AN ABSTRACT OF THE THESIS OF

Carlos Carroll for the degree of Master of Science in Wildlife Science presented on

July 1, 1997. Title: Predicting the Distribution of the Fisher (*Martes pennanti*)

in Northwestern California, U.S.A. Using Survey Data and GIS Modeling

Redacted for Privacy

Abstract approved:

Reed F. Noss

Forest carnivores such as the fisher have frequently been the target of

conservation concern due to their association with older forests and assumed sensitivity

to landscape-level habitat alteration. Although the fisher has been extirpated from most of

its former range in the western U.S., it is still found throughout much of northwestern

California. However, fisher distribution is still poorly known in the majority of this

region where surveys have not been conducted. In order to predict fisher distribution

across the region, a multiple logistic regression model was created using data from 682

previously surveyed locations and a GIS vegetation coverage created from satellite

imagery. A moving-average function was used to derive landscape level indices of

vegetation variables from the GIS layer. Moving averages of canopy closure, tree size

class, and percent conifer were found to have strong correlations with fisher presence.

Regional gradients as represented by either precipitation or a trend surface derived from

spatial coordinates were also significant predictors in the model. The model was validated

with new data collected from 240 survey locations and proved to be accurate in predicting

fisher presence in unsurveyed areas. The model was used to generate hypotheses as to the

mechanisms controlling habitat selection and the scales at which these operate and to evaluate the representation of fisher habitat in existing protected areas. These insights may be valuable in designing conservation reserve networks that insure the long-term viability of forest carnivore populations.

Predicting the Distribution of the Fisher (*Martes pennanti*)

in Northwestern California, U.S.A.

Using Survey Data and GIS Modeling

by

Carlos Carroll

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented July 1,1997
Commencement June 1998

Master of Science thesis of Carlos Carroll presented on July 1, 1997

APPROVED:

Redacted for Privacy

Major professor, representing Wildlife Science

Redacted for Privacy

Chair of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

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

Redacted for Privacy

Carlos Carroll, Author

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF FIGURES

LIST OF FIGURES CONTINUED

`LIST OF FIGURES CONTINUED

LIST OF TABLES

LIST OF TABLES

LIST OF ACRONYMS

BAAS - *Bassiriscus astutus*, the ringtail.

BIC - Bayesian Information Criterion

C_p - a statistic used for the evaluation of nested models

CAR - conditional autoregressive model

CDA - confirmatory data analysis

CONMA - Percent Conifer moving average (FOCALMEAN) variable

CRH - Cliford-Richardson-Hemon modified t-test

CWHR - California Wildlife Habitat Relationships system

DBH - diameter at breast height

DEM - digital elevation model

DENMA - Density (Canopy Closure) moving average (FOCALMEAN) variable

DOQ - digital ortho-quad

EDA - exploratory data analysis

EMAP - Environmental Monitoring and Assessment Program of the USEPA

ESA - Endangered Species Act

FOCALMEAN - a moving average function in the Arc-Info GIS software program

FOCALSTD - a function in the Arc-Info GIS software program that calculates the standard deviation of the cells within a "moving window"

GAM - generalized additive model

GAP - gap analysis project

GIS - geographic information systems

GLM - generalized linear model

LMP - Land Management Plan, also referring to a vegetation coverage developed as part of the plannning process by the US Forest Service

LSR - late-successional reserve

MA - moving-average spatial model

MAPE - *Martes pennanti*, the fisher

MLR - multiple logistic regression

NFI - National Forest Inventory grid

PRECIPANN - annual precipitation variable

QMDBH - quadratic mean diameter at breast height

SAR - simultaneous autoregressive model

SEPM - spatially-explicit populaion model

SIZEMA - Tree Size Class moving average (FOCALMEAN) variable

SPGR - *Spilogale gracilis*, the spotted skunk

SU - sample unit (a group of six trackplate stations)

TTF - Timberland Task Force, referring to the GIS vegetation coverage developed as part of the TTF study

URAM - *Ursus americanus*, the black bear

URCI - *Urocyon cinereoargenteus*, the grey fox

UTM - Universal Transverse Mercator projection

Predicting the Distribution of the Fisher (*Martes pennanti*)
in Northwestern California, U.S.A.
Using Survey Data and GIS Modeling

1. Introduction

1.1 Problem Definition

Forest carnivores such as the fisher (*Martes pennanti*) have frequently been the

target of conservation concern due to their association with older forests and assumed

sensitivity to landscape level habitat fragmentation. The fisher possesses a variety of life

history attributes that make it sensitive to anthropogenic habitat alteration. These include

a large home range, low fecundity, and limited dispersal ability across open habitat

(Buskirk et al. 1994). The same characteristics that make the fisher of conservation

concern also make it an ideal study organism for investigating the effects of landscape

composition and pattern on dispersal dynamics and population viability. Forest carnivores

such as the fisher can be seen as integrating habitat characteristics at levels ranging from

microscale (presence of large woody debris for denning and resting sites) to macroscale

(connectivity within and between metapopulations)(Thompson 1991, Buskirk 1992,

Powell and Zielinski 1994).

This study uses fisher survey data and a GIS vegetation layer created from

satellite imagery to develop a multiple logistic regression model to predict fisher

distribution across northwestern California. The model was developed by means of a

retrospective analysis using existing survey data and then validated with new field data.

In addition to its use for prediction, this type of modeling may also help generate

hypotheses as to the mechanisms controlling habitat selection and the scales at which

these operate. These insights may be critical to the design of conservation reserve networks that insure the long-term viability of forest carnivore populations.

1.2 Population Status

Historically, fishers were distributed across North America from the latitude of Hudson's Bay southward to Tennessee and Virginia in the east (Buskirk et al. 1994). Their range in the western U.S. extended down the Rocky Mountains to Yellowstone and along the west coast to the Klamath mountains and down the Sierra Nevada. By 1900 trapping and logging had led to extirpation of fishers from most of the eastern U.S.. In this century regrowth of forest in New England and the northern Great Lakes states, as well as regulation of trapping, has allowed the fisher to recolonize those areas. Populations in the western U.S., however, have continued to decline (Powell and Zielinski 1994). In recent decades the scarcity of sightings from Washington, Oregon, and the northern Sierras point to the fisher's extirpation from these areas (Aubry and Houston 1992, Zielinski et al. 1996). The population in the Klamath Province (northwestern California and southwestern Oregon) may be the largest remaining in the western U.S. (Powell and Zielinski 1994).

Efforts to supply data on the population status of fishers in the west have been hampered by the difficulties inherent in studying such a rare and secretive organism. However, the majority of studies show that fishers, especially in the western U.S., preferentially use late-successional forests, stimulating concern over the long-term viability of populations in areas subject to extensive logging (Powell and Zielinski 1994,

Buskirk et al. 1994). Selection by fishers for late-successional forests may be related to several habitat resources. Structure in the form of large woody debris and snags provides denning and resting sites. The energetic cost of foraging is lower in late-successional forest due to increased density of preferred prey species, increased prey vulnerability associated with downed logs, as well as easier winter movement due to lighter snow accumulation in closed-canopy forests (Powell and Zielinski 1994). Fishers have a well-documented preference of areas with high canopy cover (Powell and Zielinski 1994). However, it is not known if this is related to predation risk or other factors associated with open areas.

These factors have led some researchers to propose that habitat suitability is mediated by forest structure rather than species composition. Use of second-growth forest by fishers in the eastern U.S. has been attributed to eastern forests achieving the necessary structural complexity at an earlier age (Powell and Zielinski 1994, Buskirk et al. 1994).

However, several factors make it difficult to have confidence in these characterizations of the effects on fishers of habitat alteration such as logging. First, fishers are difficult to study because of their low densities and other traits that violate the assumptions of most population estimation methods (Powell and Zielinski 1994). Second, fishers respond to habitat quality at spatial scales that may not be incorporated into the study design. Third, most studies have been conducted in the east and may not generalize well to the western U.S..

Concern over the status of fishers in the western U.S. has resulted in closure of trapping seasons in all western states but Montana. The fisher is listed as a "sensitive" or "management indicator" species by the US Forest Service in all regions where it occurs (with the exception of Region 6 (Oregon and Washington))(Powell and Zielinski 1994). This concern has also prompted two petitions for listing of the western fisher subspecies (*Martes pennanti pacifica*) as "threatened" under the Endangered Species Act (ESA)(Sierra Audubon 1991, Carlton 1995). Both petitions were denied by U.S. Fish and Wildlife Service (USFWS) (USDI Fish and Wildlife Service 1996). The agency felt that evidence was lacking to demonstrate that fisher populations in the west were declining, and that it was not evident that fishers in the western U.S. belonging to the *M. p. pacifica* subspecies were geographically or genetically distinct from the more abundant eastern populations of *M. p. pennanti*. This decision has been criticized as showing a lack of awareness of recent research findings on the subject. The controversy demonstrates the need to establish a better understanding of the distributional dynamics of the fisher in the western U.S..

1.3 Goals of Study

Four broad research topics motivate this study: What is the status of the Klamath fisher population? Why do fishers seem to have persisted here but not in other regions of the west? What can this tell us about the Klamath populations' prospects for long term viability given current trends in land use? And what lessons can we draw that can be applied to predict the viability of forest carnivores in other regions? Although the results

presented here only begin to answer these questions, but will hopefully form a foundation for further research.

These four questions were addressed through the development of a multi-scale habitat model. The modeling approach was designed to fulfill the following goals:

1) Predict fisher distribution in unsurveyed areas

2) Analyze the regional distribution to identify potential reasons for concern over population viability (e.g. barriers to dispersal)

3) Generate hypotheses as to mechanisms controlling habitat selection and the scales at which these operate

4) Delineate important habitat areas for the fisher in the Klamath region for use in prioritizing conservation strategies.

5) Develop models and modeling techniques that can be applied to other regions

2. Literature Review

2.1 Conceptual Framework

Interaction across multiple scales has become a major topic in landscape ecology as the increasing rate of anthropogenic habitat alteration and the resulting extinction crisis has forced ecology and conservation biology to broaden the scale at which systems are studied (Dunning et al. 1992, Wiens et al. 1993, Wiens 1995). Theoretical concepts such as metapopulation dynamics and source-sink dynamics have focused attention on landscape-level processes as critical to long-term population persistence (Pulliam 1988, Hastings and Harrison 1994). Applied problems such as the conservation planning process for the northern spotted owl (*Strix occidentalis caurina*) have also emphasized the significance of landscape-level processes such as dispersal success (Murphy and Noon 1992, McKelvey et al. 1993).

Hierarchy theory provides a means of conceptualizing the links between processes operating at multiple scales (Allen et al. 1984). Processes at a particular scale integrate the effects of events at finer scales and are themselves constrained by processes operating at coarser scales (Wiens 1989b). This produces a landscape composed of a hierarchy of nested patches (Kotliar and Wiens 1990). Ecotones, or transition zones between patches, may also form a scale-dependent hierarchy (Gosz 1993).

Holling (1992) proposed that habitat alteration at a particular spatial scale would strongly affect only those species that sample the landscape at that scale, due to interactions between morphological constraints and the spatial structure of the

environment. "Grain response" is the term used to characterize the scale-dependent response of an organism to landscape structure (McGarigal 1993). The effects of coarse-scale fragmentation may only be evident through a focus on species with extensive area requirements. These "umbrella species" may therefore make effective targets for conservation planning (Noss and Cooperrider 1994, Noss et al. 1996).

