of accuracy known as *kappa* (Cohen 1960, Lillesand and Kiefer 1994). By chance alone, I expect some of the cells to be correctly classified. The *kappa* statistic is a measure of how well a model classifies reference data independent of chance alone (Congalton et al. 1983, Rosenfield and Fritzpatrick-Lins 1986). Prior probabilities for group membership were equal to the proportion of used and unused cells (i.e., 0.5).

RESULTS

Pellet-group Calibration

The frequency distribution of elk use among cover types (rough fescue prairie, non-rough fescue prairie, shrubland/forest) as indexed by pellet-group counts (n=138) was similar to use indexed by radio-telemetry locations (n=41) (χ^2=1.82, df=2, p=0.34) (Table 2). Both methods ranked use of cover types from least to greatest identically. Elk used rough fescue prairie more often than available (pellet-group count=1.2 [rate of % used to % available], radio telemetry=1.26) while using shrubland/forest less than available (pellet-group count=0.54, radio telemetry=0.42). Non-rough fescue prairie was used in proportion to availability (pellet-group count=1.05, radio telemetry=0.95).

Univariate Analysis

Elk used cells that were located far from roads and from cover, on gentle slopes, with close proximity to forage. Mean rankings of ROADIST, COVERDIST, FORAGEDIST, and SLOPE were significantly different between used cells ($\geq$1 pellet-group) and unused cells (0 pellet-groups) ($p<0.1$) (Table 3). I failed to detect a significant difference in the mean rankings for BUNCH ($p=0.80$) and CATTLE ($p=0.85$); subsequently, variables were excluded from model building. Based on the Spearman rank correlation, I further eliminated FORAGEDIST, because it was the most highly correlated variable, particularly with COVERDIST ($r=-0.81, p<0.01$) (Table 4).

Sensitivity Analysis

I examined the sensitivity of the univariate results relative to different cut-offs for coding pellet-group counts, by classifying a cell as a "used" cell in increments of one pellet-group for the range of 0-8 pellet-groups. For ROADDIST, COVERDIST, and SLOPE, the pattern in cell use, as measured by group means and significance of difference, was independent of the cut-offs for classifying a cell as a used cell (Table 5). At the most conservative classification of >8 pellet-groups for classifying a cell as used, cells were located further from roads and from cover, and on gentler slopes than unused cells ($p<0.10$).

Spatial Autocorrelation

I tested the 1995 sample of 50 used and 50 unused cells for spatial autocorrelation (Figure 3). For each of the three distances examined (i.e., immediately adjoining in a checkerboard pattern, one cell apart, two cells apart), paired pellet-group counts ($n=25$ each) formed a scatter around the plot's diagonal with $R^2<0.2$ for all comparisons. These results suggest that the sampling intensity of 16% (100 of the 636 cells comprising

TRMR winter range) resulted in little spatial autocorrelation among pellet-group counts. Based on my findings, I estimate spatial autocorrelation to account for 10% and 19% of the variation in adjacent pellet-group counts.

Model Validation

Mean Prediction Score: For all models, I rejected the null hypothesis that that there was no difference in the mean suitability score of used cells (n=50) and unused cells (n=50) surveyed in 1995 (p>0.05), except for EXPERT, which was significant at p=0.08 (Table 6). For all models, the mean suitability score was higher for used cells than for unused cells. The mean suitability score ranged from 0.37 to 0.47 for unused cells and 0.55 to 0.66 for used cells. The difference in prediction score between unused and used cells was largest for LOGISTIC (0.29) and smallest for EXPERT (0.10).

Use versus Availability: For all models tested, I rejected the null hypothesis of no difference between the distribution of observed use and expected use among suitability classes (p<0.05) (Figure 4). For all models, observed use of suitability classes 0-0.2, 0.2-0.4, and 0.4-0.6 was less than expected use, except for HSI, which did not predict for class 0.0-0.2. For the suitability classes of 0.6-0.8 and 0.8-1.0, observed use was greater than expected use, except for HSI, which did not predict for class 0.8-1.0.

Frequency of Use: For all models tested, I rejected the null hypothesis that there was no difference in the mean suitability score for cells used in one, two, and three years in 1995-97 (p<0.05) except for EXPERT (p=0.52) (Table 7). For all models, the mean prediction score was lower for cells used in one year than those used in two and three years (Figure 5). The difference in the mean suitability score between cells used in one year and those used in two years ranged from 0.07 for EXPERT to 0.23 for LOGISTIC.

The difference between cells used in two years and those used in three years was less pronounced.

Classification Accuracy: I compared the mean classification of used and unused cells. For comparisons among models, I present the mean accuracy for the cut-off of the suitability score that maximized the rate of correctly classifying used and unused cells. I defined used cells in one of two ways: (1) used once in three years, and (2) used three times in three years.

The mean classification accuracy in one year was similar among models (Figure 6). Mean accuracy among models ranged from a low of 51% for EXPERT (cut-offs 0.2 and 0.8), to 55% for HSI (cut-off 0.6), to 58% for PATREC (cut-off 0.6) and a high of 61% for LOGISTIC (cut-off 0.8). The corresponding rate of classification improvement over chance ranged from 2% for EXPERT to 22% for LOGISTIC. HSI and PATREC had 10% and 16% improvement over chance, respectively.

Mean accuracy and improvement over chance were markedly greater when cell use was defined as used in all three years (Figure 7). Mean accuracy was lowest for EXPERT at 58% (cut-off 0.8) and improved to 71% for LOGISTIC (cut-off 0.5), to 73% for PATREC (cut-off 0.6), and to 75% for HSI (cut-off 0.5). The corresponding rate of classification improvement over chance ranged from 16% for EXPERT to 50% for HSI. PATREC and LOGISTIC had 46% and 42% improvement over chance, respectively.

DISCUSSION

Improving the objectivity of modeling habitat suitability through more formal and verifiable approaches is often time-consuming, expensive, and difficult (Duncan et al. 1995, Morrison et al. 1998). To justify these approaches, development and application costs need to be offset with greater accuracy (Salwasser 1982, Conroy and Noon 1996, Salwasser pers. commun. 1997). By evaluating the accuracy of different modeling approaches for habitat suitability, this study provides information to determine these tradeoffs. I chose modeling approaches ranging from simple, subjective, and inexpensive expert opinion to more complex, objective, and expensive mathematical and statistical models.

For the comparison of marginally suitable habitats (one year of use) with unsuitable habitats (three years of non-use), models performed slightly better than chance alone. However, for the comparison of more suitable habitats (three years of use) and unsuitable habitats, the three field data models revealed greater accuracy than the expert model. These results have two important implications for habitat suitability modeling.

First, none of the models were able to discern marginally suitable habitat from unsuitable habitat. This has important ramifications for conservation purposes, particularly for a species that is a habitat generalist since it may use a suite of “marginally” suitable habitats rather than a few highly suitable habitats. The inability of models to detect these habitats may result in a lack of their conservation.

Second, of the three data-dependent modeling approaches (with varying degrees of complexity and subjectivity), performance was similar when given the same set of variables and data. This suggests that the actual modeling structure for aggregating variables may be less important than the selection of variables. In an era of emphasis placed on mathematical and/or statistical models (Morrison et al. 1998), the necessity of their complexity may, in some cases, not be justified. That is, the cost of objectivity required for the most advanced of these data-dependent models, such as logistic regression, may not be compensated by an increase in accuracy. Limited resources might be better directed at ensuring inclusion of biologically important habitat attributes into models. For a species as well studied as elk, this may be relatively simple.

In North America, the Rocky Mountain elk occupy the Rocky Mountains and adjacent mountain ranges from British Columbia and Alberta to New Mexico and Arizona (Boyce and Hayden-Wing 1982). Throughout this range, elk occupy a variety of environments differing in geology, climate, landform, and vegetation. Besides these landscape-level influences, the occurrence of elk in a particular habitat is the result of a multitude of interacting factors and processes including habitat, demography, predation, competition (including that from humans), disease, history, and habituation among others. This suggests that different factors and processes influence habitat use in different environments.

Yet, surprisingly, the three simple and easily measured variables I used in modeling habitat suitability on a winter range for a single elk population in Montana were the same variables used in HSIs for a western Oregon range and an eastern Wyoming range. Given the wide-ranging distribution and the few variables selected, it is not surprising to find that the models did not perfectly predict habitat suitability, but rather that the models performed as well as they did. The selection of these biologically important variables dictated the accuracy of the model.

Since expert evaluations are based on biological knowledge of habitat requirements, they should more closely model how an animal perceives its environment than a statistical model. If so, why was accuracy of the expert model lower than for the field data models, even when evaluating more suitable habitat?

Despite the fact that all models relied on the same variables, associations between those variables and elk use were not always consistent. For example, in the expert evaluations, four of the five experts stated that areas close to cover were of higher suitability than those areas further from cover. I failed to detect this relationship; based on pellet-group counts, elk used areas close to cover less often than those areas further from cover. This lower use might be explained by sparser grass cover on the rocky soils and dry slopes adjacent to cover (Ayers Baumeister unpubl. data 1997) or the possibility that cover may not be as important because of the frequent warm winds that keep foraging areas and slopes snow-free through winter. In fact, because of these winds, tree cover retains snow longer and at deeper depths than in grasslands (Ayers Baumeister and Dean 1997). As such, elk probably conserve more energy by traveling short distances between bedding and feeding areas within grasslands than in using distant cover (Parker and Gillingham 1990).

While these are biological plausible explanations, it is interesting that experts (i.e., elk biologists) suggested different elk-cover relationships. These experts may have had a different definition of cover based on personal experience, and assumed that TRMR cover, as it was described to them, fit their definition. Most experts gained their knowledge on elk-habitat relationships in regions where cover is a more important component of winter range suitability, including in western Montana (Lyon pers. commun. 1999) and in the Blue Mountains of Oregon (Thomas pers, commun. 1999).

For TRMR, I classified a habitat as "cover" if the majority was comprised of aspen, cottonwood, limber pine, and/or Douglas-fir. Limber pine is the most widespread tree species classified as cover, yet, these stands rarely exceed 50% canopy closure (Ayers Baumeister *unpubl. data* 1997). In contrast, HSIs for the Blue Mountains

(Thomas et al. 1988) and Bighorn Mountains (Burcham and Jellison 1993) assigned "cover" to those stands with >50% canopy closure. Based on their criteria, most limber pine would be classified as forage areas, with the possible exception of denser stands with a Douglas-fir component, which occur on <5 % of the winter range.

As such, TRMR may have very little "true" cover for elk. If so, the edge relationships proposed by experts (greater use of areas close to cover-forage edge) may exist only where the fescue grassland meets the Douglas-fir forests to the west and agricultural fields to the east. A site visit by experts or a presentation of an aerial photo might have helped better visualize cover availability (Holthausen et al. 1990) and may have resulted in different suitability ratings.

Although experts concurred with the data models regarding road-elk use relationships, slope associations varied widely. Two of the five experts did not consider slope important in describing habitat use and one expert suggested that elk use steeper over gentler slopes. These variations in habitat-elk use associations found in the EXPERT model are examples of the effects of subjectivity on model development based on experience, knowledge, and individual bias. In data-dependent models, associations are fitted based on data, and are, hence, considered less subjective. In terms of accuracy, objectivity ruled over subjectivity when comparing these modeling approaches. However, objectivity does not guarantee accuracy.

Statistical models require sufficient data to predict suitability and are ineffective without the appropriate data. Collecting these data is usually expensive and time-consuming. The advantage of mapping detailed habitat suitability more objectively needs to be carefully evaluated as it presents a practical problem depending on the maintenance required for habitat variables. Variables that change over time, such as road density, range condition, and cattle grazing, need to be updated regularly. Land cover types and more static variables, such as slope, aspect, and rivers have the advantage of having to be mapped only once, but are, unfortunately, of limited use in evaluating consequences of land use on habitat suitability as they are less sensitive to management activities. Thus, from an operational perspective, a statistical model may be of limited utility in evaluating elk habitat, even if the majority of predictions are empirically correct.

Furthermore, the methodology associated with a statistical model is not always readily available for intended users. For example, applying the logistic regression model requires a GIS database with model attributes described for a given winter range and, at least, a basic understanding of statistics and spatial assessments. Yet, many of the likely users of models, including wildlife biologists, ranchers, and county planners have limited access to a GIS or the technical expertise to operate such a system (Thomas pers. commun. 1999). Applications of these models on the Front would fall under the same limitations (Olson pers. commun. 1996, Peebles pers. commun. 1997). An expert model, on the other hand, can be used by nonprofessionals as it is easily understood and applied (McNay et al. 1987, Holthausen et al. 1990).

Finally, the last consideration in evaluating models is understanding the purpose behind the use of the model. Model performance varies depending on the criteria used for evaluating accuracy. For example, the expert model was able to differentiate between used and unused cells (based on prediction score) and described use versus availability similar to the field-data models. For some conservation purposes, this may be adequate. Mack et al. (1997) state that for a model "to be suitable, it must be able to account for a proportion of the variance of the ecological response which is acceptable to the user." Thus, depending on the ecological question addressed and the level of accuracy and precision needed, different modeling approaches may meet a particular objective equally well or better.

Does this improve the potential utility of expert opinion when development and applications costs are taken into account? The easiest and least expensive approach is to consult experts. If expert opinions can sufficiently meet an objective with acceptable accuracy, then building an expert model is the most prudent approach. As Wang (1997) appropriately stated: "When both a complex and a simple model can sufficiently meet a study objective, the simple model should always be the preferred choice." However, if an expert models fails to meet objectives, then a mathematical model, such as an HSI, or a statistical model, such as a logistic regression, are reasonable approaches for mapping habitat suitability.

Today, many models of habitat suitability are built relying on empirical data without first evaluating the utility of expert opinion. This apparent hesitation is related to an ongoing debate over the validity of using subjective information in species-habitat modeling (Dixon and Ellison 1996). While this debate continues, decisions are being made on the fate of species habitat, many of which only within the context of best information available. The decision to use a simple model such as expert opinion over that of a more complex, costly model is one that needs to be made by the decision-maker and the public relative to the decision, the criteria for decision-making, the availability of alternative models, financial resources, technical support, and the risk of making a wrong decision.

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TABLES

Table 1. Nested ANOVA (Sokal and Rohlf 1995) for testing different resolutions of explaining variation in pellet-groups counts of 50 m transects aggregated to 150 m squares, 450 m squares, and 1350 m squares.

Source of variation	*df*	*SS*	*MS*	*F*	*p*	Expected *MS*	% variation explained
Among 1350 m cells	2	115.4	57.7	3.58	0.070	4557	17.7
Among 450 m cells	9	145.1	16.1	1.40	>0.10	1788	7.9
Among150 m cells	24	275.5	11.5	11.3	<0.001	46.9	53.5
Within transects (error)	108	110.0	1.02			1.02	20.8
Total	143	646					

Table 2. Counts of habitat use based on 1995 pellet-group counts ($\geq$1 pellet-groups/cell = used) (n=138) and telemetry locations (n=41) (Olson et al. 1994) for 150 m GIS cells at TRMR winter range.

	Use data		
Cover type	Telemetry location (%)	Pellet-group count (%)	Availability at TRMR (%)
Rough fescue prairie	29 (71)	91 (66)	56
Non-rough fescue prairie	8 (19)	29 (21)	20
Shubland/forest	4 (10)	18 (13)	24
Total	41	138	100

Table 3. Means, S.E., mean rankings and Mann-Whitney *U*-test for ROADDIST, COVERDIST, FORAGEDIST, SLOPE, CATTLE and BUNCH of used (n=50) and unused (n=50) cells at TRMR winter range, 1995.

Variable	Mean	S.E.	Mean Ranking	*U*-statistic	*p*
ROADDIST (m)					
Used	879.5	76.7	57.2	915	0.02
Unused	680.8	79.7	43.8		
COVERDIST (m)					
Used	298.5	29.0	63.0	624	<0.01
Unused	134.1	19.1	38.0		
FORAGEDIST (m)					
Used	13.2	3.4	43.5	902	<0.01
Unused	34.2	6.1	57.5		
SLOPE (%)					
Used	13.3	0.9	39.1	680	<0.01
Unused	18.7	1.1	61.9		
CATTLE (droppings/transect)					
Used	13.5	1.6	49.9	1222	0.85
Unused	13.6	1.5	51.1		
BUNCH (% cover)					
Used	53.2	5.5	49.8	1215	0.80
Unused	54.8	5.6	51.2		

Table 4. Spearman rank correlation coefficient (*r*) and *p*-values in parentheses for ROADDIST, COVERDIST, FORAGEDIST, and SLOPE.

Variable	ROADDIST	COVERDIST	FORAGEDIST	SLOPE
ROADDIST	1.00	~	~	~
COVERDIST	-0.13 (0.21)	1.00	~	~
FORAGEDIST	0.16 (0.12)	-0.81 (<0.01)	1.00	~
SLOPE	0.09 (0.36)	-0.43 (<0.01)	0.25 (0.01)	1.00

Table 5. Means (mean rankings) of ROADDIST, COVERDIST, and SLOPE for used and unused cells relative to different cut-offs for classifying used/unused cells. *P*-values refer to Mann-Whitney *U*-test of mean rankings for used and unused cells.

Cut-off	*n*	ROADDIST	*p*	COVERDIST	*p*	SLOPE	*p*
≥1	50	879.5 (76.4)		298.5 (29.0)		13.3 (0.9)	
<1	50	680.8 (79.7)	0.02	134.1 (19.1)	<0.01	18.7 (1.1)	<0.01
≥ 2	44	916.9 (83.3)		316.2 (31.4)		13.4 (1.0)	
< 2	56	672.7 (72.9)	0.03	137.7 (17.8)	<0.01	18.1 (1.0)	<0.01
≥ 3	43	913 (85.2)		311.9 (31.9)		13.4 (1.0)	
< 3	57	679.9 (71.9)	0.04	144.1 (18.6)	<0.01	18.0 (1.0)	<0.01
≥4	37	918.0 (93.2)		330.7 (34.5)		12.8 (1.1)	
< 4	63	699.2 (68.4)	0.06	149.0 (18.1)	<0.01	17.9 (0.9)	<0.01
≥ 5	31	924.3 (102.3)		323.9 (36.2)		13.4 (1.2)	
< 5	69	715.4 (65.8)	0.08	167.9 (20.1)	<0.01	17.2 (0.9)	0.02
≥ 6	27	953.3 (111.9)		345.2 (38.2)		13.7 (1.3)	
< 6	73	716.1 (63.3)	0.06	168.5 (19.5)	<0.01	16.8 (0.9)	0.06
≥ 7	24	1002.1 (120.5)		340.6 (42.1)		13.5 (1.5)	
< 7	76	710.1 (61.3)	0.02	177.0 (19.5)	<0.01	16.8 (0.8)	0.05
≥ 8	22	1019.3 (127.9)		324.0 (43.8)		13.5 (1.6)	
< 8	78	712.7 (60.2)	0.02	185.9 (20.1)	<0.01	16.7 (0.8)	0.07

Table 6. Student's *t*-test for equality of means of used cells (n=50) and unused cells (n=50) for habitat suitability models: EXPERT, HSI, PATREC, and LOGISTIC. Group samples were randomly selected from 274 cells surveyed for elk use at TRMR winter range in 1995.

Model	Means (S.E.)		*t*-test for equality of means	Levene's test for equality of variance
	unused	used		
EXPERT	0.47 (0.04)	0.57 (0.04)	t= -1.78, p=0.08	F=1.05, p=0.31
HSI	0.43 (0.01)	0.55 (0.01)	t= -6.19, p<0.01	F=4.29, p=0.04
PATREC	0.39 (0.02)	0.55 (0.02)	t= -4.72, p<0.01	F=1.35, p=0.25
LOGISTIC	0.373 (0.03)	0.659 (0.03)	t= -6.75, p<0.001	F=1.65, p=0.201

Table 7. ANOVA table for mean probability scores of cells used by elk in one year (n=30), two years (n=30), and three years (n=30) at TRMR winter range in 1995-97.

Model	Source of variation	*SS*	*df*	*MS*	*F*	*p*
EXPERT	Between groups	0.09	2	0.04	0.66	0.52
	Within groups	5.84	87	0.07		
	Total	5.93	89			
HSI	Between groups	0.30	2	0.15	14.15	<0.01
	Within groups	0.94	87	0.01		
	Total	1.24	89			
PATREC	Between groups	0.33	2	0.17	4.49	0.01
	Within groups	3.22	87	0.04		
	Total	3.55	89			
LOGISTIC	Between groups	0.91	2	0.46	6.52	<0.01
	Within groups	6.08	87	0.07		
	Total	6.99	89			

FIGURES

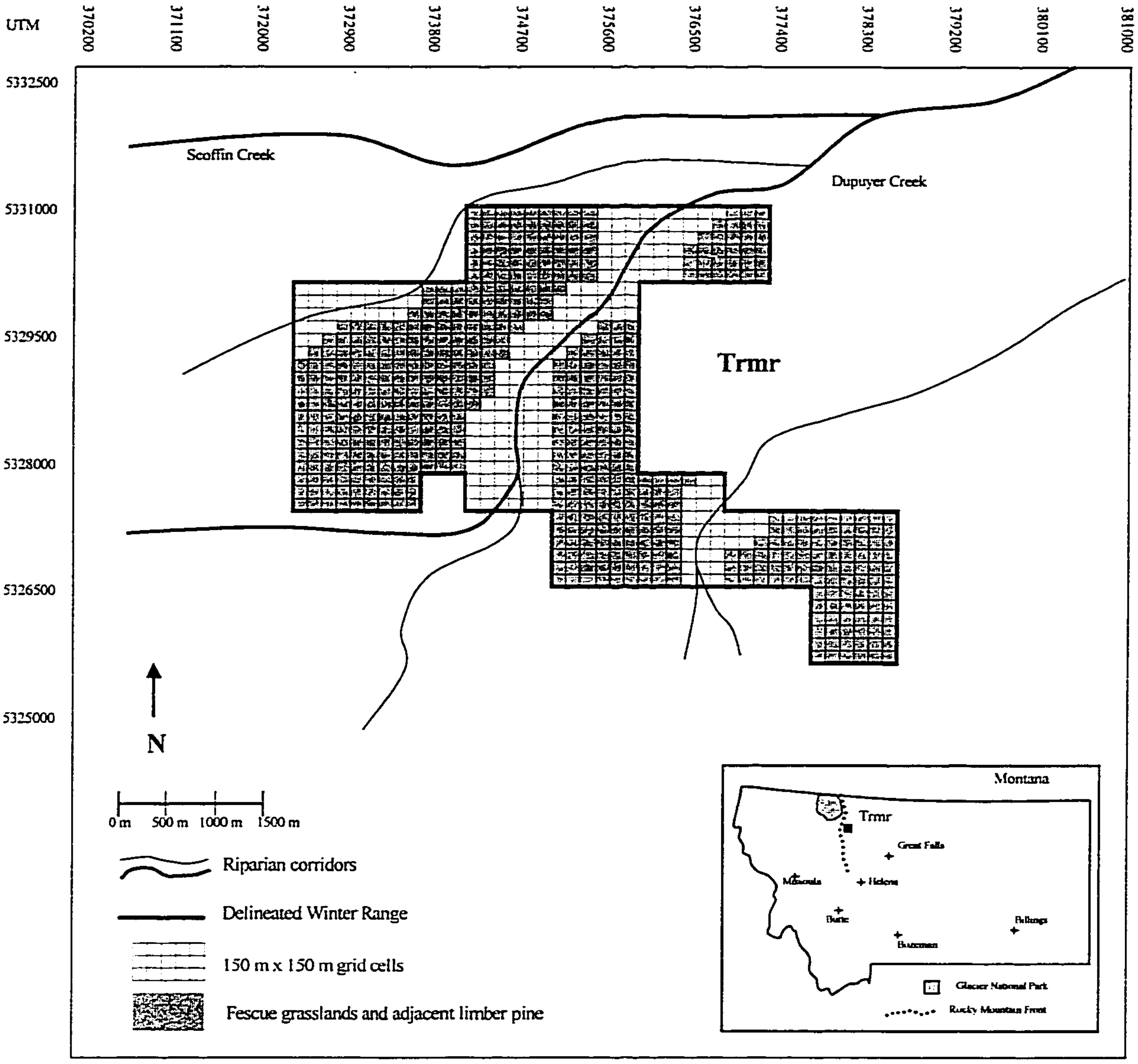

Figure 1. TRMR winter range on Montana's Rocky Mountain Front.

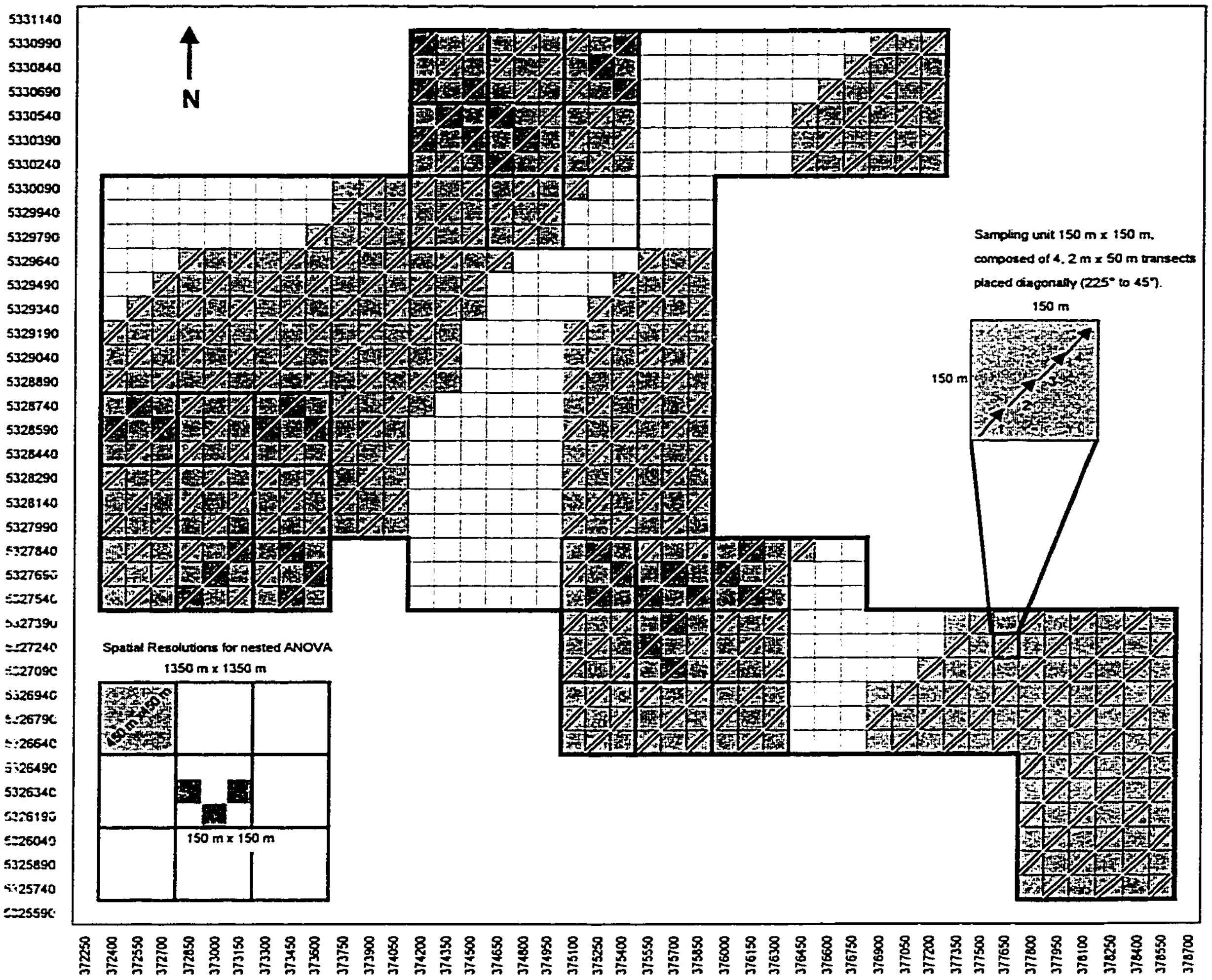

Figure 2. Location of transects (n=1096) surveyed in 1995 at TRMR winter range. Shaded areas refer to fescue grassland and adjacent limber pine. Also plotted are three 1350 m x 1350 m squares used for the nested ANOVA.

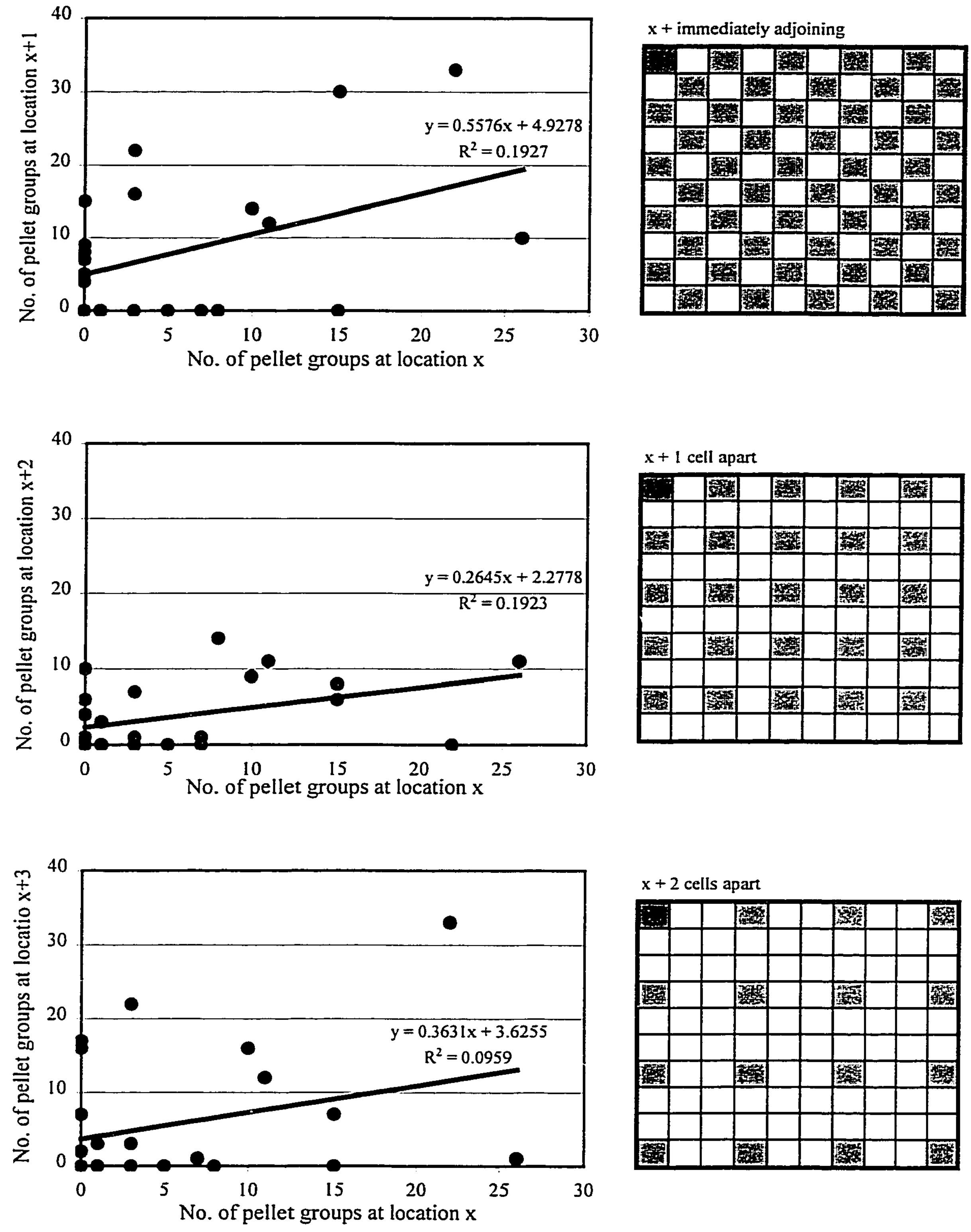

Figure 3 (a-c). Scatterplots of elk pellet group counts at cell location x (*n*=25) and x+*h*. (a: cells immediately adjoining, for a sampling intensity of 50%, b: 1 cell apart, for a sampling intensity of 25%, c: 2 cells apart, for a sampling intensity of 12.5%).