Only by analyzing environmental variation from the perspective of the organism can we build robust models that can predict species' responses to ecosystem change (Kotliar and Wiens 1990, Dutilleul et al. 1993). Rather than measuring ecological heterogeneity with metrics that are obvious or easily-measured from the investigator's perspective, it is important to identify factors leading to "functional heterogeneity" (Kolasa and Rollo 1991). This requires an understanding of the spatial and temporal scales at which an organism most strongly responds to environmental variation. Habitats that appear heterogeneous to one species may appear homogeneous to others if they select habitat based on coarser scale perceptions. Heterogeneity at scales below this minimum grain size may be de-emphasized in order to simplify modeling (Dutilleul et al. 1993).

2.2 Spatial Population Dynamics

It is increasingly evident that the species inhabiting a site may be determined as much by dispersal and other extrinsic factors as by intrinsic interactions such as competition. This has led to renewed interest in the concepts of metapopulation and source-sink dynamics, which relate the local abundance of an organism to larger-scale population processes. The classic metapopulation model conceives of a group of transient

populations interconnected by dispersal (Levins 1970). While any one population is doomed to extinction, the metapopulation as a whole persists through recolonization events. However, these classic metapopulation models may be rare in nature (Harrison 1994, Hastings and Harrison 1994). The concept has since been broadened from the classic "island-island" model to account for other combinations of patch size and isolation (Harrison 1994). "Mainland-island" metapopulations contain at least one population large enough to have low extinction risk. "Non-equilibrium" metapopulations lack the connectivity that allows for recolonization, hence they are doomed to extinction. "Patchy" metapopulations, on the other hand, have such frequent interchange that they function as one population. Real populations may show a combination of these scenarios (Stith et al. 1996).

Some authors have proposed that fishers are best managed as a metapopulation with priority given to maintaining corridors between patches or populations (Heinemeyer 1993, Heinemeyer and Jones 1994). However, data on dispersal, which are difficult to gather, will be necessary to help determine which of the various metapopulation models is most descriptive of fisher population dynamics. Different types of metapopulation structure lead to varying recommendations as to conservation priorities (Stith et al. 1996).

The concept of source-sink dynamics recognizes that the spatial juxtaposition of habitat patches, in addition their habitat suitability, can determine the actual distribution of organisms. Sink populations may persist despite a negative population growth rate due to dispersal from adjacent source populations in higher quality habitat (Pulliam 1988). Thus source-sink dynamics can lead to an "expanded niche" that includes habitats

occupied only due to immigration (Pulliam 1996). The majority of some populations may occur in such sink habitat, and other, more suitable habitat may remain unoccupied due to isolation (Pulliam 1996). The source-sink concept may be strengthened by expanding its focus to multiple scales of habitat patchiness (Kotliar and Wiens 1990).

Populations of relatively long-lived organisms may commonly show such non-equilibrium population dynamics in response to rapid habitat degradation. In the case of the northern spotted owl, local density remained at high levels in some areas in the face of larger-scale population declines due to an influx of non-reproductive "floaters" displaced from more degraded habitat (Harrison et al. 1993).

Early conceptual models of landscape structure focused on patches embedded in an inhospitable matrix and connected by corridors of favorable habitat. More recently, attention has focused on how organisms use the landscape mosaic as a whole (Wiens 1996). The concept of functional connectivity has replaced an emphasis on linear corridors (Noss and Cooperrider 1994). Landscapes can be portrayed as a surface of cost/benefit contours representing the ratio of costs such as predation risk to benefits such as food (Wiens 1996). Landscape composition and landscape pattern thus combine to create a "topography" that influences the movement decisions and distribution of organisms in a more complex manner than suggested by the patch/matrix model.

2.3 Fishers as Candidates for Landscape Level Analysis

In response to growing concern over the status of forest carnivore populations in the western U.S., Ruggiero et al. (1994) proposed a comprehensive strategy to coordinate research on four species: fisher, American marten (*Martes americana*), lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*). Extensive studies of species occurrence (i.e. using GIS) were called for in order to address information gaps in the areas of habitat requirements at multiple scales. The key to the success of efforts to conserve these species was thought to be a broader, landscape-level approach (Ruggiero et al. 1994).

The fisher's vulnerability to the effects of anthropogenic habitat alteration results from a high trophic position that leads to a variety of life-history characteristics such as large home range, low density, and low reproductive rate. Most previous studies of fishers have used telemetry to examine habitat associations at the within-home-range scale. However, it is hypothesized that dispersing juveniles may make decisions on where to establish a home range by integrating perceptions of landscape quality over a wide area (Powell and Zielinski 1994). This might result in the effects of habitat selection being most evident at above-home-range scales.

Fisher distribution thus may be influenced by processes operating at various spatial scales. At the patch level, these might include foraging site selection and denning and resting site selection. At the landscape level, the effects of home range selection by dispersing individuals and source/sink effects would dominate. At the regional level, variation in forest composition due to climate and regional patterns in land use play important roles. Regional scale processes might also include source/sink and

metapopulation dynamics, as regional barriers to dispersal may affect gene flow and recolonization of areas after extirpation. Because their distribution is likely to be strongly influenced by such coarse-scale landscape processes, fishers are good candidates for umbrella species.

2.4 Fisher Habitat Ecology

The fisher is the largest member of the genus *Martes*, which comprises 7 species of small to medium-sized carnivores that are distributed throughout the forests of the northern hemisphere. They tend to be generalist predators, feeding on small to medium-sized mammals and birds, as well as carrion (Powell and Zielinski 1994).

The fisher is sexually dimorphic with adult males weighing 3.5-5.5 kg and adult females 2.0-2.5 kg.. Fishers exhibit intrasexual territoriality, with one male sharing his home range with two to three females (Powell and Zielinski 1994). Young are born in the spring and are raised by the females in protected den sites. Large snags are often preferred as den sites to provide protection from predators while the mother is hunting. Mean litter sizes are between 2 and 3, but only one half to one third of the adult females breed in any one year. Juvenile fishers disperse from their natal area in their first winter (Powell and Zielinski 1994). Males disperse farther than females, with reported dispersal distances of 10 to 100 km. (Powell and Zielinski 1994). The spatial structure of fisher populations varies over time. Territories fluctuate in size seasonally (between breeding and non-breeding seasons) and between years (due to prey cycles and habitat change).

Habitat selection at the home range scale might be expected to be most evident at low densities[1] (Wiens 1989a). As fishers became more abundant, they would be expected to disperse and fill in the intervening suboptimal habitat. Powell (1994b) proposes the following continuum of population structure from very low to very high habitat quality: "transient -> exclusive territories, decreasing in size -> intrasexual territories, decreasing in size -> extensive home range overlap". If territory size is correlated with habitat quality, forest fragmentation may increase predation risk and the energetic cost of foraging by requiring larger home range sizes (Buskirk et al. 1994).

2.5 Landscape Level Dynamics of Fisher Populations

Although much has been written on the sensitivity of forest carnivores to landscape fragmentation, almost all of it is based on extrapolation from studies of habitat selection by animals at the within-home-range scale. An exception is a study in northwestern California that found occurrence of fisher to be strongly correlated with increasing forest stand area (up to 100 ha) and decreasing stand insularity (Rosenberg and Raphael 1986).

More compelling evidence is provided by a recent study of the American marten in the intermountain west that looked at marten abundance in 18 nine km^2 landscapes. The landscapes were composed primarily of mature conifer forests, and varied in both the portion of the landscape in openings (both natural and due to logging) and the degree of

---

1. However, in situations of low density, measurements of local density might show high temporal variability despite constant regional scale density if home range boundaries were more free to shift with time (Wiens 1989a).

fragmentation associated with habitat loss. Landscape-level habitat loss was negatively correlated with marten abundance, and landscape pattern (fragmentation) had an secondary additive negative effect (Hargis and Bissonette in press).

In assessing the effects of landscape structure on the distributional dynamics and genetic structure of fishers, it is important to recognize the differences between historical and current landscape dynamics in the forests of the region. The effects of anthropogenic fragmentation on forest carnivores may be qualitatively different from the effects of the natural disturbance regime driven by processes such as fire. A recent study in the Oregon Cascades found that current landscape conditions on public forest lands managed for timber production were distinct from those caused by pre-settlement disturbance regimes (Wallin et al. 1996). Reconstruction of pre-settlement landscapes based on fire history showed not only a greater abundance of older stands but also much larger patch size and higher spatial and temporal variability in age-class distribution.

Similar conclusions would probably hold for the Klamath region. However, its fire disturbance regime is somewhat less dominated by stand-replacing fires and effects of fire disturbance vary with fire intensity (Agee 1993). Species that prefer the interior of forest patches will be negatively affected by severe fires that fragment older forests. In contrast, they may be positively affected by moderate or low intensity fires that increase old-growth structure.

Landscape grain affects the viability of species that must disperse between patches of preferred habitat. Percolation theory predicts a critical threshold below which habitat specialists will have difficulty "percolating" or traveling across the landscape

(With and Crist 1995). This threshold might occur when the landscape shifts from a matrix of older forests to a matrix of early seral patches caused by logging or fire. During initial stages of fragmentation the effect of habitat loss (landscape composition) might be expected to dominate. In later stages, landscape pattern in the form of habitat isolation might become important (Wiens 1996). Studies of the effects of habitat loss on mustelids, however, have shown declines in abundance long before a 'percolation threshold' is reached (Hargis and Bissonette in press). The dispersal dynamic found in the fisher may have been adaptive in pre-settlement landscapes. However, it may become non-adaptive as human-induced fragmentation increases. In highly fragmented landscapes, dispersal to sink habitat may further reduce population viability (Pulliam 1996).

2.6 Simulation Modeling

Simulation models incorporating parameter estimates from intensive studies of mustelids have been used to explore the effects of habitat change on population dynamics. Several generally available simulation models, such as VORTEX (Lacy 1993) and RAMAS (Akcakaya 1994), can be used to simulate the effects of genetic, demographic, environmental, and catastrophic stochasticity, as well as deterministic pressures, and predict extinction probabilities. Lacy and Clark (1993) used VORTEX to simulate the effect of varying levels of trapping and logging on American marten. Trapping was modeled as a harvest of 20% of the population annually. Logging was modeled as a loss of 1% of habitat per year over 50 years. Mean annual population growth rate was 29.2% in untrapped populations and 3.4% in trapped populations.

However, despite their positive growth rate, isolated populations of 50 or 100 animals had high probabilities of extinction due to stochastic processes, pointing to the importance of dispersal in ensuring population persistence.

Schneider and Yodzis (1994) developed a model that used the concept of "Optimum Territory Size" to address the influence of spatial dynamics (i.e. habitat quality and heterogeneity) on energy balance and reproductive output. A 32 year record from standardized trapping of *Peromyscus* species in Algonquin Park, Ontario was used to parameterize a marten population model and successfully mimic the cycles of marten abundance taken from trapping records during the same period (Schneider 1994). As prey abundance and/or habitat area decreased, martens increased territory size and associated energy cost, resulting in lower fecundity. Three types of extinction scenarios were demonstrated by the model:

1) Extinction due to negative growth rate

2) In populations with strongly positive growth rate, deterministic extinction due to habitat loss. The extinction threshold was reached at $N = 75-125$.