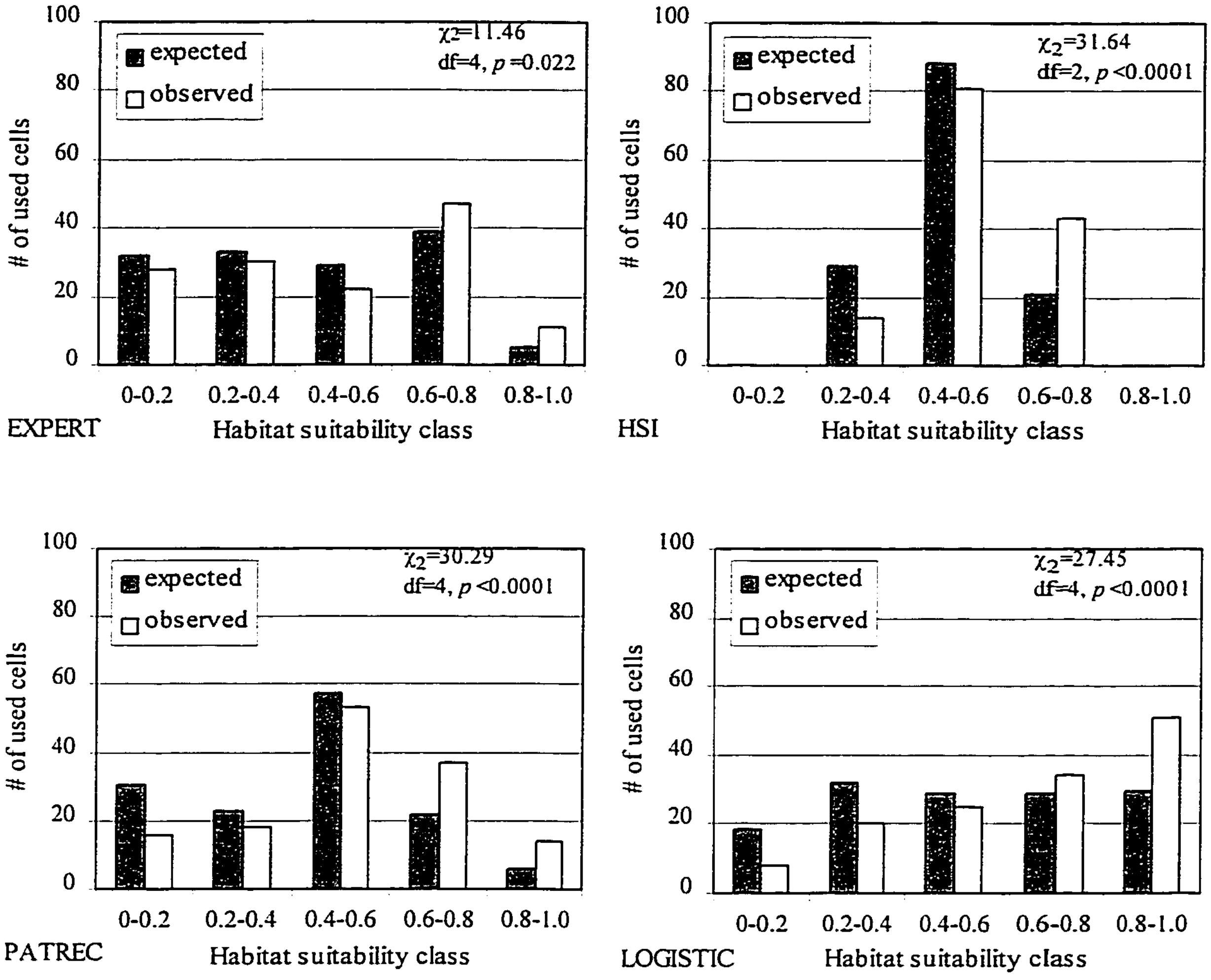

Figure 4. Comparison of EXPERT, HSI, PATREC, and LOGISTIC models for observed use versus expected use of habitat suitability classes at TRMR winter range in 1995. Distribution of observed use among habitat suitability classes was based on 138 used cells in 1995. Expected use was based on the availability of habitat suitability classes for 636 cells comprising TRMR. Observed use and expected use were tested for difference using the chi-square test.

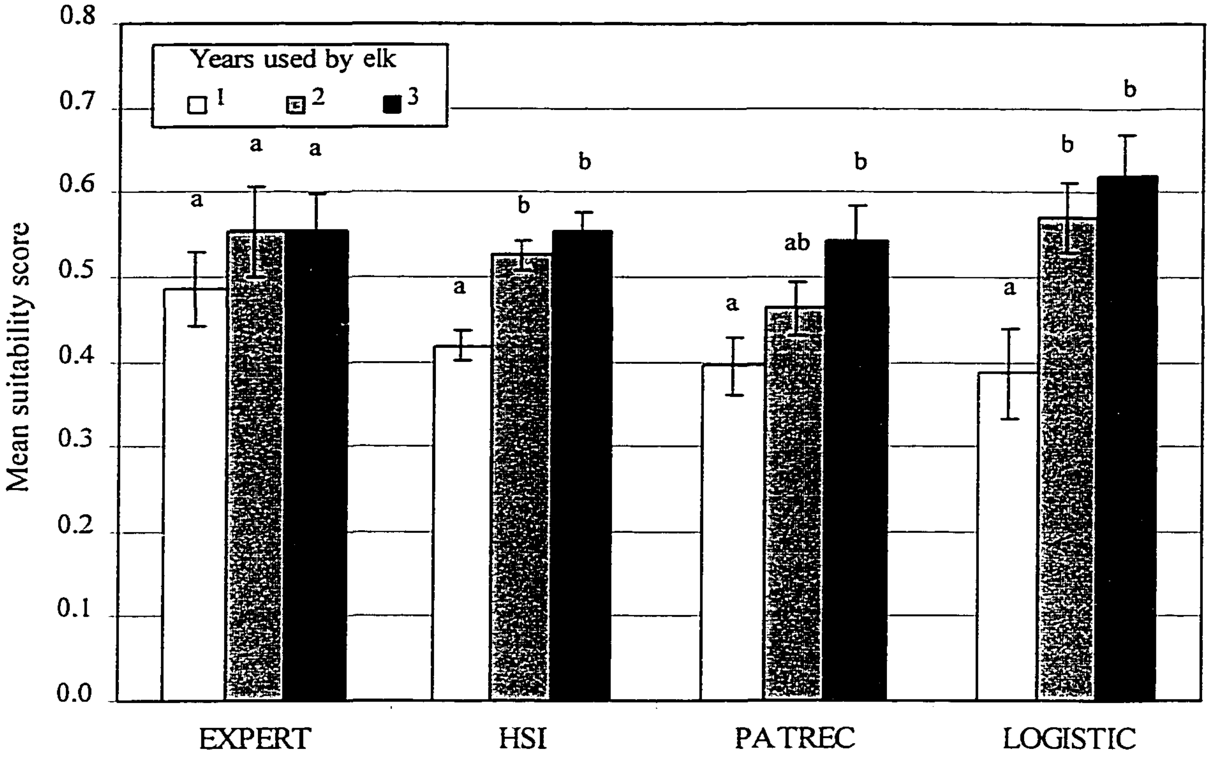

Figure 5. Mean prediction score and S.E. of cells used by elk in one year (*n*=30), two years (*n*=30), and three years (*n*=30) at TRMR winter range in 1995-97. For each model, group means were tested for difference using a one-way ANOVA. Different letters above a bar denote significant difference at $p<0.05$ within each model.

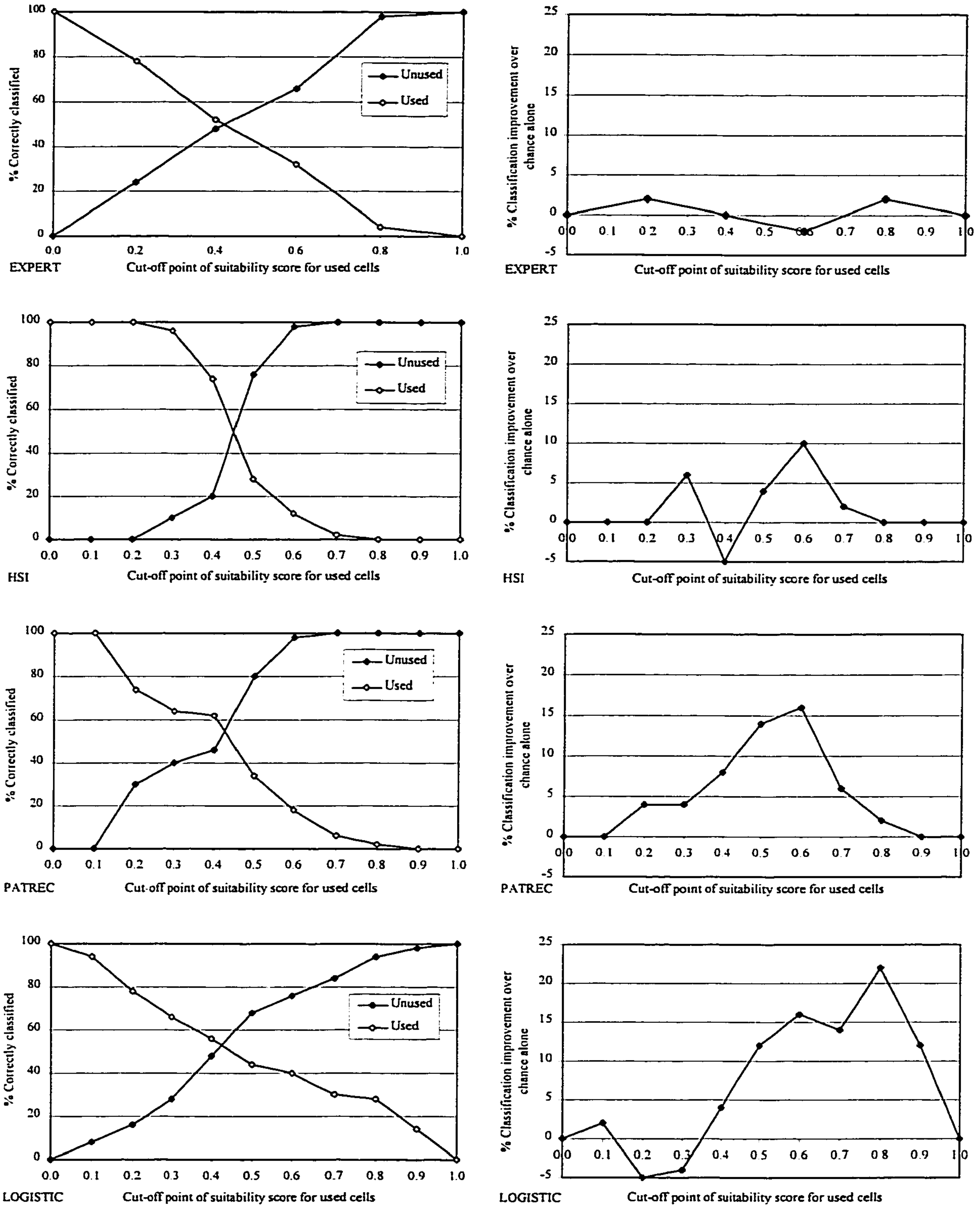

Figure 6. Classification accuracy and improvement over chance of habitat suitability models for predicting cell use by elk at TRMR winter range during 1995-97. Accuracy and chance improvement are presented for used cells (*n*=50) (i.e. used only once in three years) and unused cells (*n*=50) (i.e. no use in three years) relative to different cut-offs for classifying a cell as a used cell.

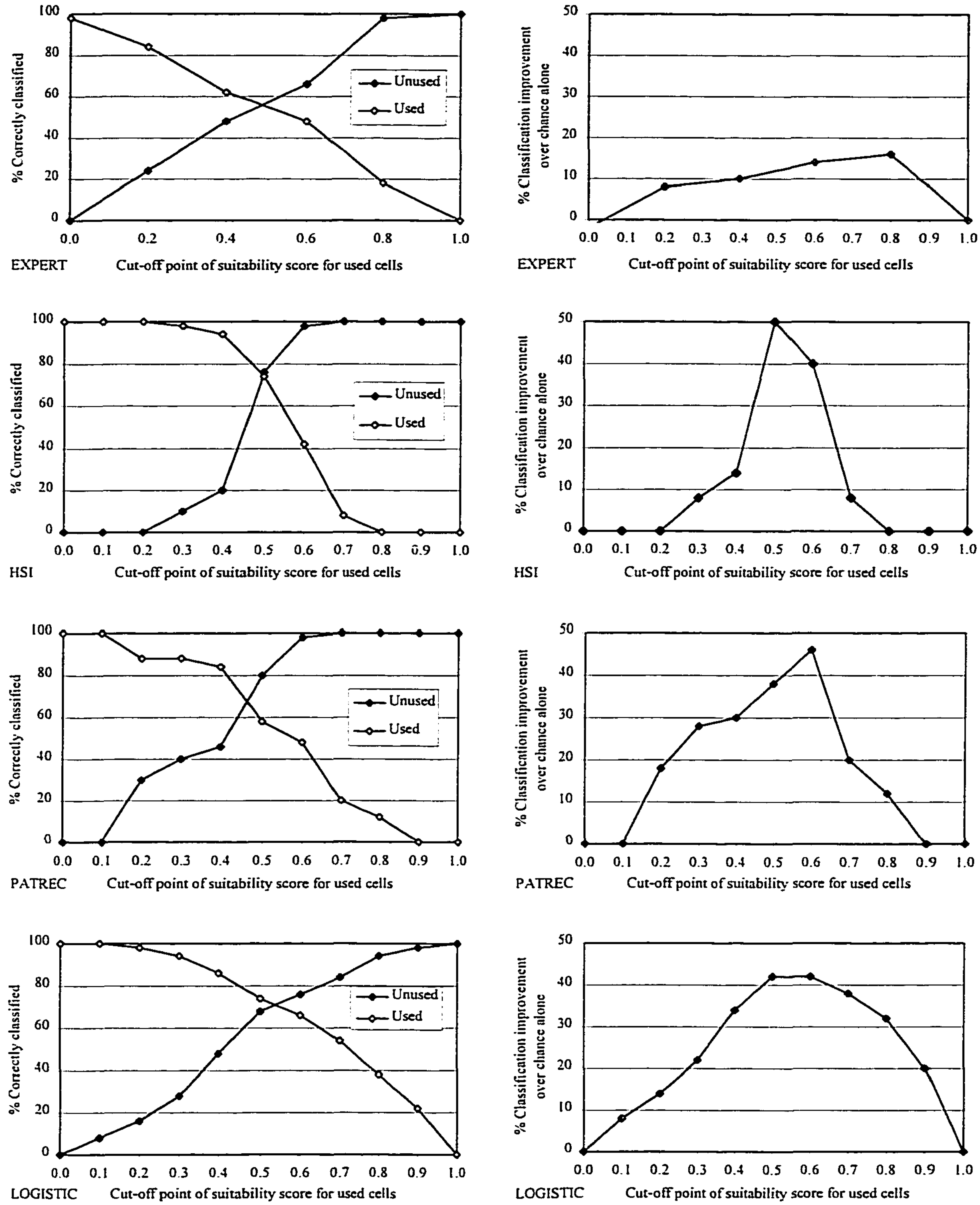

Figure 7. Classification accuracy and improvement over chance of habitat suitability models for predicting cell use by elk at TRMR winter range during 1995-97. Accuracy and chance improvement are presented for used cells (*n*=50) (i.e. used thrice in three years) and unused cells (*n*=50) (i.e. no use in three years) relative to different cut-offs for classifying a cell as a used cell.