3) In populations with a slightly positive growth rate, stochastic processes result in significant probabilities of extinction even in large populations.

The effect of increasing habitat fragmentation on dispersal and predation risk was identified as a missing parameter in this study. Accurate parameter estimation in these type of models often requires long-term data on difficult to measure quantities such as prey abundance or dispersal distance.

2.7 Statistical Habitat Models

Although habitat selection studies have been a research topic since the era of

Grinnell, they gained increasing popularity with the focus on niche theory by MacArthur

and his colleagues (Wiens 1989a). Due to the inability of univariate analyses to resolve

the intercorrelations among habitat variables, multivariate models were increasingly

favored. Using a variety of regression and ordination techniques, these models explored

correlations between the distribution or abundance of a species at a series of sites and

habitat variables measured at these locations. Significant correlations were often detected,

as might be expected when examining a large number of variables. However, models

constructed from one data set often proved unable to predict the presence or abundance of

a species at other sites. They also often performed poorly at prediction at the same site at

a later date. In a study of shrubsteppe birds, Wiens (1989a) found correlations of over

70% between abundance of seven species and habitat floristics. Only two of the seven

models performed well when applied to other nearby sites in similar habitat. Experiences

such as this led to some disenchantment with multivariate habitat modeling.

One problem with models based on abundance is that density may often be an

inaccurate measure of habitat quality (Van Horne 1983). This is more likely to be the case

when "environments are strongly seasonal, temporally unpredictable, or spatially patchy,

and in species that are ecological generalists and have a social dominance structure and a

high reproductive capacity" (Wiens 1989a). Of these characteristics, social dominance

structure and habitat patchiness are most applicable to fishers. Density in sink habitats is

expected to show higher temporal variability than that in source habitats (Wiens 1989b).

Thus models developed from data collected in these habitats will have poor temporal predictive power. The difficulties in inferring habitat suitability from distribution or abundance have prompted criticisms of GAP analysis and similar rapid biodiversity assessment startegies that use this approach (Conroy and Noon 1996).

To explain the low generality of the observed correlations between species and their habitat in his shrubsteppe study, Wiens (1989a) suggested the following factors:

1) Interspecific interactions (competition, predation, etc.)

2) Dispersal from other areas

3) Environmental stochasticity (e.g. weather extremes)

4) Temporal variation in habitat resources

5) Temporal lags in response to habitat change

6) Habitat factors acting at a scale not measured in the study

All of these factors, except for the first, can be grouped as due either to inappropriate temporal or spatial scale. Thus if habitat data could be gathered on a larger spatial scale, it is possible that model generality could be significantly improved.

2.8 Spatial Statistical Habitat Models

Spatial heterogeneity is often seen as an obstacle to the understanding of ecological processes, to be avoided through proper selection of study sites or ignored through simplifying assumptions. Many spatial analysis techniques seek only to account for and remove the effects of spatial autocorrelation in order to prevent misleading conclusions about the significance of variables. Recently, there has been increased

recognition that incorporating spatial pattern into ecological analysis can provide more powerful insights into process questions (Karieva and Wennergren 1995, Dutilleul and Legendre 1993). If the interest is in robust prediction and a functional understanding of the process, it is important to find a model that explicitly represents the spatial correlation structure of the data (Haining 1990). Unfortunately, there is usually more than one plausible model available, a situation that is compounded by the correlative, rather than experimental, nature of the analysis. "[M]odels... for representing spatial variation will often provide only crude approximations to the real patterns of variation encountered and the analyst needs to consider the extent to which results may prove sensitive to different but equally plausible representations of this variation" (Haining 1990).

The evaluation of multiple plausible models requires an integration of exploratory and confirmatory data analysis into a process termed "data-adaptive modeling" (Haining 1990). Exploratory data analysis (EDA) seeks to find patterns in the structure of the data using a variety of methods that are robust and resistant to data outliers and violations of parametric assumptions (Tukey 1977). EDA may be especially useful in ecology, where data often violate the assumptions of parametric tests (e.g. multivariate normality). Confirmatory data analysis (CDA) refers to what is traditionally thought of as statistical inference, e.g. providing p-values and confidence intervals.

Many advocates of the strict Popperian hypothetico-deductive method feel that EDA is equivalent to "data-dredging" and should play only a minor role in analysis. Inductive inference, in which falsifiable predictions, or pattern hypotheses, are derived by means of statistical analysis and tested on new data, is not considered a legitimate form of

hypothesis testing by Popperian standards (Wiens 1989a). Others feel that, on the contrary, alternating between EDA and CDA in the course of analysis is preferable to relegating EDA to a purely preliminary role (Haining 1990).

Because it may be difficult to choose between multiple plausible models, validation is a critical component of this type of analysis. If the model successfully predicts the pattern when compared with new data or a portion of the data that was not used in the initial analysis, we can be more confident of its generality. The validation conclusions will be more robust if the validation data set encompasses a range of the possible environmental and spatial variation in the population. This highlights the importance of a sampling design tailored to the questions being asked. In addition, although the generality of the observed pattern may be validated, it is more difficult to conclude that this has confirmed any process hypotheses about the causes of that pattern (Wiens 1989a). A model may have high predictive power but lack a clear functional interpretation. This may or may not limit its usefulness, depending on the goals of the analysis.

A strict Popperian approach may be problematic when the process being studied occurs at a large spatial scale. Possible experimental manipulations may be so difficult as to make replication impractical. An alternative is a comparative study that takes advantage of the range of conditions already present on the landscape due to natural or anthropogenic "experiments" (Carpenter 1990, Walters and Holling 1990).

In a recent symposium volume on large-scale ecology, Robert May criticized the tendency for ecological studies to focus exclusively on smaller spatial scales.

Many such studies are entirely appropriate to the questions being asked, but others derive more from the financial and time constraints of grants (often reinforced by current fashions for Popperian 'falsifiable hypotheses', which themselves owe more to philosophical musings than any real appreciation of how physical scientists actually work), than from careful assessment of the spatial scales that govern the system in question. ...While there are many interesting and practically important questions that can sensibly be pursued on these scales, many others cannot. I fear that, in recent years, too many ecologists have yielded to the temptation of finding a problem that can be studied on a conveniently small spatial and temporal scale, rather than striving first to identify the important problems, and then to ask what is the appropriate spatial scale on which to study them (and how to do this if the scale is large)(May 1994).

2.9 Retrospective Modeling

The strength of the statistical inferences drawn from a habitat association study depends, to a large degree, on the attention paid prospectively to sampling design. However, pre-existing survey information collected for other purposes may often be the only data available for such analysis. The use of such data requires the analyst to confront the problems created by variations in protocols and sampling strategies. The heterogeneous character of such data sets may violate assumptions of standard statistical tests, such as random sampling. Generalizations of the correlations between species presence/absence and habitat characteristics to the entire study population must be model-based due to the lack of a probability-based sampling design.

Several distinct strategies have been used to investigate habitat selection using survey data. A basic choice is between comparisons of survey locations where the organisms were detected to either 1) random points or 2) those survey locations without detections. The first option requires the choice of the area considered available habitat

from which random points are drawn (Manly et al. 1993). The second option also benefits from defining the comparison data, though in a different way. Absence records from areas outside of the range boundaries or environmental tolerance of the species may distort the analysis and may need to be excluded (Austin and Meyers 1996).

The use of random points approximates the case-control retrospective design common in medical applications. It is most useful when the study organism selects for rare habitat types or resources (Ramsey et al. 1994). The use of random points circumvents the question of whether survey intensity was sufficient to detect the organism at all survey locations. However, it assumes that the organisms are rare enough that random points are probably unoccupied (Ramsey et al. 1994). A comparison of sites with detections versus sites without detections avoids this assumption, but at the cost of reducing the generality of the observed habitat associations. The latter approach seems preferable when the surveys have the potential to detect animals over most of their home range (e.g. during foraging) as is the case with bait stations. The former approach may be more appropriate when the sites represent nesting locations. Habitat data from foraging locations has inherently less biological significance than that from nesting site locations. However, it may be he best alternative when studying species (such as fishers) that require intensive telemetry studies to detect denning locations.

Organisms that are difficult to detect due to inaccessible habitat and cryptic or nocturnal behavior may be good candidates for retrospective analyses. These constraints were encountered in the case of the marbled murrelet (*Brachyramphus marmoratus*). A retrospective analysis of murrelet survey data was used to generate hypotheses as to

selection of nesting habitat at the landscape scale (Raphael et al. 1995). "Occupied" sites were compared to sites where transient birds were detected and to sites without detections. Two scales of analysis were employed: large watersheds and circular 2 km² landscapes delineated around survey sites. Both landscape composition and pattern were analyzed through the use of the FRAGSTATS program (McGarigal and Marks 1995). The circular landscapes around occupied sites contained more older forest than those around comparison sites. Watershed level and landscape pattern analyses proved inconclusive (Raphael et al. 1995).

FRAGSTATS was also used to examine correlations between the abundance of various breeding bird species and metrics of landscape composition and pattern (McGarigal 1993). The low explanatory power of landscape pattern found in this study, as in Raphael et al. (1995), was attributed to the effects of regional scale dynamics, as well as to differences between measured and functional heterogeneity.

A similar retrospective analysis was performed using data on the northern spotted owl and a variety of other species (Ramsey et al.1994). Logistic regression was found to be a widely applicable method for analysis of species-environment relationships.

In a comparison of landscape composition and pattern in circular landscapes of 3 sizes around owl nest sites and random sites, Lehmkuhl and Raphael (1993) found that circles of 36 km^2 around a nest site approximated the landscape characteristics of the owl's home range better than larger or smaller circles. The authors used a moving average (MA) function in GIS to model average habitat quality within an owl's foraging radius. Landscapes around owl sites had a significantly higher percentage of suitable habitat and a larger mean patch size than those at random sites.

In order to develop a map of predicted sighting potential, Agee and Stitt (1989) analyzed historic sighting records of grizzly bears in the North Cascades. An MA function was used to measure interspersion of habitat types. Land-cover type and interspersion at sighting locations were compared to those at random locations. Contingency table analysis demonstrated that sightings were more common than expected in certain habitats and at higher interspersion levels. These findings were incorporated in a non-statistical scoring process to create the predictive map. Use of this type of sighting data risks selection and detection bias but was perhaps the only data available in this instance.

In a analysis of winter habitat of deer (*Odocoileus virginianus*), Milne (1989) found that the accuracy of the model was highly dependent on choosing the scale at which the organisms perceived resource distribution. Since this scale might not be known beforehand or might change with time, the use of indices such as fractal dimension that are theoretically scale-invariant was advocated. However, other landscape metrics have been proposed as more robust and biologically meaningful than fractal dimension

(Schumaker 1996). In addition, metrics derived from edge measurements are inherently sensitive to fine scale error in the delineation of patch boundaries. Metrics derived from area (such as patch size) might be expected to be robust for this type of analysis

Researchers in Australia have made widespread use of predictive modeling to study relationships between species distribution and environmental variables. Most efforts have sought to relate plant distributions to abiotic variables (e.g. Austin and Meyers 1996). The method has also been applied to examining associations between birds and a variety of biotic variables including vegetation structure and floristics, as well as abiotic variables such as minimum temperature and topographic position (Neave et al. 1996). Model performance was improved by deriving synthetic variables such as insolation from raw variables such as topography and latitude. These synthetic variables are thought to be more process-oriented and less location-specific (Austin and Meyers 1996).

These studies have also helped demonstrate the value of several lesser-known analytical techniques for ecological research. Generalized linear modeling (GLM), of which logistic regression is a special case, allows regression analyses of a variety of non-linear relationships (Hastie and Pregibon 1993). Generalized additive modeling (GAM) is an even more flexible method that fits smoothed curves to the data with few assumptions as to the form of the response (Hastie 1993).

A Bayesian approach was used by Aspinall and Veitch (1993) to model associations between bird survey data and environmental variables. Correlations between bird presence/absence and both elevation data and spectral bands of unclassified satellite

imagery were analyzed iteratively to produce maps of conditional probabilities of species

presence for each environmental layer. These were then combined using Bayes' Theorem

to produce a composite probability map. By directly modeling species distribution from

raw imagery, this method avoids a additional source of classification error. The cost is a

loss of the ability to interpret the functional relationship between land-cover and species

distribution. Bayesian modeling is a widely used technique in remote sensing

applications, and is increasingly popular in ecological studies (Johnson 1989, Link and

Hahn 1996).

A model combining multiple logistic regression with Bayesian modeling was used

to develop a multi-scale model of the distribution of the Mt. Graham red squirrel

(*Tamiasciurus hudsonicus grahamensis*) (Periera and Itami 1991). The study is unusual

in that it explicitly addresses the spatial context of the habitat model. The model

combined first-order trend surface and second-order environmental variation through the

development of two separate models representing large-scale spatial trends and

environmental variation, respectively. Their conditional probabilities were then combined

by means of Bayes' theorem. Squirrel activity sites were compared with sites

systematically "sampled" from the GIS layers. The spatial autocorrelation structure of the

environmental variables was used to specify a lag distance between sampled points large

enough to avoid autocorrelation problems. Elevation, slope, aspect, and canopy closure

class were retained as variables in the best environmental model. The predominance of

abiotic variables was partially attributed to the low resolution of the biotic data.

A regional scale analysis of wolf distribution in the north central U.S. used multiple logistic regression to compare landscape composition and pattern within wolf pack territories against that within areas of similar size (153 km^2) randomly chosen from the remaining region (Mladenoff et al. 1995). The variables analyzed included human population density, prey density, road density, land cover, and land ownership, as well as 5 landscape pattern indices. The final model included only road density, although fractal dimension was marginally significant. The road density model was used to predict potential wolf habitat in the region in order to devise a conservation strategy to aid recovery of this threatened species. The study produced significant insights into regional-scale population dynamics and the importance of coordinating conservation planning across multiple ownerships.

2.10 The Role of Modeling in Conservation Planning

As the preceding examples demonstrate, spatial statistical habitat modeling is an attractive alternative to other methods such as analytical or simulation modeling. Parameterization of analytical models such as age-structured matrices requires data gathered from intensive demographic studies. Recently, the development of spatially explicit population models (SEPM) has allowed demographic data to be combined with GIS maps of landscape composition and pattern (Murphy and Noon 1992, McKelvey et al. 1993). Despite the attraction of SEPM's for predicting the impacts of landscape change, they may be too 'data-hungry' for use with all but the most well-studied of species. This, coupled with the need for multi-species conservation planning, has led to

the search for modeling techniques that can use coarser-resolution data such as presence/absence records (Hanski 1996, Karieva 1996).

The type of spatial modeling used in this study has the potential to play a important role in conservation planning in these 'data-poor' situations. An example is the use of statistical modeling of the predicted distribution of endemic species to perform "GAP analysis" in northern Mexico (Bojorquez-Tapia et al. 1995). Faced with a lack of detailed survey data, the analysis used modeling based on geo-referenced collection site data and maps of climatic variables to produce maps prioritizing the relative conservation value of lands in the region.

A recent study of the endangered red-cockaded woodpecker (*Picoides borealis*) used the term "Species-Centered Environmental Analysis" to refer to their use of statistical modeling in a similar context (James et al. 1997). By regressing the viability of a focal species on a variety of biotic and abiotic factors at multiple sites, they hoped to relate population-level trends to changes in landscape and ecosystem-level processes such as fire disturbance regimes.

Recently, ecosystem management strategies have been advocated in a move away from a focus on single species (Grumbine 1994). However, incorporation of species level analysis into ecosystem management may provide insights into the "functional integrity" of landscapes that is not available by other means (Murphy and Noon 1992, McKelvey et al. 1993). This suggests that an approach to conservation planning that integrates species-level and ecosystem-level analysis will be most successful in maintaining biodiversity and ecosystem integrity (Franklin 1993, Noss and Cooperrider 1994).

3. Methods

3.1 Study Region

3.1.1 General Description

The area analyzed in this study consists of the California portion of the Klamath Ranges and adjacent portions of the northern California coast (Figure 3.1). The analysis area, which covers 26,600 km^2 of public and private lands, was defined based on current knowledge of the distribution of the Klamath fisher population, probably the most abundant in the western U.S. (Powell and Zielinski 1994). The extent of the retrospective data set is approximately 15,000 km^2, or 56% of the analysis region. The model created in this analysis was also extrapolated southward into the northern California Coast Range as well as northward to encompass the Oregon portion of the Klamath ranges. These regions presently lack substantial survey data, so conclusions for these areas are more speculative in nature.

The Klamath region of southwest Oregon and northwest California lies at the junction of several biogeographic provinces. Its high plant diversity (3500 taxa, 280 endemic) has been attributed to its "central" location at the hub of several mountain ranges, each with its characteristic forest communities (Whittaker 1961, Vance-Borland et al. 1996). High topographic, climatic, and edaphic diversity lead to steep environmental gradients that bring together forest types that elsewhere are widely separated. The survival in this region of forest types that were widespread during the
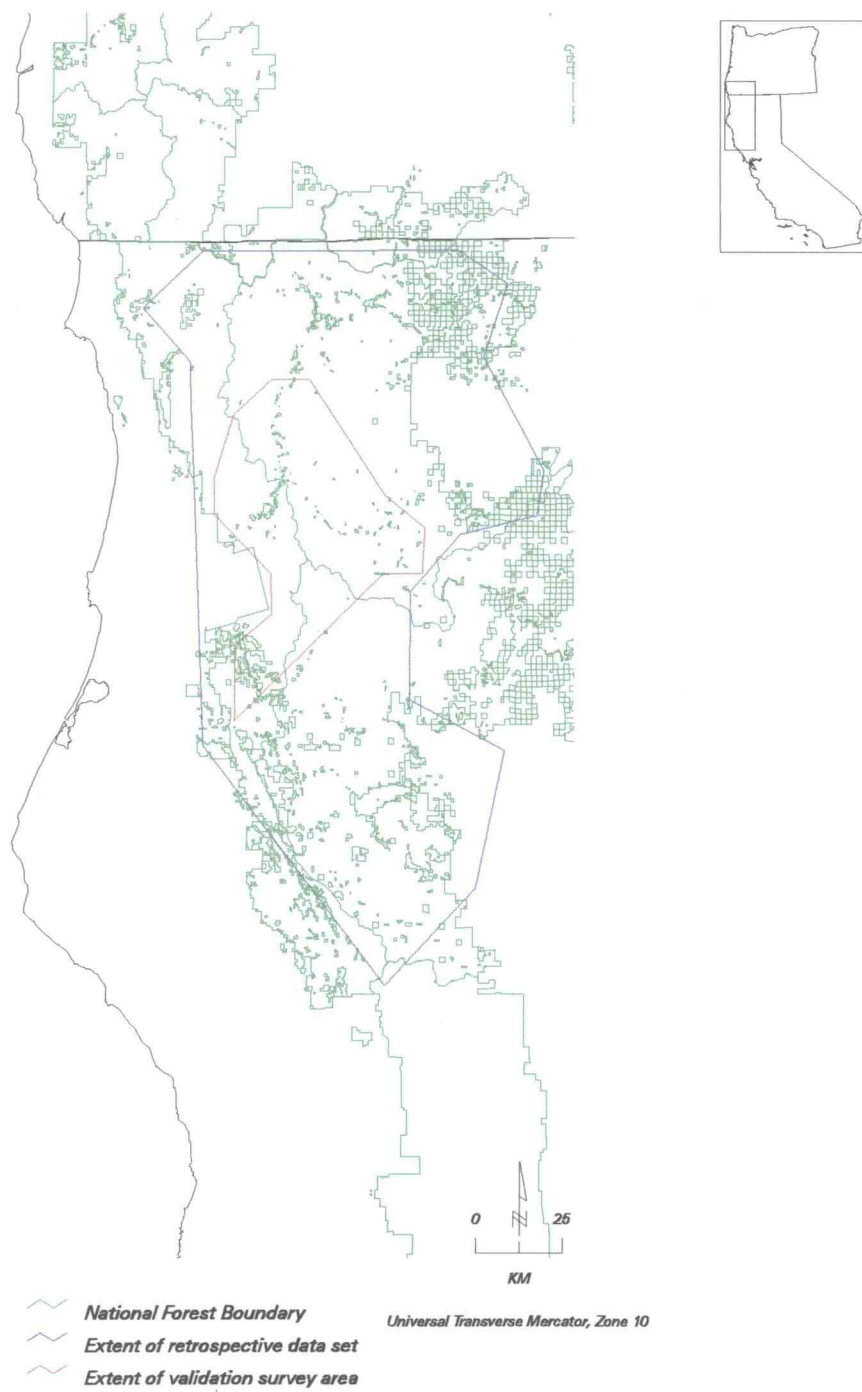
Figure 3.1 Map of study area

National Forest Boundary
Extent of retrospective data set
Extent of validation survey area

Universal Transverse Mercator, Zone 10

0   25

KM

warmer and wetter climate of the Miocene (26 to 7 million years B.P.) is due to a combination of factors (Whittaker 1961):

1) Maritime influence insuring adequate moisture

2) Sufficient warmth due to its latitude and coastal location

3) Lack of recent geologic upheaval due to glaciation or volcanism

4) Edaphic (parent material) diversity, especially the presence of serpentinite and peridotite

Average precipitation is highest at over 3000 mm a year in the coastal ranges near the northwest corner of the region. It decreases sharply eastward and less strongly southward, reaching a minimum of around 500 mm in the southeast corner of the region (Whittaker 1961, Daly et al. 1994). Orographic effects on precipitation are strong due to the dissected topography. Heaviest rainfall occurs in the winter months.

Many of the endemic flora of the region occur on ultrabasic parent material such as serpentinite and peridotite. The forests on these soils often show a low tree canopy cover due to the effects of the chemical content of these minerals. However, the scattered trees may attain a large size and often co-occur with a well-developed shrub layer. These unique plant communities present a problem both for remote sensing classification (W. Cohen, pers. comm.) and for habitat analysis.