APPENDIX

Expert Opinion Worksheet

Introduction

As an expert on elk-habitat relationships, you have been asked to evaluate elk occupancy on a 1,700 ha winter range on Montana's Rocky Mountain Front between Teton River and Birch Creek. Collectively with four other expert opinions, your evaluation will be compared to other approaches for modeling elk habitat occupancy including an HSI model and a regression-based analysis.

Background

The winter range is located in fescue-dominated grasslands of the foothills separating Douglas-fir forests to the west and wheatfields to the east. Grassland comprises 80% of the area. The remaining area is vegetated with cover patches (generally <5 ha) of limber pine, aspen, and cottonwood. Up to 400 elk use the range year-round with greatest use occurring during winter (December-May). The range is lightly grazed by 120-150 cow-calf pairs in spring and early summer. The area is closed off to human activity during winter except for daily cattle feeding in the center of the winter range (100 ha) and a county road located on the eastern portion of the range.

Methods

The winter range was mapped in GIS as grid cells of 150 m x 150 m. Each cell was described by three habitat variables: (1) mean distance (m) to nearest road traveled by vehicles, (2) mean distance (m) to nearest cover patch ($\geq$ 0.5 ha of limber pine, aspen, cottonwood), and (3) mean slope (%). Each variable was categorized into 3-4 groups, resulting in 48 unique combinations describing cells comprising winter range habitat. Your task is to rate each combination for the likelihood of elk occupancy during an "average" winter. Elk use is indexed by the presence of pellet-groups along a 200 m long and 2 m wide belt-transect placed diagonally across each cell. Each transect was read by one observer in May by walking slowly the length of the transect and recording winter pellet-groups. Used was defined by $\geq$1 pellet-groups and unused by 0 pellet-groups. Please classify each cell combination as used or unused with 1 and 0, respectively. Thus, for each combination ask yourself whether an area with this combination of habitat characteristics would be used ($\geq$1 pellet-groups) or unused (0 pellet-groups) by elk during an average winter from December through May.

Mean distance (m) to road traveled by vehicles	Mean distance (m) to cover patch (limber pine, aspen, cottonwood)	Mean slope (%)	Used (≥1 pellet-group) = 1 OR Unused (0 pellet-groups) = 0
0-500	1-180	0-10	
		11-20	
		>20	
0-500	181-360	0-10	
		11-20	
		>20	
0-500	361-540	0-10	
		11-20	
		>20	
0-500	>540	0-10	
		11-20	
		>20	
501-1000	0-180	0-10	
		11-20	
		>20	
501-1000	181-360	0-10	
		11-20	
		>20	
501-1000	361-540	0-10	
		11-20	
		>20	
501-1000	>540	0-10	
		11-20	
		>20	
1001-1500	0-180	0-10	
		11-20	
		>20	
1001-1500	181-360	0-10	
		11-20	
		>20	
1001-1500	361-540	0-10	
		11-20	
		>20	
1001-1500	>540	0-10	
		11-20	
		>20	
> 1500	0-180	0-10	
		11-20	
		>20	
> 1500	181-360	0-10	
		11-20	
		>20	
> 1500	361-540	0-10	
		11-20	
		>20	
> 1500	>540	0-10	
		11-20	
		>20	

CHAPTER 3: TESTING THE GENERALITY OF LOGISTIC REGRESSION MODELS FOR PREDICTING MULE DEER OCCURRENCE ON WINTER RANGES ALONG MONTANA'S ROCKY MOUNTAIN FRONT

INTRODUCTION

Logistic regression (LR) is a widely applied statistical technique for predicting species distribution based on the relationship between environmental features and species presence/absence (Brennan 1991, Buckland and Elston 1993, Austin et al. 1996, Munger et al. 1997, Massolo and Meriggi 1998). For a particular area, LR yields a value for the probability of species presence by capturing that part of the variation in occurrence explained by one or more species-habitat associations (Van Horne and Wiens 1991). These associations are then used to (1) determine the location and suitability of habitat, (2) predict species distribution, and (3) assess consequences of habitat alterations on species distribution (Pereira and Itami 1991, Buckland and Elston 1993, Stowe et al. 1993, Fielding and Haworth 1995, Bian and West 1997, Milsom et al. 1998, Mladenoff and Sickley 1998).

For example, Mladenoff and Sickley (1998) used road density in a LR to estimate the location and suitability of habitats in Maine and upstate New York for restoring the endangered eastern timber wolf (*Canis lupus*). Pereira and Itami (1991) used LR to predict habitat suitability for the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) and evaluated likely consequences of habitat loss due to development.

LR has been used to model species-habitat associations because it (1) generates probabilistic predictions ranging from 0 to 1 (Brennan et al. 1986), (2) allows for analysis of continuous (e.g., elevation) and categorical (e.g., cover types) data (Press and Wilson

1978, Trexler and Travis 1993), and (3) offers a wide range of post-hoc diagnostics for model testing (Hosmer and Lemeshow 1989, Pereira and Itami 1991). LR is often preferred over alternative approaches, such as discriminant function analysis (DFA), because it requires fewer assumptions regarding data distribution (Hair et al. 1995). Data that are skewed and include many zeros are unsuitable for DFA and other statistical procedures requiring normality and homogeneity of variance, but can be analyzed using LR.

One objective for modeling species-habitat associations, LR included, is to predict the distribution of a species at times and places different from those for which a model was originally developed (Hayes and Jowett 1994, Fielding and Haworth 1995, Mladenoff and Sickley 1998). The confidence that can be placed on these predictions is a function of the degree of empirical correctness (Marcot et al. 1983). However, because of the time and cost of collecting data, few validation studies are replicated across time or space. As such, the generality of models is seldom known (North and Reynolds 1996, Morrison et al. 1998). Generality was defined by Marcot et al. (1983) as the ability of a model to represent how a species selects habitats over a broad range of similar systems.

The generality of species-habitat associations depends on the consistency of habitat use among areas, populations, and through time (Wiens 1989). Brennan (1991), Fielding and Haworth (1995), and Leftwich et al. (1997) tested the generality of LR models for different populations. Brennan (1991) tested a mountain quail (*Oreortyx pictus*) model developed with data from California at sites of known species presence in Idaho, Washington, Oregon, and Nevada which correctly predicted occurrence in 15 of 16 sites. Fielding and Haworth (1995) investigated the generality of locally derived LRs to predict nest site location for golden eagle (*Aquila chrysaetos*), raven (*Corvus corax*), and buzzard (*Buteo buteo*) among five geographic subregions in northwest Scotland. Models ranged in accuracy from 6% to 100% of nest sites. Leftwich et al. (1997) examined transferability of a LR for the tangerine darter (*Percina aurantiaca*) at rivers in southwestern Virginia. For the test rivers, the local model failed to predict presence in 83% of the habitat samples where tangerine darters were present. Fielding and Haworth (1995) and Leftwich et al. (1997) suggested caution in transferring local models to other areas. However, these and other similar studies (Grohsens and Orth 1994, Hayes and Jowett 1994) differ greatly in design, data, species, and spatial scales. This makes it particularly difficult to predict when a local LR will fail as a predictor of habitat use for other populations.

OBJECTIVES

My objective was to quantify the generality of locally developed mule deer (*Odocoileus hemionus*) habitat associations to other mule deer populations. My approach was to test the ability of a multivariate LR developed in one winter range to predict habitat use by mule deer at adjacent winter ranges in the foothills of Montana's Rocky Mountain Front. I attempted to reject a model in several ways using test designs varying in place and time, including (1) different year, same range, (2) same year, different range, and (3) different year, different range. If local mule deer-habitat associations, as described by a LR, were similar among winter ranges and/or years, I expected a statistically similar model accuracy (Fielding and Haworth 1995). I tested the hypothesis that the mean accuracy of predicting habitat use and non-use was not different between years and winter ranges based on survey data of mule deer habitat use collected at three distinct winter ranges in 1995-97. Statistically similar mean accuracy and improvement over chance in predicting used and unused habitats were used as criteria for measuring generality. The more often I failed to reject the hypothesis, the greater my confidence that a locally-developed LR can yield accurate predictions of mule deer occurrence across winter ranges and years tested. Thus, the model has generality.

STUDY AREA

I selected three adjacent mule deer winter ranges in the foothill region of Montana's Rocky Mountain Front for study, located along a north-south orientation in the narrow ecotone between the Rocky Mountains and the Great Plains (Figure 1). The winter ranges are referred to as Blackleaf Wildlife Management Area (Blackleaf) (2165 ha), Theodore Roosevelt Memorial Ranch (TRMR) (1681 ha), and Scoffin Butte (Scoffin) (1575 ha). In 1995-97, mule deer populations approximated 225 at Blackleaf, 600 on TRMR, and 550 deer at Scoffin (Olson pers. commun. 1998).

Each winter range is occupied by a population of mule deer with unique migration and distribution patterns (Kasworm 1981, Ihsle Pac 1982, Kasworm et al. 1984, Ihsle Pac et al. 1988). Overlap of populations is considered minimal, despite close proximity (the greatest distance between ranges is 30 km) (Baumeister 1994, Olson pers. commun. 1995).

Topographical attributes and associated vegetation communities delimit winter ranges. Blackleaf Creek, Dupuyer Creek, and Scoffin Creek separate winter ranges. Blackleaf and TRMR are designated as conservation areas by Montana Fish, Wildlife and Parks and Boone and Crockett Club, respectively, with winter restrictions on human access and livestock grazing to protect wintering mule deer. Scoffin is privately-owned with restricted human access, but with locally concentrated livestock grazing in bottomlands—which are little used by mule deer—during winter.

The winter ranges have similar environmental conditions. Long, cold winters and short warm summers characterize the climate. Temperatures vary considerably, ranging from -30° to 37° C annually (Aune and Kasworm 1989, R. Peebles, pers. commun. 1995). Annual precipitation ranges from 30-40 cm, with the greatest amount of precipitation occurring between April and July (Moeckel 1997). Warm winter winds often raise the temperature dramatically in a matter of a few hours, leaving the ground free of snow.

Each range encompasses floristically and structurally diverse habitats, dominated by limber pine (*Pinus flexilis*) and bunchgrass prairie, predominantly *Festuca* spp.. Bottomlands are comprised of bunchgrass prairie, irrigated hay meadows, and alfalfa fields that grade into limber pine forest on western exposures, ridge lines, and plateaus (Mueggler and Stewart 1980, Offerdahl 1989, Ayers 1996). Along creeks, cottonwood (*Populus* spp.) and willow (*Salix* spp.) communities (Moeckel 1997) dominate the vegetation.

Historically, fires on the bunchgrass prairie occurred at intervals of 5 to 10 years (Arno 1980). The absence of fire over the last century has allowed limber pine communities to become established in grasslands, resulting in a temperate savanna landscape (Ayers 1996). Besides mule deer, the range provides wintering habitat for elk (*Cervus elaphus*), white-tailed deer (*O. virginianus*), wolf (*Canis lupus*), mountain lion (*Felis concolor*), and golden eagle. Up to 400 elk use the winter ranges from December to May (Olson pers. commun. 1998). White-tailed deer are present in low densities (<50 animals/winter range) and are associated primarily with cottonwood habitats along creeks (Peebles pers. commun. 1995, Olson pers. commun. 1995).

A GIS database was available for the region with information on (1) biophysical attributes (slope, aspect, land cover type), (2) human land use (roads, buildings, administrative boundaries), and (3) spatial measures (size, shape, proximity of cover type patches) (Boone and Crockett 1994). Interpreted aerial photography (1:24,000) was used to map land cover types. The classification keys for interpreting photos were developed at TRMR (Offerdahl 1989). Data on slope and aspect were derived from a 7.5-minute Digital Elevation Model (DEM) (U.S. Geological Survey). The database was mapped at a resolution of 30-m pixels.

METHODS

Pellet-group Counts

The generality of a multivariate LR was tested by comparing predicted habitat suitability to mule deer habitat use. To test the model, a grid of cells was superimposed on a winter range, with cells described for predicted and observed values. As an index of mule deer presence, I counted the number of pellet-groups along transects. Predicted presence was based on a LR developed from a set of used and unused cells and associated environmental attributes.

I used pellet-group counts to index habitat use. Such counts are inexpensive, easily interpreted, and widely applied for evaluating habitat use by ungulates (Leopold et al. 1984, Loft and Kie 1988). I did not assume that pellet counts reflected amounts of time spent in a habitat, biological need, population densities, or indication of use of a habitat for a particular function such as resting or browsing. Pellet-group counts simply determined whether or not deer were present in a habitat.

I counted pellet-groups along rectangular 0.01 ha belt transects (50 m long and 2 m wide) (Neff 1968, Freddy and Bowden 1983). Pellets were counted as one group if ≥ 5 pellets of the same general size, shape, and color were present within a 0.5 m^2 area (Bowden et al. 1969). Deer pellets were distinguished from elk pellets based on size and shape differences. "Winter" pellets were separated from "non-winter" pellets by color, vegetative overgrowth, and signs of deterioration (Loft and Kie 1988), the former of which were counted.

Sampling took place over a variety of limber pine/bunchgrass communities and adjacent habitats over a 30-day period. Transects were read in spring after deer left the range (after May 15th) and prior to "green-up" (approximately June 15th). Using the GIS, diagonals were graphically superimposed over TRMR winter range at 200 m intervals except for patches >5 ha of riparian vegetation which were seldom used by mule deer in winter (Ihsle Pac 1982). I avoided backtracking and, thereby, increased efficiency by systematically placing transects along parallel diagonals oriented from southwest (225°) to northeast (45°) (Figure 2). Starting coordinates for each transect were generated using the GIS (Boone and Crockett 1994) and located in the field using a Global Positioning System. I read all transects thereby eliminating inter-observer bias.