The Douglas-fir (*Pseudotsuga menziesii*) type is the most extensive forest community in the Klamath region. The Douglas-fir/mixed conifer type can be distinguished from a Douglas-fir/mixed evergreen type containing a greater hardwood component (Sawyer et al. 1977). Douglas-fir is also an important member of neighboring

forest types. Upslope it becomes a member of the white fir (*Abies concolor*) forests and other high elevation types that have little hardwood component (Sawyer and Thornburgh 1977). To the east it grades into forests dominated by ponderosa pine (*Pinus ponderosa*) and gray pine (*P. sabiniana*). These forests also have a stronger component of deciduous oaks such as Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*). To the west it becomes a member of the redwood (*Sequoia sempervirens*)/western hemlock (*Tsuga heterophylla*) forest (Zinke 1977). The redwood forest is often part of a landscape mosaic with patches of oak woodlands. To the north, the boundary of the Klamath Province marks a transition to the western hemlock/Sitka spruce (*Picea sitchensis*) forests of the Oregon Coast Ranges (Franklin and Dyrness 1973). The hardwood species of these forests are primarily deciduous and form a minor component when compared to their role in the Klamath region. To the south, the Douglas-fir/mixed evergreen type loses its conifer component to become a mixed evergreen hardwood forest (Sawyer et al. 1977).

The Klamath region experiences twice the frequency of lightning ignitions found in the Cascade Range to the north (Agee 1993). The fire regime is composed of a higher proportion of low to moderate intensity fires than Cascade forests. Thus fire disturbance in the Klamath has a more important role in creating old-growth structure than do the stand-replacing fires in more northern forests.

The spatial and temporal variability of fire frequency and intensity created by the diverse plant communities of the region in turn leads to further diversity in landscape pattern and composition. The dominant conifer species of these forests (Douglas-fir,

ponderosa pine, sugar pine (*Pinus lambertiana*), and incense cedar (*Calocedrus decurrens*)) become fire "resisters" with age (Agee 1993). Their hardwood associates (madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*), chinquapin (*Chrysolepis chrysophylla*), and canyon live oak (*Quercus chrysolepis*) are fire "endurers" by means of epicormic sprouting. This, along with the predominantly evergreen nature of the hardwood species, makes these landscapes more resilient to fire disturbance. This has important habitat implications for forest wildlife.

3.1.2 Ownership and Landuse Patterns

The majority of the analysis area is comprised of public forest lands administered by three national forests, the Six Rivers, Klamath and Shasta-Trinity, as well as a small proportion of lands administered by the Bureau of Land Management. Public forest lands administered by the Forest Service comprise approximately 62% of the analysis region. Public forest lands are divided into three main management categories:

1) Protected areas (wilderness, research natural areas) where no timber harvest takes place. These areas cover 26% of Forest Service land, or 16% of the region.

2) Late-Successional Reserves (LSRs), where some timber harvest may occur but where non-timber resources are nominally the primary management concern. These are of recent designation (1995) and so may have more or less extensive previous logging history. They cover 27% of Forest Service land, or 17% of the region.

3) General forest or matrix, where timber is the primary management emphasis. These lands cover the remaining 47% of Forest Service land, or 30% of the region.

The coastal portion of the study area contains the redwood parks, administered by either the National Park Service or the California State Parks. Although these areas cover only 3% of the region, they play a critical role in protecting remnants of the old-growth redwood ecosystem. They are primarily composed of older forest. However, much of the Redwood National Park addition of 1978 was logged prior to acquisition.

Private landholdings comprise 35% of the region. Most of the coastal section is in private ownership, primarily large timber holdings. Private timber inholdings in the eastern section of the study area form part of a "checkerboard" ownership pattern with public lands. Some areas of primary forest (such as the Headwaters Forest area) still remain on private lands. However, timber management practices on private lands are generally more intensive than on public lands. Shorter rotations and less retention of older trees creates a more simplified forest structure.

Second growth stands of redwood, however, often retain significant amounts of residual structure in the form of snags and downed logs. This may help explain the presence of late-successional forest associated species such as the spotted owl and the fisher in these areas (Noon and McKelvey 1996b). Redwoods, as stump sprouters, also recover canopy closure more quickly after logging than do non-sprouting conifers. However, this residual habitat value has not been sufficient to prevent the decline of the Humboldt marten (*Martes americana humboldtensis*). This congeneric to the fisher was once widespread in the redwood region (Slauson et al. 1996). Although trapping appears responsible for its decline before 1946, logging is implicated as the most likely cause of the lack of population recovery in the last 50 years (Zielinski and Golightly 1996).

3.2 Study Design

The data used in this study consisted of field survey data used in the retrospective analysis, GIS data on environmental variates, and validation field data collected to test the results of the retrospective model.

3.2.1 Survey data

The retrospective survey data were collected under several protocols that differed in the type of survey apparatus, the duration of the survey and the dispersion of sampling sites. Survey stations were of three types: 35mm cameras, 110 cameras, and track plate stations (Zielinski and Kucera 1995). 35mm camera stations are designed to take photos automatically when an infrared sensor is triggered by an animal investigating the bait. Multiple events can be recorded between visits, so these cameras only need to be checked weekly. 110 line-triggered cameras, however, must be reset after each photo. Similarly, sooted track plate stations must be visited regularly to replace bait and trackplate. These types of stations are more labor-intensive and are left in place for shorter periods. Types of bait and the use of lure also varied between surveys.

Average duration for the retrospective surveys was 18.4 days. Most trackplate and line-triggered camera surveys run under Forest Service protocols (Zielinski 1991, Zielinski and Kucera 1995) ranged in duration from 12 to 18 days (Zielinski et al. in press). Trackplate surveys run under a non-Forest Service protocol lasted 22 days (Beyer and Golightly 1995). 35mm camera stations were generally left in place for longer periods of 30 days or more.

The sampling design of surveys varied according to the goals of the study. Most surveys were performed by Forest Service and Hoopa Indian Reservation biologists, rather than by research biologists. Funding was primarily due to project-level planning needs, often connected with timber sales. Early surveys, therefore, dispersed stations on roads throughout the project area (Zielinski 1991). As awareness of the need for landscape-level planning grew, the focus shifted to dispersing stations throughout a 10 km² survey unit (Zielinski and Kucera 1995). An alternate protocol dispersed stations along roadside transects (Beyer and Golightly 1995).

This variation in sampling methods reduces the power of the retrospective analysis to detect habitat associations. Analysis of the effect of increased survey duration in both the retrospective data and in the validation study indicates that there is little effect of increased duration after 12 days (Figures 3.3 and 4.8). Therefore, rather than adding duration as an additional variable to the model, the 84 locations with surveys of less than 12 days were removed from the analysis. These locations were primarily from sites surveyed in the early 1980s (Raphael 1988). Their age relative to the other data could have introduced temporal effects, as significant habitat change due to logging occurred in the decade leading up to the spotted owl injunction in 1991. Data from the survey locations used in the retrospective analysis were collected during the period 1991-1995 (Zielinski et al. in press).
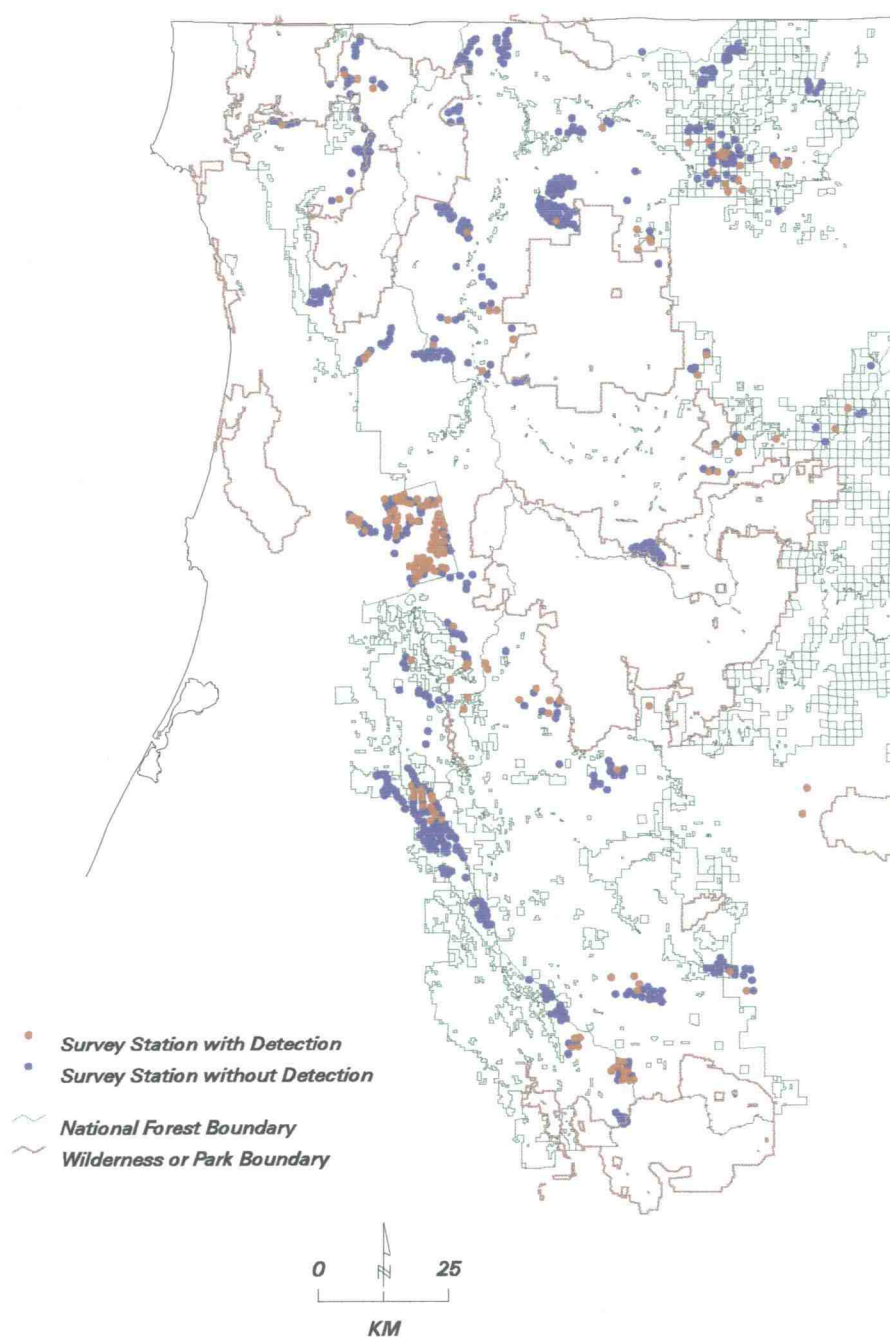
Figure 3.2 Map of survey station locations in retrospective data set.
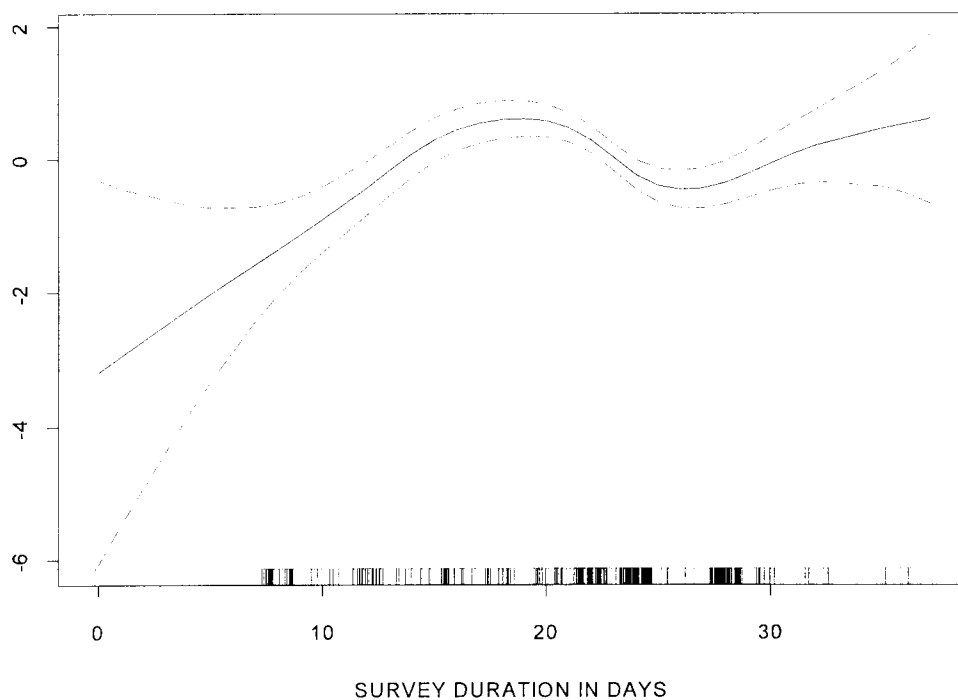
Figure 3.3 Survey duration versus function of survey duration in univariate
GAM model