Spatial Resolution

Comparison of predicted habitat suitability to observed habitat use required matching the grid cell size to variation in pellet-group counts (Block and Morrison 1991). To determine if the pattern of use as described by pellet-group counts was scale-dependent (Hutto 1985, Porter and Church 1987, Morrison et al. 1998), I tested different spatial resolution to identify where variation in pellet group counts was greatest. Kasworm (1981), Ihsle Pac et al. (1988), and Pac et al. 1991 suggested that mule deer in this region of Montana select habitats at several spatial scales. This selection is akin to the hierarchical model of progressively finer and inclusive scales of selection, down to the level of individual feeding and bedding sites (Johnson 1980). This suggests that there is a spatial resolution at which variation in pellet-group counts is greatest.

However, selecting this level of resolution *a priori* would be subjective since the scales at which habitat selection occurs likely form a continuum or a hierarchy (Wiens et al. 1987). No obvious structure or composition within limber pine communities appeared that might automatically and conclusively be considered important or correlated with important factors on selection patterns. Instead, I tested the null hypothesis that there is no variation in the number of pellet-groups for a series of inclusive resolutions using a nested analysis of variance (nested ANOVA). A nested ANOVA is a suitable statistical technique to test for significant differences in the variation of pellet-group numbers between two nested spatial resolutions (Sokal and Rohlf 1995). For each resolution, the nested ANOVA computed the amount of explained variation (Underwood 1997).

Using 1995 data, I aggregated individual transect readings, which represented a 35 m cell in GIS, into progressively larger cells. While there may be a finer resolution operative in habitat use by mule deer than that of transect-level counts, I considered this to be the finest resolution at which to model habitat use given the resolution of the existing GIS habitat database (30 m pixel). I used the mid-way point to spatially reference each transect in GIS. The GIS pixel within which the mid-way point was located provided the habitat attributes for a particular transect. A shorter transect (< 50 m) would have resulted in identical habitat information. Also, moving to a shorter transect would have increased the chance of adjacent transects sharing the same GIS pixels (Pereira and Itami 1991).

For the nested ANOVA, I randomly selected 4 transects as starting locations within 4 different limber pine communities of >50 ha and ≥2 km apart. At each starting transect, I aggregated pellet-group transects into larger blocks of 150 m x 150 m, 450 m x 450 m, and 900 m x 900 m, resulting in four adjacent transects/150 m square, nine, 150 m squares/450 m square, and four, 450 m squares/900 m square (Figure 2). Within each resulting 900 m square, I randomly chose two of four, 450 m blocks. In each of these, I randomly chose three of nine, 150 m squares; and each was described by four replicate transects. Thus, each pellet-plot was described in terms of its nested location within progressively coarser resolutions.

I present the results here, because the resolution chosen is essential for the remaining methods (Table 1). Most of the variation in pellet-group counts (45.8%) was explained by the 150 m squares as compared to 27.1 % for transects, 14.3 % for 450 m squares, and 12.8 % for 900 m squares. Based on these results, I chose the 150 m square as the resolution for describing habitat use by mule deer using pellet-group counts. These 150 m squares are hereafter referred to as "cells."

In GIS, I mapped winter ranges at 150 m resolution. Resulting cells were described for mule deer use, habitat characteristics, and model predictions. Use of a cell by deer was quantified by summing pellet-group counts of four adjacent transects. Cells were described for habitat characteristics using the GIS database. Model predictions were developed by using LR to analyze the association of habitat characteristics with deer use by cells. I surveyed 274 cells in 1995.

Since LR requires a binary input for use (dependent variable), I had to select a cut-off value from my continuous pellet-group count data to split the sample. To minimize bias, I looked for "natural patterns" in the frequency distribution of the data such as a sharp decline between two adjacent counts (North and Reynolds 1996, Munger et al. 1997). The frequency distribution of 1995 pellet-group counts revealed a positively skewed distribution with many 0s (Bliss 1953, Bowden et al. 1969). I used the difference in counts of 0s and 1s as a "natural pattern" suggesting a cut-off of ≥1 pellet-group would signify use. I assumed that those cells with ≥1 pellet-groups were used more often by wintering mule deer than those cells with 0 pellet-groups.

Univariate Analysis

LR includes variables in a model based on how well they improve the fit between dependent and independent factors. Prior to building a multivariate LR, I examined habitat variables for their ability to differentiate between used and unused cells (Pereira and Itami 1991). If mule deer used a cell (i.e. habitat) based on a habitat variable (e.g., distance to cover), then I expected to find differences in the mean values between used cells and unused cells. I reviewed literature on mule deer-habitat associations during winter to identify a set of test variables (Pac et al. 1988, Pac et al. 1991).

One categorical and ten continuous variables were selected (Table 2). Five variables measured coverage by land cover types (e.g., prairie grasslands), and two measured topography (slope, aspect). Two continuous variables measured proximity: (1) distance to nearest conifer cover, and (2) distance to nearest road traveled by vehicles in winter. One variable measured habitat diversity.

I included the presence of elk as a variable because recent work on elk-mule deer interactions suggests that in those habitats where the species are sympatric and abundant, inter-specific competition can force mule deer to use less suitable habitats than in areas where elk are less abundant (Thomas pers. commun. 1998). I quantified elk use by the number of pellet-groups counted on each 150 m cell transect (0 pellet-groups = unused, $\geq$1 pellet-groups = used). The methodology of reading transects for elk pellet-groups was identical to that for mule deer pellet-group counts.

I randomly selected 50 used ($\geq$1 pellet-group) and 50 unused (0 pellet-groups) cells for the univariate analysis. Where appropriate, I compared group means using the Student's *t*-test and mean ranking using the Mann-Whitney *U*-test. The categorical variable was analyzed using a chi-square test. I selected those variables for inclusion into the regression model that most differentiated between used and unused cells using the significance level *p* as a criterion. I set α=0.1 to reduce the likelihood of a Type II error i.e., failing to include a potentially important predictor in the multivariate suitability model to a 10% level (Capen et al. 1986, James and McCullough 1990, Green et al. 1994). This may have resulted in some Type I errors because I did not adjust α for multiple tests (Thomas and Taylor 1990, Mills pers. commun. 1999).

I attempted to build parsimonious multivariate LRs by including only three significant variables. As more variables are included, the probability of a correlation between variables increases and the predictive power of individual variables decreases (Bunnell 1989, Van Horne and Wiens 1991). Also, overfitted models tend to be less applicable to areas for which they were not originally developed (James and McCullough 1990). I reduced the set of significant variables using the Spearman rank correlation coefficient for bivariate combinations by removing variables most correlated with other variables. From a pair of correlated variables, I selected the one with greater between-group statistical significance using *p* as a criterion (Block et al. 1998). The set of significant and only weakly correlated variables was used for building LR models.

Sensitivity Analysis

The variables in the LR were selected based on a univariate analysis of mean rankings between used cells ($\geq$1 pellet-groups/cell) and unused cells (0 pellet-groups/cell). As such, I assigned equal weight to cells with one or several pellet-groups. Conceivably, different use versus non-use cut-offs of pellet-group counts may yield a different set of variables. I evaluated the sensitivity of univariate results relative to different cut-offs for coding pellet-group counts. I classified a cell as used in increments of four pellet-groups for the range of 0-12 pellet-groups. A classification of used as >12 pellet-groups resulted in too few used samples (<20).

Spatial Autocorrelation

To test for sample independence, I examined whether the random sample of 50 used and 50 unused cells was spatially autocorrelated. Surveying many cells in a relatively small area, even if randomly selected, can result in spatially autocorrelated samples since cells closer together are more likely to be similar in their measurement values than those farther apart (Swihart and Slade 1985, Legendre 1993). For mule deer, these "neighborhood effects" (Chou and Soret 1996) may result from social interactions as well as from similar responses to environmental conditions.

I tested for spatial autocorrelation by determining the degree of correlation between pellet-group counts of cells at fixed distances from one another (Real and McElhany 1996). I randomly drew a sample of 25 cells from cells surveyed in 1995 and paired each pellet-group count with one count randomly drawn from the four cells that immediately adjoined the cell in a checkerboard pattern (50% sampling intensity). I repeated this process for cells that were separated by one cell (25% sampling intensity) and two cells (12.5% sampling intensity).

I graphically examined the degree of correlation between paired cells by plotting the number of pellet-groups at location x against the number of pellet-groups at location x + distance h using an h-scatterplot (Hair et al. 1995). If perfect correlation exists, the number of pellet-groups in a pair of cells is identical and the line has a slope of 1. Any deviation from that pattern is defined by a scatter of points around the diagonal.

Suitability LR Model

For each year of survey data collected at TRMR (1995-97), I built a multivariate LR to predict the probability that mule deer pellet-groups are present in a cell based on a set of explanatory variables. LR assigns weights to individual variables based on their contribution in differentiating between used and unused cells (Green et al. 1994, Brennan 1991). I chose 50 used ($\geq$1 pellet-group) cells and 50 unused (0 pellet-groups) cells, because it is desirable to have equal group sizes when building LR to avoid attributing accuracy to chance alone caused by disparate sample size (Capen et al. 1986, Mills et al. 1993).

I built a model by entering (forcing) into the equation the set of three variables selected from the univariate and correlation analyses. Forcing variables into the model was preferred over a stepwise process to ensure consistency in use of variables when testing accuracy (Fielding and Haworth 1995). For different years of survey data, the stepwise process may result in different sets of variables, which may make it difficult to attribute a classification error to a particular source.

Given inventory data for a cell, the probability P that $\geq$1 pellet-groups are present in a cell (P) was computed as: $P = \dfrac{1}{1 + e^{-\beta_0-(\beta_1 * x_1)-(\beta_2 * x_2)-(\beta_3 * x_3)}}$, where x_n are the data values from a cell, β_0 is the y-intercept, and β_n are the regression coefficients for each variable. Equation parameters were estimated using the maximum likelihood method (Hosmer and Lemeshow 1989).

I tested the hypothesis that none of the variables influenced the probability of cell use (i.e., regression coefficient is 0) using the Wald chi-square statistic. I compared mean prediction scores for used and unused cells using the Student's *t*-test. I examined each LR for goodness-of-fit by (1) examining residuals for outliers, (2) performing a goodness-of-fit test, and (3) computing classification accuracy.

A basic assumption of LR is that the relationship between the dependent and independent variables follows the sigmoid growth curve (Marzluff 1986). As such, I tested the assumption that the sigmoid curve is an appropriate model for describing the association of pellet-group presence with cell attributes. This required grouping cells. Cells were ordered by their respective prediction score *P* and the lowest 10% were assigned to the first group, the next 10% to a second group, and so on until all cells were assigned to a unique group and 10 equally-sized groups were formed (Hosmer and Lemeshow 1989, Loftsgaarden and Andrews 1992).

For each group, I summed the number of cells with pellet-groups and compared it to an expected count, which was computed by summing prediction scores for all cells in a group multiplied by the total number of cells in a particular group. I then tested whether the expected count differed from the observed count by more than can be attributed to chance alone using the Pearson chi-square goodness-of-fit test for all 10 groups simultaneously. A model that fit the data well was expected to show a small chi-square value and a large *p*-value.

The goodness-of-fit test examines how well the model fits the data. However, the test does not reveal how well a model can classify used and unused cells. With a large sample size, there is a high likelihood of obtaining a significant model, while actual classification accuracy may be low (Hair et al. 1995).

Calculating accuracy involved constructing a cross-tabulation of predicted with observed cell use. This required converting the prediction score (scaled from 0 to 1) into a binary variable of used (0) and unused (1) through specification of a cut-off value. Below this value, all cells are considered unused (0), while all above are considered used (1). Depending on the cut-off value selected, the classification accuracy can vary widely (Pereira and Itami 1991). I accounted for this sensitivity by presenting classification accuracy relative to all cut-offs at 0.1 increments.

I also calculated a chance-corrected measure of accuracy known as *kappa* (Cohen 1960, Lillesand and Kiefer 1994). By chance alone, I expect some of the cells to be correctly classified. The *kappa* statistic is a measure of how well a model classifies reference data independent of chance alone (Congalton et al. 1983, Rosenfield and Fritzpatrick-Lins 1986). Prior probabilities for group membership were equal to the proportion of used and unused cells (i.e. 0.5).

Model Validation

Following the development of a "good" fitting model, the next step was to test the generality of each local regression model at other winter ranges and years. The evaluation of accuracy focussed on a model's ability to predict actually used and unused cells. If model accuracy varied with place and time, I expected classification accuracy and error to differ among winter ranges and years. I tested differences in model accuracy using test designs of (1) different year, same range (DYSR), (2) same year, different range (SYDR), and (3) different year, different range (DYDR) (Table 3). I compared the results of these designs to those of the same year, same range tests (SYSR) using data not previously used in model development. No chronological order was placed on the 1995, 1996 and 1997 data sets. Thus, a model developed with data in 1997 could be tested with data from 1995 and 1996. For each test design, the procedure resulted in several comparisons.

Methods for surveying cells at Blackleaf and Scoffin were identical to those employed at TRMR. For each winter range and year, I randomly selected cells to result in 50 used cells and 50 unused cells. I built a classification error matrix and computed a chance-corrected agreement for each comparison. Results were summarized for all comparisons of a test design and presented relative to all cut-offs at increments of 0.1. In my text, I report on the cut-off, which simultaneously maximized the rate of correctly classifying used and unused cells.

RESULTS

Univariate Analysis

All variables were non-normally distributed, so the Mann-Whitney *U*-test was used for the univariate analysis. However, I present means for clarity in comparing groups (Table 4). The mean rankings of used and unused cells were significantly different ($p<0.05$) for SHRUB, ASPEN, LIMBER, ELK, COVER-DISTANCE, and SLOPE. On average, used cells were located on steeper slopes with greater shrub and limber pine cover than unused cells. Used cells consisted of less aspen/willow/ cottonwood cover, on average, than unused cells. The number of cells with habitat diversity ≥ 2 was greater for used cells than for unused cells. There was, on average, a greater number of elk pellet groups in unused cells than in used cells.

I failed to detect a significant difference in mean rankings for GRASS, CONIFER, ROAD-DISTANCE, ASPECT, and DIVERSITY ($p>0.1$) and these variables were subsequently removed from further analyses. I also removed SHRUB and ASPEN from the analysis because fewer than 15% and 10% of the cells had values >0, respectively. I eliminated the variable COVER-DISTANCE because it was highly correlated with the variables SLOPE, ELK, and LIMBER (Table 5). I selected SLOPE, LIMBER, and ELK for inclusion in the LR.

Sensitivity Analysis

I detected similar patterns in cell use at other pellet-group cut-offs (Table 6). At the most extreme classification of >12 pellet-groups required for classifying a cell as used, I found that LIMBER, ELK, COVER-DISTANCE, and SLOPE differentiated significantly between used cells and unused cells ($p<0.1$). Similarly, I failed to detect a significant difference in mean rankings for GRASS, CONIFER, ROADDIST, ASPECT, and DIVERSITY ($p>0.1$). This sensitivity analysis suggests that mule deer have a strong preference for habitats on steep slopes with abundant limber pine and shrub communities and little use by elk. This pattern was independent of the number of pellet-group counts/cell for the ranges of values examined.