Environmental variance	(Non-environmental spatial variation)	Unexplained variance	
(Non-spatial environmental variation)	Spatial Structure		
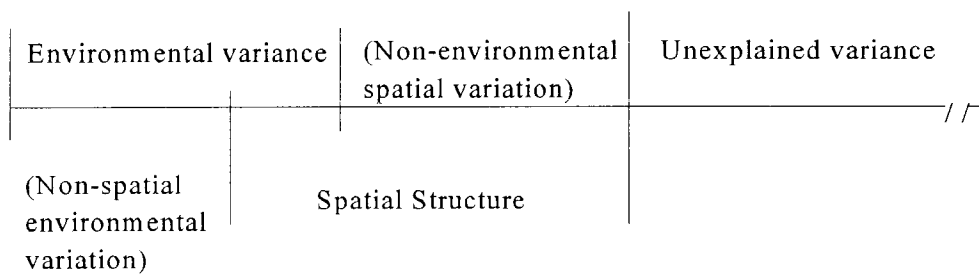
Figure 3.4 Partitioning the spatial and environmental components of variance. After
Borcard et al. (1992).

The distribution of the survey locations across the study area is highly non-uniform (Figure 3.2). Some areas have high concentrations of survey effort while large regions such as the Shasta-Trinity National Forest and private lands lack survey data. A non-uniform distribution of detections is also evident from the figure. Detections appear to be most concentrated in the central part of the region, and to decline to the north. Due to the large areas without survey data, it is difficult to generalize this conclusion to the region as a whole before model development.

3.2.2 GIS data

A variety of GIS data sources were available for analysis of the data. These included layers containing information on vegetation, roads, hydrology, precipitation, elevation, and land management category. One of the vegetation layers available was the Land Management Plan (LMP) data developed by individual national forests from timber type records as part of the forest planning process, and later standardized for use in the development of the Northwest Forest Plan (U.S. Forest Service, unpublished data). This data set covered only Forest Service lands. The second layer was developed as part of the Timberland Task Force (TTF) study (Cal. Timberland Task Force 1993). This vegetation layer is based on an unsupervised classification of Landsat Thematic Mapper (TM) imagery combined with "groundtruthing" of vegetation attributes. The extent of the TTF layer is California north of San Francisco and west of Interstate Highway 5. The classification includes both continuous and categorical vegetation attributes. The classification accuracy was estimated at 60-80% for each categorical attribute, based on

validation plots sampled by the contractor. Its intended use is limited to regional and landscape-level analysis such as performed here, rather than project level analysis (e.g. estimation of stand volume) (Cal. Timberland Task Force 1993).

GIS vegetation layers derived from satellite imagery have several advantages and limitations when compared to traditional vegetation maps based on ground surveys. The advantages include seamless coverage of multiple ownerships, standardized and replicable classification techniques, and current and updatable mapping that allows multitemporal analyses. The limitations include the fact that these layers are more appropriate for landscape and regional-level than for patch-level analysis, and that attempts to extract more than a few size or closure classes or floristic (species) differences will seriously reduce accuracy (Cohen et al. 1995).

A qualitative comparison of the two vegetation layers showed good agreement at the coarse scales used in the landscape analysis. The LMP layer, although based on ground surveys, was gathered over an extended period and intended primarily for timber inventory purposes (U.S. Forest Service, unpublished data). For these reasons, it also lacks the level of accuracy that would permit its use in patch-level analysis.

A third vegetation layer was used to extrapolate predicted habitat suitability to the Oregon Klamath Ecoprovince. This layer was supplied in a draft form by researchers at Oregon State University (W. Cohen, unpublished data). Vegetation was classified as a categorical attribute following the classes of Cohen et al. (1995). Because of the differences between these classes and the TTF class attributes, as well as the draft form of the data, predictive modeling in the Oregon Klamath is expected to have larger errors.

The attributes analyzed in the retrospective analysis included the following from the TTF data layer: density (canopy closure), TTF tree size class (Table 3.1), percent conifer, quadratic mean diameter at breast height (QMDBH) of hardwoods, CWHR Type, and CWHR Closure Class. These were analyzed at both point (or "patch") and landscape levels.

Table 3.1 TTF Size Classes.

Class	Average Tree Size
1	0 - 14 cm qmdbh
2	14 - 25 cm qmdbh
3	25 - 60 cm qmdbh
4	60 - 90 cm qmdbh
5	>= 90 cm qmdbh

The CWHR, or California Wildlife Habitat Relationships system, uses current knowledge of wildlife habitat associations to assign habitat values to vegetation types (Meyer and Laudenslayer 1988). The vegetation is classified into four closure classes, six tree size classes, and a variety of forest and non-forest floristic types. Since this system is commonly used by agency and private wildlife biologists to evaluate fisher habitat suitability for planning purposes, CWHR types were evaluated in the analysis.

Other TTF attributes that were not analyzed are: percent hardwood, QMDBH, and QMDBH of conifers. These were redundant with variables already in the analysis. In addition, several attributes from other GIS data sources were evaluated. A late-successional forest data layer was developed based on a MA of "old growth" habitat selected from the LMP layer.

Hydrologic data was available from the 3 national forests at 1:24,000 scale. It was analyzed as distance from streams. Road data for national forest lands was also available at 1:24,000 scale. This was analyzed as road density using a MA function. Road data for the entire region was only available at a coarser scale (1:100,000) and was not used in this analysis. Differences in the quality and resolution of the available data for public and private lands would have created problems for predictive modeling if these variables (roads and streams) had proved significant.

A digital elevation model (DEM) at 90 meter resolution was used to derive the elevation of survey locations (U.S. Geological Survey, unpublished data). Other variables, such as aspect and slope, could also have been derived from this source.

Mean annual precipitation was derived from a precipitation layer of the U.S. at 6 km resolution (Daly et al. 1994). This model interpolates values for the area based on weather station data and modeled effects of elevation and other variables. Because of the scarcity of weather stations in the region, its complex topography, and the coarse resolution of the layer, it is likely that the precipitation estimates contain substantial error. This would pose an obstacle to the development of predictive models for species (e.g. plants) whose distributions are more directly limited by climatic factors.

GIS layers containing information on land ownership, as well as management categories for public lands, were available at 400 meter resolution (U.S. Forest Service, unpublished data). Management category information (e.g. LSR, matrix) may be provisional due to ongoing modifications to the Northwest Forest Plan.

3.3 Analytical Approach

3.3.1 Multiple Logistic Regression (MLR)

Multiple logistic regression was chosen as the appropriate method for the statistical analysis due to the binary nature of the response variable (presence/absence). MLR, unlike discriminant function analysis, is robust to violations of multivariate normality in the predictor variables (Ramsey et al. 1994). Species distributions along environmental gradients may be expected to be show a variety of non-normal distributions for theoretical reasons, so such violations may be frequent in these types of analyses (Austin 1985).

The potential predictor variables derived from the GIS analysis were first assessed for significance in a univariate analysis. Generalized Additive Modeling (GAM) was then used to assess the need for polynomial terms in the model. GAM fits smoothed curves to the data without assumptions as to the linearity of the response (Hastie 1993).

The best multivariate model does not necessarily contain the variables that are most significant in the univariate analysis. This may be due to correlation between variables, or it may indicate that these variables have a more complex effect due to interactions with other variables. Variables that lack significance in the univariate analysis may be included in the final model due to their significance in a multivariate context. However, this would suggest caution in assigning a functional interpretation to these variables.

Stepwise model fitting, using both backward and forward selection, was used to help construct a model with good fit to the data. However, to create the final model, output from the stepwise procedure was assessed with other diagnostics as well as according to criteria such as biological significance. In addition to seeking a model with good fit to the data, the following goals influenced model selection:

1) Simplicity: models with fewer variables are better.

2) Generality: variables that are available for the entire study area and can be expected to be available for other areas are preferable. In addition, variables such as elevation and trend surface variables whose effect cannot be generalized to other areas are undesirable.

3) Interpretability: Process variables, in addition to generality, also have better interpretability. This facilitates making process hypotheses about the observed patterns.

Although p-values for the significance of individual variables were produced, the C_p statistic for inclusion of the variables provides a better comparison of sets of nested models as it controls for reduced degrees of freedom (Statistical Sciences, Inc. 1995). However, not all the comparisons in this study are between nested models. Therefore the use of other diagnostic statistics was explored.

A measure that has been used in the literature to compare alternative MLR models is a version of the R^2 statistic commonly encountered in linear regression (e.g. Bojorquez-Tapia et al. 1995). The formula is:

R^2_k = 100([log-likelihood of null model] - [log-likelihood of model k])/[log-likelihood of null model]

However, this statistic actually compares the fitted values of two models without reference to the observed data, and is thus not recommended as a measure of goodness-of-fit in the case of logistic regression (Hosmer and Lemershow 1989).

Recently, the Bayesian Information Criterion (BIC) has gained popularity as a measure for comparing non-nested models (Raftery 1994). Like the C_p statistic, BIC assesses penalties for inclusion of too many variables. Its formula is $BIC_k = L^2_k - df_k \log n$ where L^2_k is the deviance, n is the sample size, and df_k is the number of residual degrees of freedom in the model. More negative BIC values indicate better models.

3.3.2 Spatial Autocorrelation Analysis

Analysis of spatially structured data raises problems not normally addressed in multivariate analyses (Legendre 1993). If locations near one another are more similar (or different) than locations far from one another, the data violate one of the central assumptions for parametric statistical tests: the assumption of independence. Each new observation contributes less than a full degree of freedom to the analysis. This can result in spurious correlations, as "successive aggregation of regionalized variables tends to increase correlations even though correlation at the disaggregated level is zero" (Majure et al. in press). The attention focused on "pseudo-replication" in the design of field experiments recognizes the problems caused by spatial autocorrelation in environmental variables (Hurlbert 1984). However, the solutions proposed to remedy this problem, such as randomized blocks, only account for spatial structure at the scale of the block size employed (Fortin and Gurevitch 1993).

Due to these problems, various methods have been developed to detect spatial structure in ecological data. Among these is the Mantel test, which tests the degree of association between two or more distance matrices, one of which may be based on geographic distance while the others are based on dissimilarities in some other variable. Since the values in a distance matrix are not independent, randomization methods must be used to test the significance of the observed association between the matrices. This involves permuting the rows and columns of one matrix many times (usually 1000 or more) and remeasuring the correlation between the matrices. In this manner, a distribution is created against which the observed correlation value can be compared for significance (Manly 1991).

In this study, the Mantel test was used as an exploratory tool to assess the significance of the correlation between the individual variables and species presence. The test was implemented using a routine in Splus (Statistical Sciences, Inc. 1995 and J. Van Sickle, unpublished). Both the simple two-matrix test and the partial Mantel test were performed.

The partial Mantel statistic allows the correlation to be tested for significance with and without the effects of geographic distance (Smouse et al. 1986). This allows the partitioning of the correlation into components of "spatially structured" environmental variation and "non-spatial" environmental variation (Figure 3.4)(Borcard et al. 1992). Dominance of the spatial component would be a warning sign that the observed correlation may be spurious due to the effects of other variables with a common spatial structure.

For example, simple and partial Mantel tests have been used to assess the correlations between regional scale landscape patterns and the population trends of neotropical migrant birds (Flather and Sauer 1996). Because of strong spatial structure in the population densities of such highly vagile species, it was important to test for correlations both with and without the effects of geographic distance.

A second method for testing for significance in the presence of spatial autocorrelation is the CRH method (Cliford et al. 1989). The CRH method involves a modified test for the significance of the correlation between two variables at a network of sites whose spatial coordinates are known. The effective sample size used in the test is reduced (for cases of positive autocorrelation) based on a measure of the spatial covariance of the variables. This method has proved useful in distinguishing between alternate hypotheses when environmental variables show strong patchiness (Thomson et al. 1996). However, the CRH test assumes stationarity in the spatial correlation structure and should be applied with caution if strong trend or anisotropy is suspected (Cliford et al. 1989). In addition, the correlation coefficient is an aggregate measure and cannot provide information on a process that has distinct effects at different scales (Cliford et al. 1989).

The CRH modified t-test was used here to assess the significance of the observed correlations between fisher presence and environmental variables after accounting for spatial autocorrelation (Cliford et al. 1989). It was implemented by means of a Fortran routine (N. Oden and B. Thomson, unpublished). Spearman rank correlation coefficients (r_s) were chosen due to the non-normal distributions of some variables.

3.3.3 Models of Spatial Structure

Methods such as described above are helpful as exploratory tools and when the goal is limited to testing for significance in the presence of spatial autocorrelation. However, it is often more useful to create an explicit model of the spatial correlation structure of the data. This structure may be modeled as a combination of large-scale trend and small-scale variation, referred to as first and second-order effects. These are similar to the components of "spatially structured" and "non-spatial environmental" variance used by Borcard et al. (1992). However, this division of the process into first-order and second-order effects is somewhat arbitrary (Bailey and Gatrell 1995).

First-order trend may be modeled through the use of linear and higher-order polynomial functions of the spatial coordinates - a technique known as trend surface analysis (Haining 1990). Environmental variables be included as covariates at this stage. However, it may be more realistic to model them as spatially autocorrelated mesoscale or second-order variation.

The covariance structure of this second-order variation is commonly modeled by either a simultaneous autoregressive (SAR), conditional autoregressive (CAR), or moving average (MA) function (Haining 1990). The distinction between the covariance structure of a SAR and MA model is illustrated in Figure 3.5. These are counterparts of the better-known autoregressive and ARIMA models used in time-series analysis (Mathsoft, Inc. 1996)

In the majority of analyses, both the first and second-order components are unknown and must be estimated from the data. This presents difficulties in that the mean

or trend of a spatial process cannot be accurately estimated without a knowledge of the spatial covariance structure and this structure cannot be estimated without a knowledge of the mean (Bailey and Gatrell 1995). This problem can be circumvented by performing the analysis iteratively. The first-order trend may be extracted by ordinary regression of the response on variables consisting of spatial coordinates with or without environmental covariates. Then the residuals are used to estimate the covariance structure through the use of a variogram.

A variogram plots the semivariance between points separated by different lag distances (Figure 3.6). The semivariance is lowest at a lag of zero. This nugget variance represents within-site variation. In geostatistics, the nugget effect is often attributed to measurement error. However, in ecological studies a variety of sources are possible, such as temporal variation in habitat resources. The semivariance increases from the nugget until it reachs a maximum at the sill at a lag distance termed the range. Points separated by distances greater than the range are not spatially autocorrelated. A theoretical variogram drawn from one of several models (spherical, circular, exponential, Gaussian, linear) is then fit to the empirical variogram derived from the data. The accuracy of the covariance structure estimation may depend on choosing the correct theoretical variogram model (Bailey and Gatrell 1995).

SAR

☐	1.1677
▨	1.2674
▨	1.2726
▨	1.2729
▨	1.3934
▨	1.40129
▨	1.40171
▨	1.4095
▨	1.41001
▨	1.41004

Moving average

☐	1.045
▨	1.067
▨	1.090
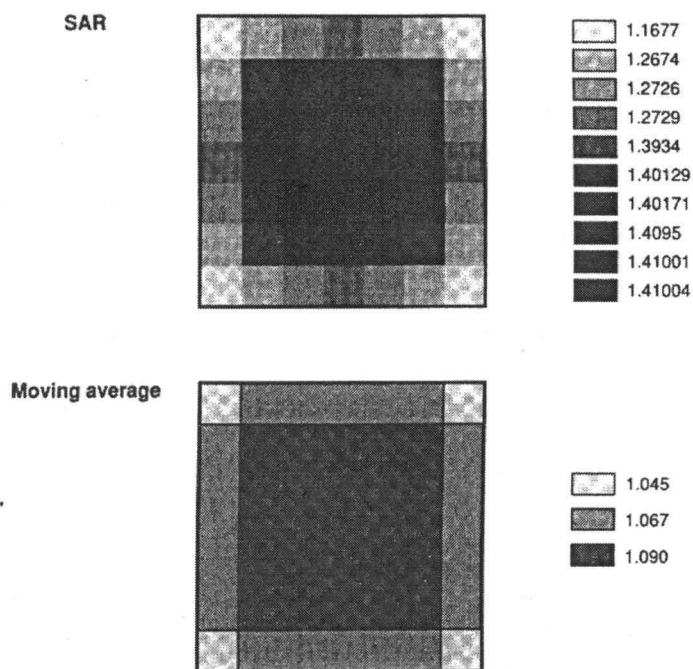
Figure 3.5 Spatial covariance structure of SAR and MA models (from Haining 1990).
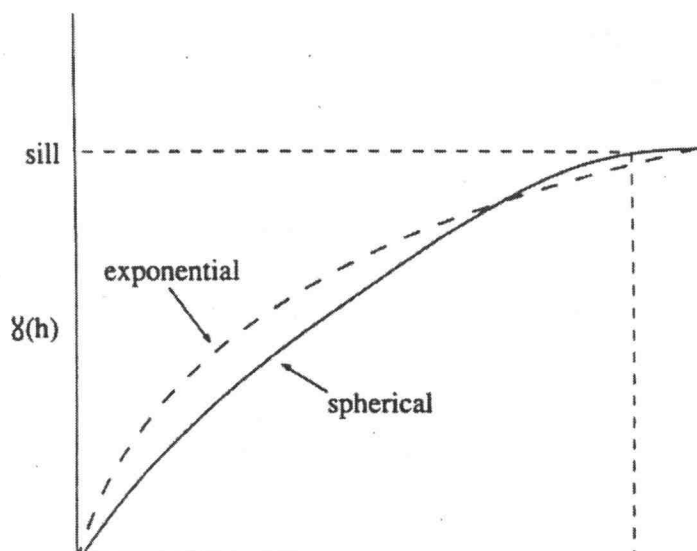
Figure 3.6 Theoretical variogram (from Bailey and Gatrell 1995).

This covariance structure may then be used to construct a weights matrix which is incorporated back into the regression model to improve the estimation of the first-order trend (Bailey and Gatrell 1995). The process is iterated until parameter estimates stabilize (Ver Hoef and Cressie 1993). This method is referred to as generalized least squares (GLS)-variogram estimation.

Kriging is an alternate method of spatial interpolation that, like GLS-variogram estimation, involves fitting a theoretical variogram to the data. Ordinary kriging requires an assumption of stationarity, that is the removal of any large-scale trend. Universal kriging relaxes this requirement and models trend and second-order effects in one step. However, if the object of the analysis is not only prediction but a functional or descriptive understanding of trends, it is better to follow a two-step process and obtain an explicit estimate of the trends (Bailey and Gatrell 1995).

Ideally, it would be possible to extend logistic regression and other forms of the generalized linear model to spatial data within the context of a spatial autoregressive model. For example, the spatial autologistic model is the spatial counterpart to logistic regression (Haining 1990). However, the non-diagonal weight matrices used in these models present problems for the model-fitting algorithms used in statistical programs (Bailey 1993). These programs use a maximum likelihood estimator (Chambers and Hastie 1993). Although the likelihood in the spatial autologistic function is intractable, it may be possible to create a model-fitting algorithm using the "pseudo-likelihood" (B. Ripley, pers. comm.). However, currently such functions are unavailable in spatial statistical software packages.

One possible solution is to perform non-spatial logistic regression incorporating

spatial coordinates as trend surface variables, with the awareness that spatial

autocorrelation may present problems for tests of significance (Bailey and Gatrell 1995).

However, this approach of modeling second-order spatial dependence as a first-order

spatial trend is not ideal. The future development of spatial generalized linear models will

allow more robust prediction and functional interpretation of spatial effects such as are

now possible with spatial linear regression models (Mathsoft, Inc. 1996).

3.3.4 Moving Average Models

The "moving-window" functions found in some GIS software (e.g. Arc-Info)

provides a method of incorporating the MA model within the logistic regression analysis

(ESRI, Inc. 1996). These functions allow the analyst to specify the shape and size of a

"window" around each cell within which the averaging of cell values will be performed.

Each cell in the input raster GIS layer is evaluated and a new layer is produced containing

the output values.

In this study, the MA function in Arc-Info (FOCALMEAN) was used to average

vegetation characteristics over a "landscape" whose size was varied during the analysis.

A series of multivariate models was created that contained vegetation variables averaged

over landscapes of varying scales. FOCALMEAN's of 10, 30, 50, 100, and 1000 km^2 in

size were evaluated, along with a model based on site level vegetation. Moving average

models were also created using the fisher habitat suitability values assigned to vegetation

types by the CWHR system. These models were then compared with the BIC statistic.