Spatial Autocorrelation

I tested for spatial autocorrelation by using a sample of 25 cells from the 1995 data (Figure 3). For each of the three distances examined (immediately adjoining in a checkerboard pattern, 1 cell apart, 2 cells apart), paired data points (n=25 each) formed a scatter around the scatterplot's 45° line with $R^2 <0.3$ for all comparisons. These results suggest that the sampling intensity of 16% (100 cells of 636 cells) resulted in low spatial autocorrelation among pellet-group counts (between 11% and 27%).

Suitability LR Model

Three LRs were built for TRMR using the 1995, 1996, and 1997 survey data of pellet-groups counts/cell and their associated GIS cell attributes. The probability that a cell is used ($\geq$1 pellet-group) was predicted using an identical set of variables: SLOPE, LIMBER, and ELK. All models predicted a non-uniform distribution of mule deer. Because variables were forced into the model, I failed to reject the hypothesis that the regression coefficient is zero for some variables (p>0.1) (Table 7). In 1995, only the regression coefficient for LIMBER was significantly different from zero (p<0.01). In 1996, only SLOPE was significantly different (p=0.03) and in 1997, LIMBER (p<0.01) and ELK (p=0.02) were significantly different from zero. The sigmoid curve of the regression model fit the data well in 1995 (p=0.78) and 1997 (p=0.15), but less well in 1996 (p=0.04). For each survey year, used cells had a greater mean probability score than unused cells (p<0.01) (Table 8). The mean difference between probability values ranged from 0.17 in 1997 to 0.34 in 1996.

The number of correctly predicted used cells and unused cells was similar among models when tested using the SYSR design (Figure 4). For all models, the probability cut-off of 0.4 maximized the number of correctly classified used and unused cells. At that cut-off, the mean accuracy of correctly classifying used and unused cells averaged 68.7% (S.E.=2.3%, range 65%-73%), which was an improvement over the probability of chance alone ranging from 30% to 46%. The 1996 model performed slightly better than the 1995 and 1997 models.

Model Validation

Models performed similarly in all test designs (Figure 5). At the probability cut-off 0.4, the DYSR comparisons (n=6) resulted in the greatest mean accuracy of 65% and an improvement over chance of 30%. Similarly, the SYDR (*n*=4) and the DYDR (*n*=8) comparisons revealed a mean accuracy of 67% and 66% and an improvement over chance agreement of 35% and 33% at the 0.3 cut-off, respectively. The sensitivity of results for mean accuracy and improvement over chance were little affected by the selection of a probability cut-off. For each probability cut-off within the range of 0.4 to 0.9, mean accuracy and improvement over chance were not significantly different among test designs ($p>0.05$).

DISCUSSION

LRs identify from a set of field data significant species-habitat associations that are used to predict species occurrence at a future time or different place (Fielding and Haworth 1995). In my study, the presence of limber pine, slope, and elk significantly correlated with mule deer presence. However, building the LR with these variables occurred with limited regard for appropriate representation of the processes that are actually operating in habitat use—i.e., the goal is prediction, not explanation (Shrader-Frechette and McCoy 1994). This is true for almost all statistical models built for conservation and management purposes. Thus, interpreting a multivariate model based on biological plausibility can be difficult (Morrison et al. 1998). Yet, modeling habitat suitability explicitly assumes that in future applications the conditions correlating with species occurrence remain unchanged (Stowe et al. 1993). This assumption requires testing. In testing the generality of local LRs, I employed a biological, as well as a statistical, approach.

The degree to which a model yields accurate predictions for different areas, times, and populations depends on the similarity in the suite of factors influencing habitat use, including habitat availability, biotic interactions, demographics, and history. It is unlikely that two populations are ever exposed to identical opportunities and constraints when selecting habitat, although this does not imply ecological dissimilarity. The ability of a local model to capture ecological similarity can be evaluated by testing its robustness and the consistency in describing habitat use (Wiens 1989).

Building a LR that has generality requires that species-habitat associations are representative of conditions at different application areas. However, because factors actually influencing habitat selection are unknown, a suite of variables is selected for potential inclusion. A significant drawback of this exploratory approach is that as the number of variables measured becomes great, the chance of detecting spurious relationships increases and the statistical power of detecting real relationships declines (Rexstad et al. 1988, Bunnell 1989, Van Horne and Wiens 1991). Thus, accepting a statistical null hypothesis is unlikely, even if the true effect is small and biologically, as well as practically, insignificant (Farmer et al. 1982). The challenge in building a local model that is generalizable is balancing specification error (an error of not including an important predictor variable) with overfitting the model (the error of fitting too many, often interrelated, predictor variables into the model).

To achieve this balance, statistical analyses are employed to sort through variables and select those that explain most of the variation in species occurrence (Irwin and Cook 1985). For example, I began with a limited set of eleven variables, which was reduced to four through univariate analyses. Although four variables seem minimal, I eliminated one more due to strong correlations with other variables. This was essential because correlated "significant" variables can lead to a well-fitting, site-specific model, but may also result in one that performs poorly when tested against an independent data set not used in model building (Buckland and Elston 1993). Such an over-fitted model has poor generality for different applications (Hair et al. 1995). I attempted to balance overfitting the model while avoiding a specification error by including only three variables. I evaluated model accuracy to assess how well balance was achieved.

TRMR models transferred well to other winter ranges and years. These findings contrast with other studies where generality was poor (e.g., Groshens 1994, Fielding and Haworth 1995, Leftwich et al. 1997). Local models may fail because the relationship of habitat and species occurrence varies over time and place (Block and Morrison 1991). Leftwich et al. (1997) suggested that poor generality of the tangerine darter model may have resulted from not including factors limiting the occurrence of the fish. Since I included only three variables in my models, I may have missed some essential factors as well. However, the strong association of mule deer occurrence with limber pine suggests that this cover type plays an important role in influencing winter habitat use. This association has both statistical and biological implications.

In winter, mule deer survival is a delicate balance between energy intake and energy expenditure (Hobbs 1989, Pac et al. 1991). Forage quality tends to be low, while costs of traveling in snow are high, especially in the snow-drifted bottomlands (Parker et al. 1984). Because of their morphology (relatively small body size), means of conserving energy are expected to override that of forage selectivity (Parker and Gillingham 1990). Nudds (1980) suggested that mule deer specialize in winter by selecting habitat for energy conservation and diet generalization as opposed to forage selectivity, typical during less severe seasons. At TRMR winter range, mule deer appear to be habitat specialists keying in to environmental conditions associated with limber pine. It is probable that mule deer use limber pine habitats based on a beneficial energy balance.

In these habitats, energy costs for travel are low since limber pine communities tend to be diverse in browse availability and are often fringed by shrub communities of serviceberry, chokecherry, and rose (Offerdahl 1989). The combinations of a snow intercepting canopy, proximity to forage, and sheltering from wind and cold (Ayers Baumeister and Dean 1997) make limber pine an essential component of winter habitat. At a time of decreased browse availability in winter and increased travel costs in snow, it is unlikely that mule deer leave thermal cover to acquire sufficient energy to meet thermoregulatory requirements (Parker and Gillingham 1990).

The biological basis for the strong association between limber pine and mule deer is also explicit statistically. Because limber pine stands are patchily distributed on winter range and easily mapped in GIS (Offerdahl 1989), the predictive power of a LR was relatively high (Block et al. 1998). Modeling of habitat suitability for mule deer was, thus, relatively easy.

The equally high accuracy achieved at other winter ranges suggests that the LR included those environmental factors, or ones correlated with them, that limit mule deer distribution in all three winter ranges (Hayes and Jowett 1994, Leftwich et al. 1997). Due to geographic proximity, winter ranges were ecologically similar in terms of vegetation, topography, geology, soils, and climate. As such, similar constraints and opportunities influence selection of a winter range by mule deer. I suspect that within a range, the suitability of a habitat is governed by how well mule deer maintain a positive energy balance. In all three winter ranges, stands of limber pine appear to meet these needs. As such, limber pine was a strong predictor of use. Other factors, such as the influence of predators and competitors on habitat use could not be comprehensively addressed using survey methods of pellet-group counts and modeling methods of GIS. The univariate analyses revealed a negative association between deer and elk. However, in the LR this association was weak and masked by the influence of limber pine and/or slope.

If the limiting factors of species occurrence are included in a model, why isn't accuracy greater? Though models were statistically significant, they nevertheless only accounted for a portion of variation in species occurrence. Is it reasonable to expect higher accuracy from these models? Probably not. Perfect correspondence between model predictions and field observations should not be expected. Mule deer, like most species, respond to a myriad of biophysical resources, environmental conditions, and biotic interactions when selecting habitat (Diehl 1986, McCullough 1994, Morrison et al. 1998). For mule deer, these interactions are complex and only poorly understood (Pac et al. 1991). Simplifications or abstractions in the form of a LR are not error free, and, as such, there is significant uncertainty inherent in natural systems modeling (Fielding and Haworth 1995, Aber 1997). By the nature of their design, these models are speculative. Furthermore, use of a habitat is also influenced by spatial relationships (Chou and Soret 1996). These spatial relationships provide two alternative explanations for model inaccuracy. These are spatial autocorrelation and spatial resolution.

Species-habitat associations occur across many different spatial scales (Wiens et al. 1987). For mule deer on TRMR, the 150 m cell size accounted for only half of the variation in pellet-group counts, combined finer and coarser resolutions accounted for the other half. Thus, the selection of a habitat is not only influenced by the biophysical attributes of a particular site, but concurrently by the decisions and factors influencing habitat use at other scales. Modeling species occurrence more accurately would require complex models to account for this variation at multiple scales (Leftwich et al. 1997).

Similarly, spatial autocorrelation accounted for some of the variation in pellet-group counts and may have limited the utility of LR by not meeting all assumptions. Combined, these spatial relations may account for a considerable portion of unexplained variation in my regression models. These spatial relations combined with only few simple measures of habitat suitability explain model accuracy reasonably well.

To what extent can a local model be applied to other situations (winter ranges) before it fails to produce accurate predictions? I presented evidence that a local model can accurately predict mule deer presence in habitats on adjacent winter ranges that are subject to similar climatic, topographical, and geological influences. However, at what point are site differences too great to maintain accuracy? The hierarchical approach to understanding habitat selection helps define model generality (Leftwich et al. 1997, Block et al. 1998).

Mule deer select habitat at various spatial scales ranging from the geographic to a specific site used for a particular activity. These scales are inclusive (Johnson 1980). Within a geographic range, habitat suitability is governed partially by biophysical factors. However, two geographic ranges may not have the same biophysical characteristics. Thus, habitat suitability within these ranges will be influenced by different factors. This suggests testing for ecological similarity between ranges prior to model transfer. For example, applying a TRMR model to a mule deer winter range in the agricultural lands of eastern Montana would probably result in poor generality. However, transferring the model to other winter ranges in the ecotone zone along the Front may produce similar accuracy.

To increase generality, sampling should occur over a wider range of conditions on several different mule deer winter ranges. However, all things being equal, as samples are distributed over a larger geographic area, fewer samples are collected at each site resulting in large sample variances. In turn, this leads to more general species-habitat associations possibly at the expense of greater precision in predicting actual site occurrence when compared to those models developed from a narrower range of habitat conditions (Hayes and Jowett 1994). Thus, there is a tradeoff in accuracy between generality and site-specificity.

For a LR to serve as a reliable tool for conserving and managing wildlife species and their habitats, generality must be evaluated (Noon 1986). Validation requires testing models with data collected at other times and at other places (Bolger et al. 1997). This allows for an assessment of consistency of species-habitat associations across broader scales. Given the array of factors that likely influence habitat use by mule deer, it is not surprising to find that a three-variable regression model lacks perfect accuracy. Rather, it is surprising that such a high level of accuracy can been achieved. This might be a function of the high degree of fidelity that deer show for the same habitats over time, the fact that deer move little among cover types, and that mule deer are habitat specialists in winter. The modeling approach presented here might perform less well for wide-ranging species (e.g., elk) that use a variety of cover types within winter range (Harris and Kangas 1988).

Because of the costs and time involved in conducting field tests, few regression-based models in use today will ever be field-evaluated. However, without sufficient validation, the risk of relying on potentially incorrect model predictions needs to be weighed against the benefits of using a particular model. The accuracy of regression-based models needs to be carefully evaluated against the costs of developing, applying, and tuning such a model for most planning and management purposes. The decision to use a regression model is one that needs to be made by the manager and the public relative to the decision, the criteria for decision-making, the availability of alternative modeling approaches, financial resources, and the risk of making a wrong decision.

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TABLES

Table 1. Nested ANOVA (Sokal and Rohlf 1995) of testing different resolutions for explaining variation in pellet-groups counts of 50 m transects aggregated to 150 m squares, 450 m squares, and 900 m squares.

Source of variation	df	SS	MS	F	*p*	Expected *MS*	% variation explained
Among 900 m cells	3	119.3	39.8	1.80	0.490	2063.0	12.8
Among 450 m cells	4	88.2	22.1	1.81	0.190	1109.0	14.4
Among150 m cells	16	194.5	12.2	7.76	0.001	50.2	45.8
Within transects	72	112.8	1.57			1.6	27.1
Total	95	514.8					

Table 2. Habitat variables used to describe 150 m cells at TRMR winter range. Continuous variables were generated from GIS database (Boone and Crockett 1994). The categorical variable DIVERSITY was based on data collected at 200 m cell transects (*n*=274) surveyed in 1995.

Variable name	Description
GRASS	% cell in prairie bunchgrass[a]
SHRUB	% cell in chokecherry (*Prunus virginiana*) and serviceberry (*Ameliancher alnifolia*)[a]
CONIFER	% cell in dense limber pine/Douglas-fir (*Pseudotsuga menziesii*) (>50% canopy closure)[a]
ASPEN	% cell in aspen (*Populus tremuloides*)/ willow (*Salix spp.*)/ cottonwood (*Populus spp.*)[a]
LIMBER	% cell in open limber pine (<50% canopy closure)[a]
COVER-DISTANCE	mean distance to nearest conifer or limber pine cover (m)[a]
ROAD-DISTANCE	mean distance to nearest road traveled by vehicles during winter (m)[a]
ASPECT	% cell in southeastern to southwestern aspect (135°-225° magnetic azimuth)[b]
SLOPE	mean slope (%)[b]
ELK	number of elk pellet-groups/transect [c].
DIVERSITY	number of 50m transect-segments in different plant communities (range 1-4)[c]. Plant communities included: prairie grassland, hayfield, limber pine, aspen, chokecherry/serviceberry, and cottonwood/willow. Classes tested: 1 and ≥ 2.

[a]= interpreted aerial photography Offerdahl (1989)

[b]= digital elevation model (U.S. Geological Survey 1993)

[c]= data from 200 m x 2 m transect placed diagonally from SW to NE in each 150 m cell surveyed in 1995 (*n*=274).

Table 3. Designs for testing generality of logistic regression models developed at TRMR winter range (1995-97): SYSR= same year, same range, DYSR= different year, same range, SYDR= same year, different range, and DYDR= different year, different range. All combinations were tested at TRMR, Blackleaf, and Scoffin with survey data collected in 1995-97.

		Winter range and survey year						
		TRMR 9	TRMR 96	TRMR 9	Blackleaf 96	Blackleaf 97	Scoffin 96	Scoffin 97
Model	TRMR 95	SYSR	DYSR	DYSR	DYDR	DYDR	DYDR	DYDR
	TRMR 96	DYSR	SYSR	DYSR	SYDR	DYDR	SYDR	DYDR
	TRMR 97	DYSR	DYSR	SYSR	DYDR	SYDR	DYDR	SYDR

Table 4. Means, S.E., mean rankings, Mann-Whitney *U*-statistics, and *p*-values of variables for used cells (n=50) and unused cells (n=50) surveyed in 1995 at TRMR winter range. Also, counts and chi-square test for categorical variable.

		Means (S.E.)		Mean rankings		Mann-Whitney	
		used	unused	used	unused	*U*	*p*
GRASS		49.5 (5.8)	49.5 (5.7)	51	50	1227	0.87
SHRUB		8.2 (3.3)	1.0 (0.7)	53.6	47.4	1096	0.04
CONIFER		32.7 (4.8)	30.1 (5.1)	51.8	49.2	1187	0.65
ASPEN		3.0 (1.8)	14.3 (3.3)	42.8	58.2	865	<0.01
LIMBER		32.0 (5.9)	3.0 (1.5)	60.0	41.0	774	<0.01
ELK		3.5 (1.1)	5.8 (1.0)	58.4	42.6	853	<0.01
COVER-DISTANCE		208 (27)	298 (33)	44.3	56.7	940	0.03
ROAD-DISTANCE		844 (82)	746 (69)	52.0	49.0	1174	0.60
ASPECT		33.3 (4.8)	29.2 (5.4)	53.4	47.6	1104	0.31
SLOPE		15.4 (0.9)	13.1 (1.0)	56.7	44.3	941	0.03
		Count				χ^2	*P*
DIVERSITY	1	30	37			2.22	0.14
	≥ 2	20	13				

Table 5. Spearman rank correlations of continuous variables ELK, SLOPE, COVER-DISTANCE, and LIMBER for 150 m cells (*n*=274) surveyed in 1995 at TRMR mule deer winter range (*p*-value).

	Variable			
Variable	ELK	SLOPE	COVER-DISTANCE	LIMBER
ELK	1.0	~	~	~
SLOPE	-0.32 (<0.01)	1.0	~	~
COVER-DISTANCE	0.30 (<0.01)	-0.46 (<0.01)	1.0	~
LIMBER	-0.27 (0.01)	0.12 (0.23)	-0.38 (<0.01)	1.0

Table 6. Sensitivity of univariate analysis relative to different cut-offs for classifying pellet-group counts as used (P) and unused (N): (1) P=0, N≥1, (2) P=0-4, N>4, (3) P=0-8, N>8, and (4) P=0-12, N>12. Continuous variables were tested using the Mann-Whitney *U*-test and the categorical variable using the chi-square test.

		Cut-offs for classifying pellet-group counts as used (P) and unused (N)										
		N=0, P>0			N=0-4, P>4			N=0-8, P>8			N=0-12, P>12	
Variable		Mean	*U*	*p*	Mean	*U*	*p*	Mean	*U*	*p*	Mean	*U*	*p*
GRASS		P=N	1227	0.87	P<N	1034	0.13	P>N	1113	0.33	P>N	1244	0.97
SHRUB		P>N	1096	0.04	P>N	1242	0.92	P>N	1220	0.70	P>N	1147	0.17
CONIFER		P>N	1187	0.65	P>N	965	0.04	P<N	1171	0.57	P<N	1223	0.86
ASPEN		P<N	865	<0.01	P<N	1076	0.09	P<N	1107	0.12	P<N	1111	0.15
LIMBER		P>N	774	<0.01	P>N	721	<0.01	P>N	865	<0.01	P>N	834	<0.01
ELK		P<N	853	0.01	P<N	822	<0.01	P<N	978	0.04	P<N	973	0.04
COVER-DISTANCE		P<N	940	0.03	P<N	903	0.02	P<N	899	0.02	P<N	984	0.07
ROAD-DISTANCE		P>N	1174	0.60	P<N	1107	0.32	P>N	1154	0.51	P>N	1095	0.29
SLOPE		P>N	941	0.03	P>N	917	0.02	P>N	998	0.09	P>N	941	0.03
ASPECT		P>N	1104	0.31	P>N	1182	0.62	P>N	1058	0.17	P>N	1172	0.58
		Count	χ^2	*p*	Count	χ^2	*p*	Count	χ^2	*p*	Count	χ^2	*p*
DIVERSITY	1	P<N	2.22	0.14	P<N	2.00	0.16	P<N	2.15	0.14	P<N	0.37	0.54
	≥	P>N			P>N			P>N			P>N		

Table 7. Logistic regression models to predict probability of cell use by mule deer in 1995, 1996, and 1997 based on 50 used cells and 50 unused cells and their associated variables (LIMBER, SLOPE, ELK) at TRMR winter range.

Model	Regression coefficient	S.E.	χ^2	p
1995 (*-2 Log Likelihood* = 113.7, $\chi^2 = 24.9$, $df = 3$, $p<0.01$)				
Constant	-1.24	0.57	4.7	0.03
LIMBER	0.04	0.01	10.1	<0.01
SLOPE	0.05	0.04	1.7	0.19
ELK95	0.02	0.02	0.6	0.44
1996 (*-2 Log Likelihood* = 95.9, $\chi^2 = 42.8$, $df = 3$, $p<0.01$				
Constant	-1.81	0.60	9.1	<0.01
LIMBER	0.34	1.02	0.1	0.74
SLOPE	0.07	0.04	4.5	0.04
ELK96	0.02	0.02	0.9	0.35
1997 (*-2 Log Likelihood* = 110.9, $\chi^2 = 27.8$, $df = 3$, $p<0.01$				
Constant	-1.34	0.60	5.0	0.03
LIMBER	0.04	0.02	9.7	<0.01
SLOPE	0.03	0.03	0.9	0.35
ELK97	0.14	0.06	5.8	0.02

Table 8. Probability of cell use by mule deer for cells classified as used (n=50) and unused (n=50) in 1995-97 at TRMR winter range.

	Used cells		Unused cells		
	Mean	S.E.	Mean	S.E.	t-test of equality of mean
1995	0.40	0.02	0.60	0.03	$t=-4.88$, $df=80.5$, $p<0.01$
1996	0.33	0.02	0.67	0.05	$t=-7.02$, $df=62.7$, $p<0.01$
1997	0.41	0.02	0.59	0.03	$t=-4.75$, $df=66.7$, $p<0.01$

FIGURES

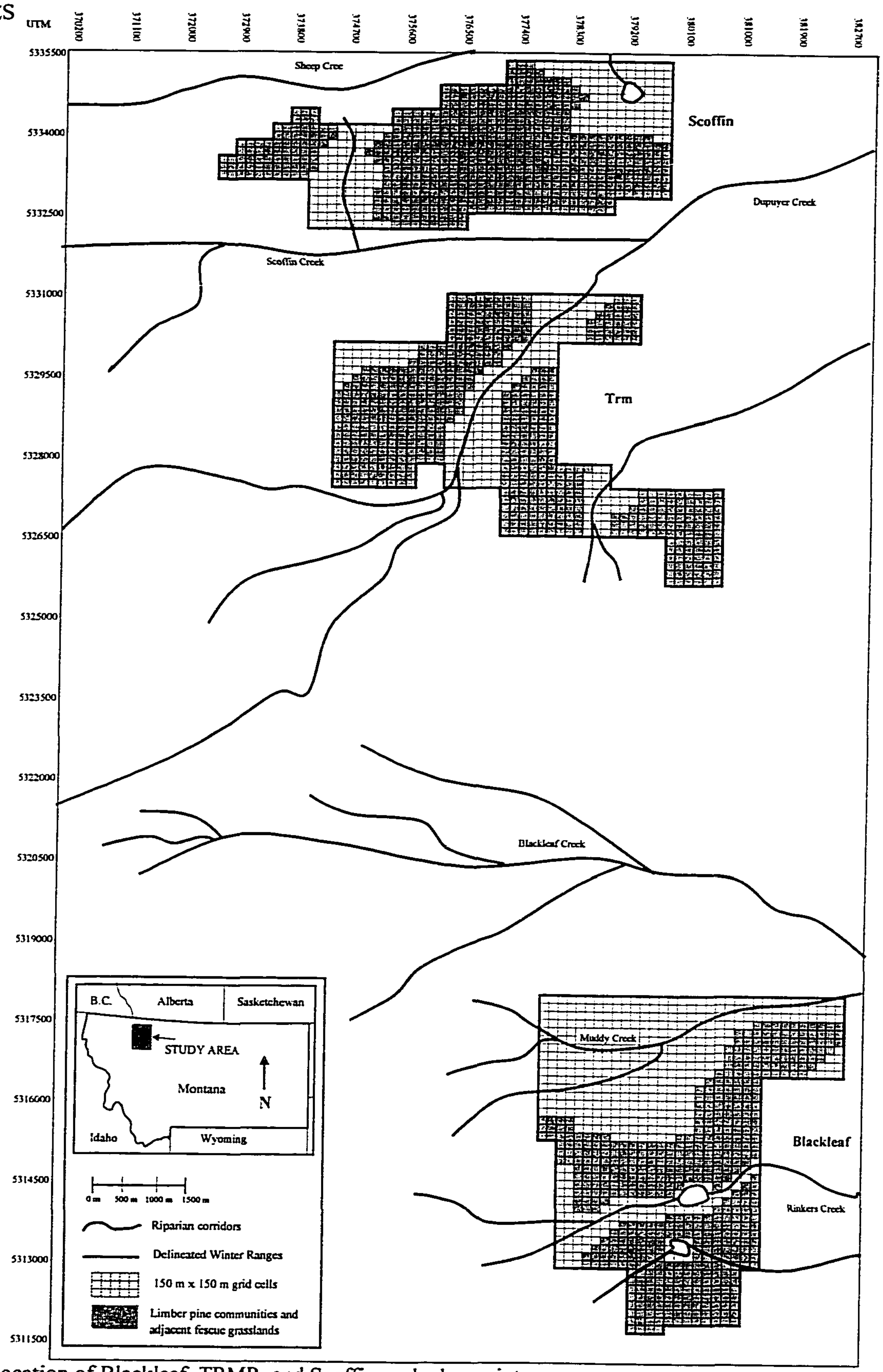


Figure 1. Location of Blackleaf, TRMR, and Scoffin mule deer winter ranges.

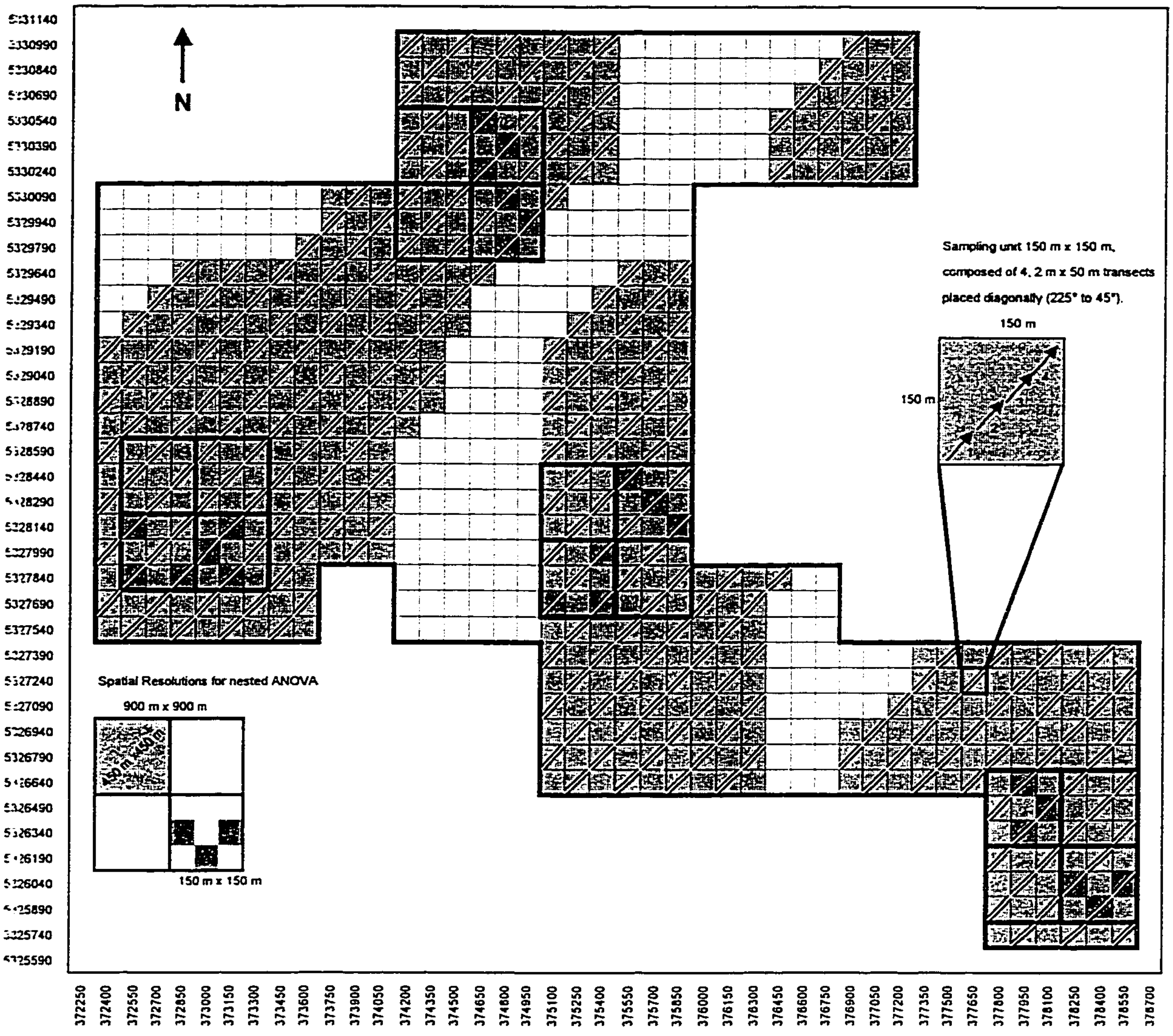


Figure 2. Location of transects (n=1096) surveyed in 1995-97 at TRMR winter range. Shaded areas refer to limber pine and adjacent fescue grassland. Also plotted are four 900 m x 900 m squares used for the nested ANOVA.

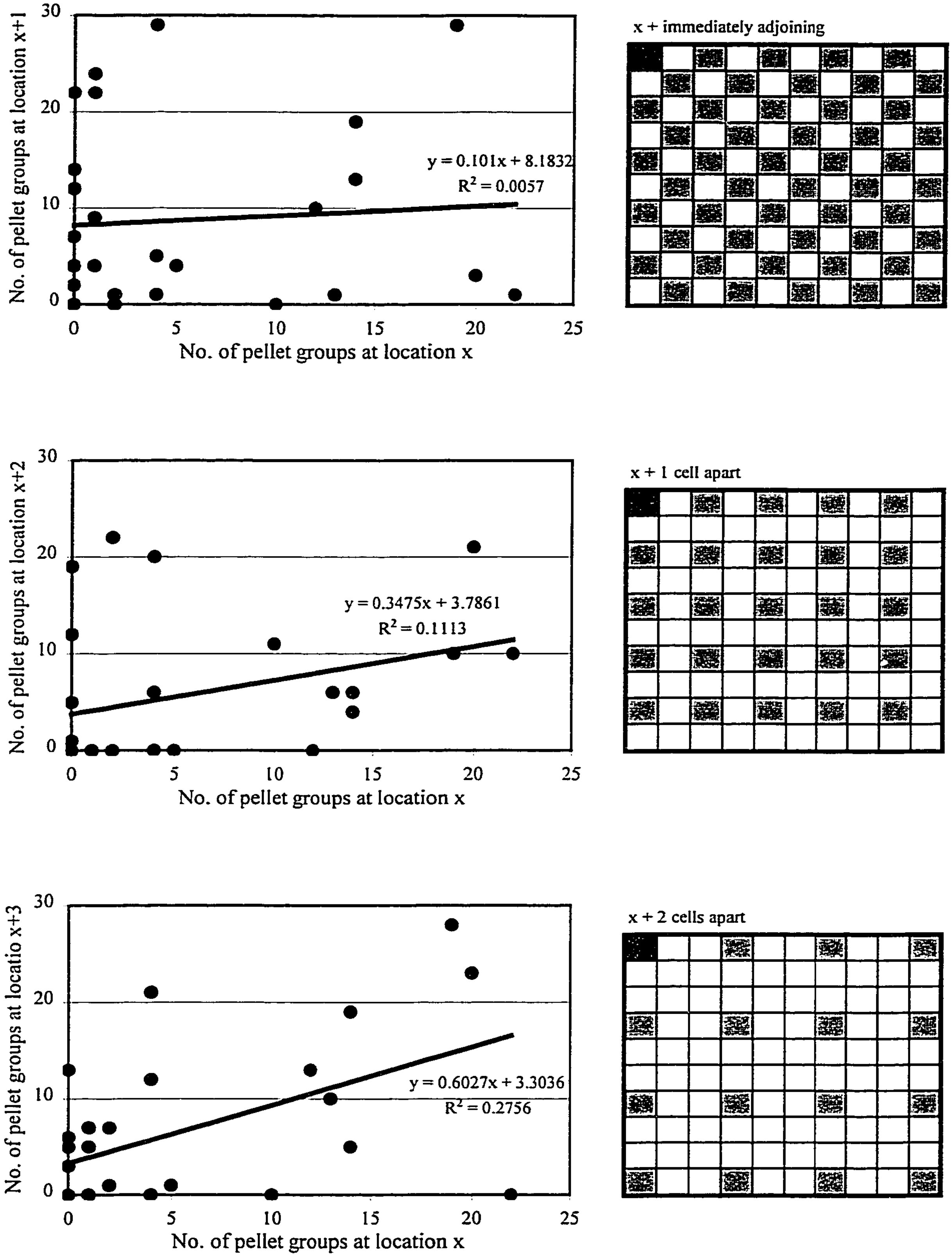


Figure 3 (a-c). Scatterplots of mule deer pellet group counts at cell location x (n=25) and x+h. (a: cells immediately adjoining, for a sampling intensity of 50%, b: 1 cell apart, for a sampling intensity of 25%, c: 2 cells apart, for a sampling intensity of 12.5%).

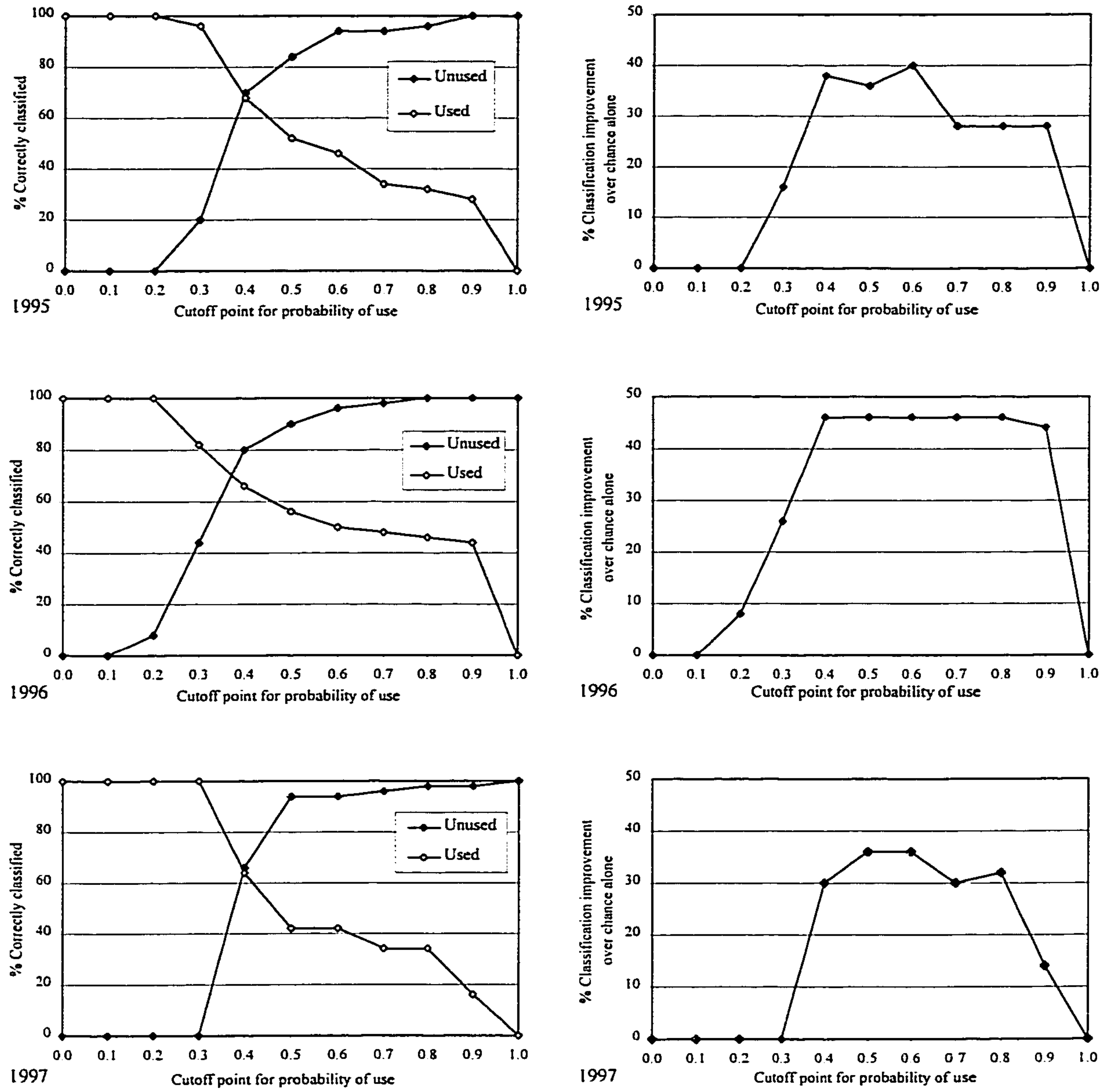


Figure 4. Percent correctly classified and % classification improvement over chance alone for logistic regression models developed in 1995-97 at TRMR winter range and tested using survey data from 1995-97 (SYSR: same year, same range).

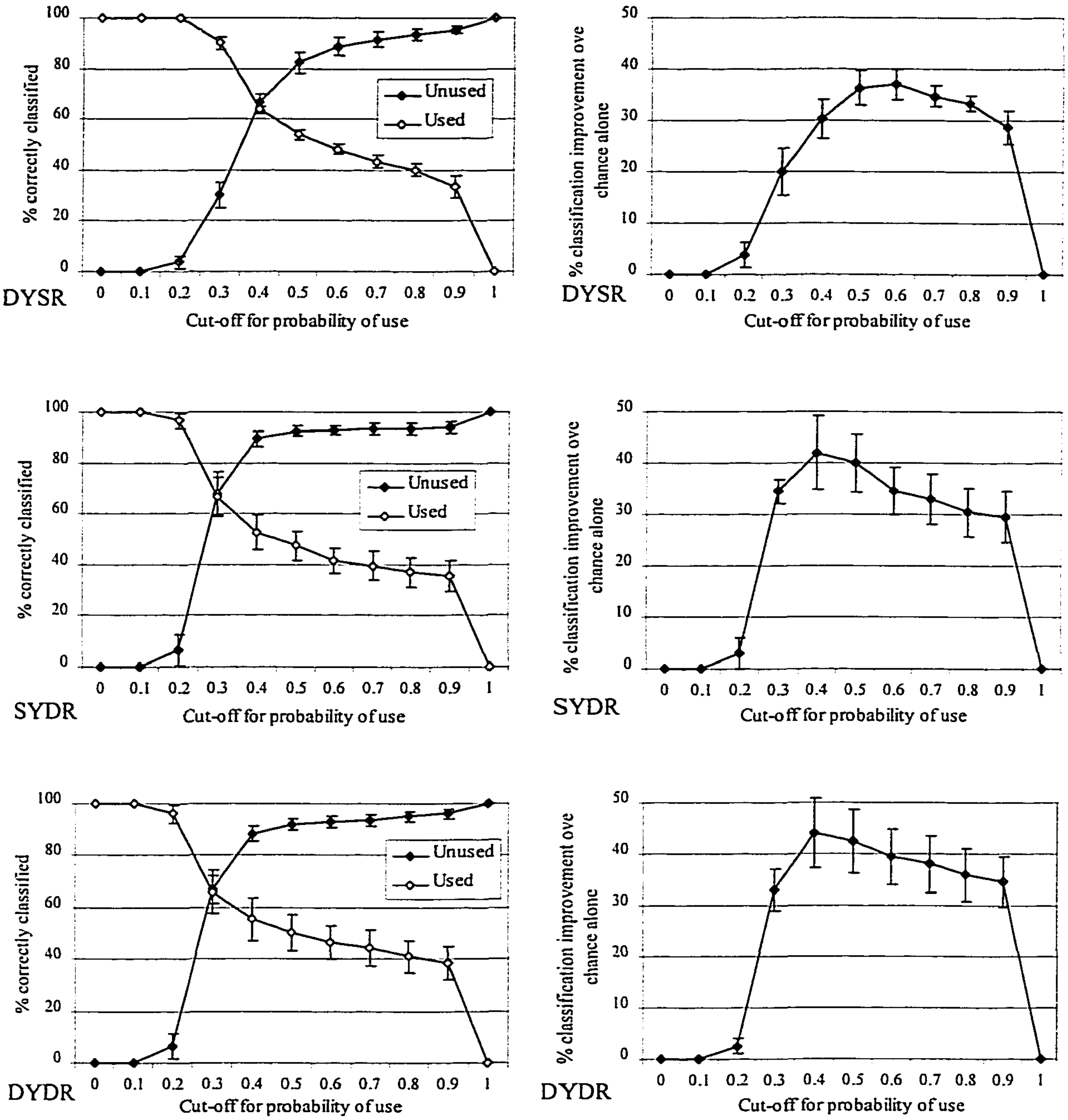
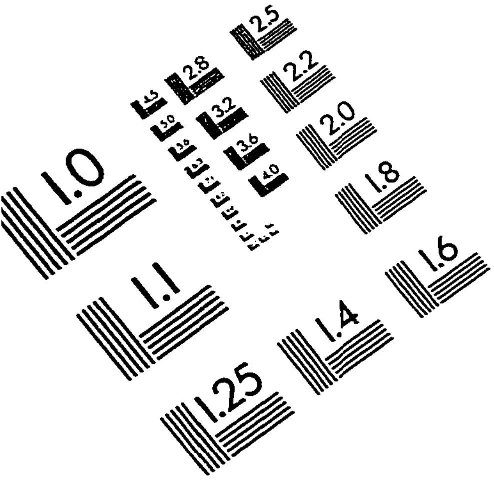
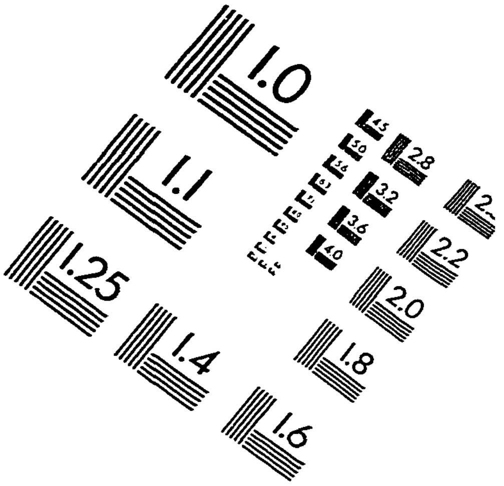
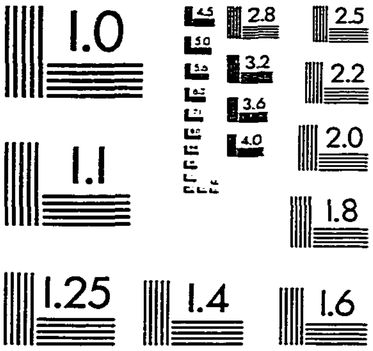


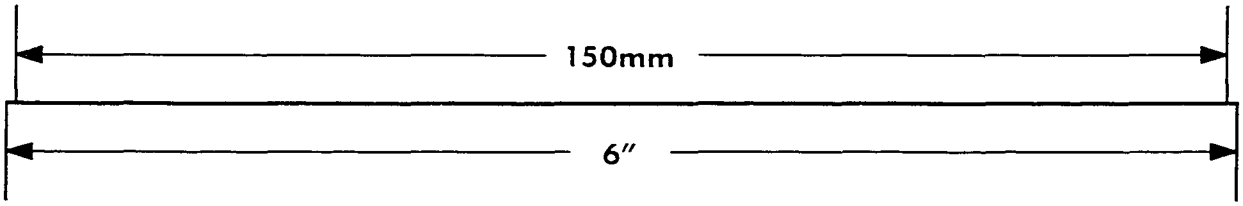
Fig. 5. Percent correctly classified 150 m cells and % classification improvement over chance alone for logistic regression models developed at TRMR winter range (1995-97) and tested at TRMR, Scoffin, and Blackleaf according to test design: DYSR, SYDR, or DYDR. DYSR= different year, same range (*n*=6), SYDR= same year, different range (*n*=4), and DYDR= different year, different range (*n*=8).

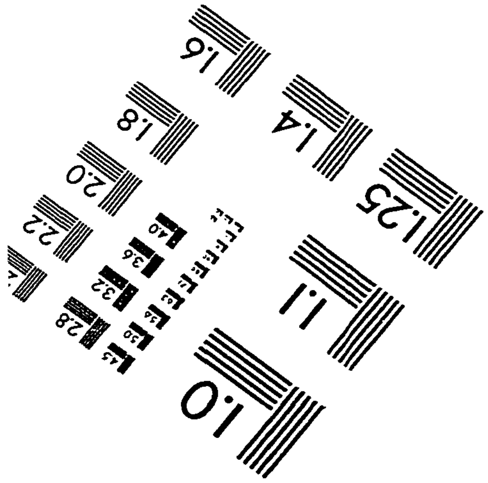
IMAGE EVALUATION
TEST TARGET (QA-3)

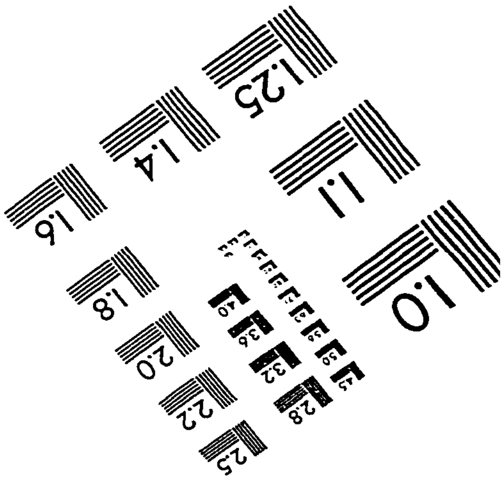












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