The variance in habitat suitability within the area of the "moving window" may be as biologically significant as the mean. The FOCALSTD function in Arc-Info computes the standard deviation within the analysis window in a similar fashion as FOCALMEAN computes the mean value (ESRI, Inc. 1996). This FOCALSTD value was used as a crude estimate of landscape diversity. However, it does not measure another aspect of landscape structure, the degree of spatial aggregation of similar patch types. This would require use of a landscape pattern analysis program such as FRAGSTATS (McGarigal and Marks 1995).

The MA model has weaknesses when compared with a SAR or CAR model. It is difficult to integrate the effects of multiple scales of habitat selection in the MA model as correlation quickly decays to zero with distance (Figure 3.5) (Haining 1990). The MA approach might be expected to work best for organisms that select strongly at a particular scale such as the home range and only weakly at scales above and below that.

It might seem possible to perform a multi-scale analysis by incorporating sets of variables derived from a particular attribute averaged over multiple window sizes. This approach, however, results in the creation of groups of highly collinear variables. This creates serious problems in interpretation of the coefficients. Although it would also have been possible to build models where each separate vegetation variable was averaged at a different scale, this would have limited interpretability of the results. MA analysis is also possible using a annulus, or ring-shaped window (ESRI, Inc. 1996). This would extend the technique used in Ramsey et al. (1994) to analyze landscape pattern around spotted owl nest sites and might be expected to reduce but not eliminate problems of collinearity.

A more promising method uses an "irregular" moving window which derives its size and the weighting given to various parts of the "window" from a kernel file created by the user (ESRI, Inc. 1996). This would allow the incorporation of weight matrices derived from variograms or other spatial analyses. The integration of these spatial statistical methods with GIS, however, is still in its initial stages (Bailey 1993).

3.3.5 Combining MLR and Spatial Modeling

The final strategy used in this analysis is a hybrid of several methods. In order to model fisher distribution at multiple scales, the following type of spatial model was employed. The probability of fisher detection, p, is modeled as a logistic function of three scales of variation and two sources of error.

logit (p) =
regional trends (trend surface) +
landscape (mesoscale) environmental attributes +
point ("patch") level attributes +
spatially autocorrelated error +
non-autocorrelated error (nugget variance)

The output of the MA analysis of the environmental variables was added to the MLR model to predict fisher distribution at the scale of the home range. The spatial coordinates (in a Universal Transverse Mercator (UTM) projection) were added as covariates to the environmental model to create a trend surface component corresponding to regional scale first-order variation. Models with and without the trend surface component were fitted for all environmental models.

If accurate plot level habitat measurements are available, they can also be incorporated in to the MLR equation to increase predictive power. In this study, accurate plot scale data were available for the validation field data, but not for the retrospective data set. An approximation of site or "patch" scale vegetation characteristics was derived by overlaying the survey locations on the TTF layer. These variables were assessed for significance during model fitting. However, these values can be expected to have low accuracy due to two factors: 1) inaccurate recording of the survey location, and 2) fine-scale error in the TTF layer. These fine-scale errors become less significant when the data are averaged to a landscape scale, due to the effects of the Central Limit Theorem. In the retrospective analysis, it is not possible to distinguish between lack of biological significance or data inaccuracy as the cause of any lack of significance of "patch"-level vegetation in the retrospective analysis.

If the species of interest exhibits hierarchical habitat selection, it is possible that the same resource may have contrasting effects in different habitat types (Ramsey et al. 1994). In that case, analysis of fine-scale habitat features might be performed separately, or with a method such as regression tree analysis that allows for such hierarchical effects (Clark and Pregibon 1993). In the MLR model used here, this type of cross-scale effect would be incorporated through interaction terms.

The error component can be broken into a spatially autocorrelated term as well as a non-autocorrelated nugget effect. Because a spatial covariance structure was not directly incorporated into the analysis, the residuals from the MLR model might be expected to be autocorrelated. Although this presents a problem for parameter estimation, it also means

that the residual values at a data point provide information about values at neighboring points. This information can be extracted through spatial modeling of the residuals, either through spatial autoregressive models or through kriging. Although spatial autoregressive modeling requires use of a specialized spatial statistical software (Mathsoft, Inc. 1996), a kriging function is available in some GIS software.

Residuals from the retrospective model were interpolated across the region using the KRIGING function in Arc-Info (ESRI, Inc. 1996). The exponential model was chosen as the best theoretical variogram based on examination of the empirical variogram values. The interpolated residual values obtained through kriging were then added to the predicted values from the MLR model. Results from the validation surveys were compared with the values predicted by the "MLR plus kriging" model to see if this model performed better than the MLR model alone.

3.3.6 Additional Details of Analysis

Many methods of spatial modeling are best suited for analysis of a regular lattice of points such as might result from a systematic sampling design. In retrospective studies, the data set usually consists of irregularly spaced sample sites. This may result in the model being primarily a characterization of heavily surveyed areas. One option to remedy this problem is to weight the data points during the model-fitting process. Points in areas of high sampling intensity would be weighted less than those in sparsely sampled areas. Dirichlet tesselation is an optimal method of dividing a surface into "tiles" surrounding a set of points (Figure 3.7) (Bailey and Gatrell 1995). Simple spatial smoothing methods

often interpolate values across regions defined by such Dirichlet tiles. The corners of the tiles are the midpoints of lines connecting a point with its nearest neighbors. By weighting points based on the area of their Dirichlet tiles, the effect of densely clustered points is reduced. In this study, data points were differentially weighted in the model-fitting algorithm based on the area of their Dirichlet tile. The tile area was computed by means of a function in Splus (T. R. Turner, unpublished).

However, if spatial autocorrelation drops to zero after a certain distance, we might want to place an upper limit on the weight allowed isolated points. The maximum value allowed for a Dirichlet tile in this analysis was the area of a tile surrounding a validation sample unit (approximately 60 km^2). This was an estimate of the area any one survey station could be thought to represent. This weighting method unavoidably gives high leverage to isolated points, so they should be examined during exploratory data analysis and model fitting. Cook's distance was used to assess the robustness of the model to outliers (Hastie 1993).
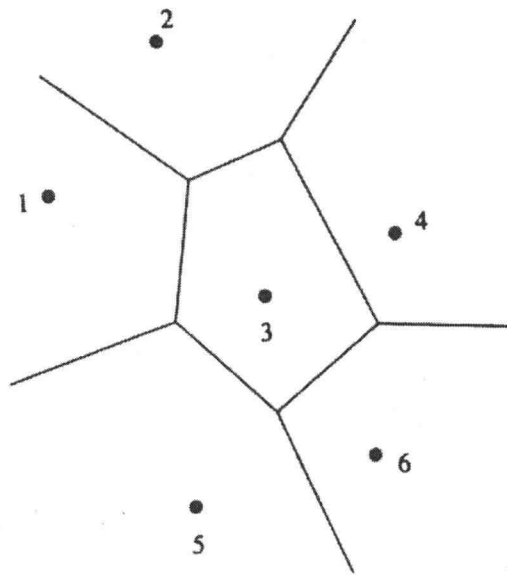
Figure 3.7 Dirichlet tesselation (from Bailey
and Gatrell 1995).
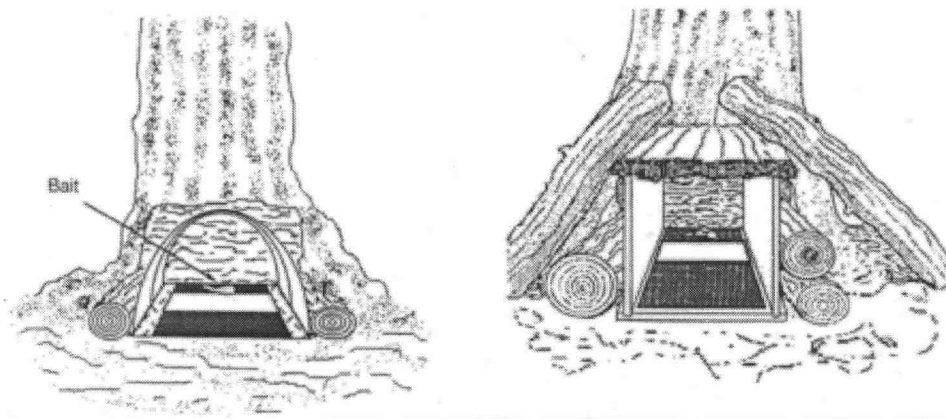
Figure 3.8 Design of trackplate stations; plastic on left, wooden on right
(from Zielinski and Kucera 1995).

3.4 Validation of Retrospective Model

3.4.1 Selection of Survey Area

A portion of the analysis region was selected as a target of the validation surveys based on lack of previous survey effort. Since little data from such an area would have been incorporated into the retrospective analysis, it would represent a stronger validation test. The area chosen covers 20% of the total area covered by the retrospective data set, but holds only 7% of the survey points in that data set (48 out of 682) (Figure 3.1).

The area covered in the 1996 validation surveys lies near the center of the analysis region. It covers approximately 2300 km^2, or about 9% of the total region and 14% of the total Forest Service land. Elevation in the survey area ranges from about 120 meters along the Klamath River to 2600 meters at the summit of Thompson Peak in the Trinity Alps. Survey station elevations ranged from 120 to 1900 meters.

The topography of the survey area is dominated by the valleys of three rivers, the Klamath, Trinity, and the Salmon, and their numerous tributaries. The higher elevations lie in four protected areas, the Trinity Alps, Marble Mountains, the Siskiyou, and the Russian Wilderness Areas. Few sample units were placed in these and other roadless areas due to logistical constraints. Large areas of the survey area burned in 1977 and 1987, particularly in the Salmon River basin.

Because over 95% of the validation survey area is in public ownership, human population density is low and there are few paved roads. The survey area is bisected in the south by State Highway 299 (2 to 4 lane) running east to west, in the north by State

Highway 3 (1 to 2 lane) running east to west, and by State Highway 96 (2 to 3 lane) running north to south. Willow Creek is the largest town in the survey area, with a population of approximately 1000 people.

3.4.2 Sampling Design and Protocol

Survey protocol generally followed Zielinski and Kucera (1995). Tracks were recorded on a Contact paper surface as animals approached the bait after crossing a sooted aluminum plate. The station enclosure was constructed of either flexible plastic with a metal base or plywood (Figure 3.8) (Zielinski and Kucera 1995). Stations were checked every other day, with an occasional delay until the third day on 17% of the visits. Sites were checked 8 times after setup, for an nominal survey duration of 16 days. Bait consisted of chicken. A commercial trapping lure was applied on the fourth visit to sample units that had not received a fisher detection at any of the 6 stations. This delay was intended to avoid weakening inferences about plot-level habitat associations due to long-distance attraction by the lure.

The sampling design used in the validation surveys was a nested design based on a systematic grid. The National Forest Inventory (NFI) grid is a system of locations covering all public forest lands in the U.S (U.S. Forest Service, unpublished data). It is similar to the sampling designs developed by other agencies (e.g. the U.S. Environmental Protection Agency's EMAP program) in that it is based on a surface of hexagonal cells (Stevens 1994). The cells form a nested hierarchy so that different sampling scales can be chosen by selecting a systematic subset of the cells. The smallest cells have a diameter of

1.35 km. Point locations are randomly selected within these smallest cells to permit probability-based inference about the cell as a whole and to avoid coincidence of multiple points with linear landscape features such as ownership boundaries. This has been termed a tesselation stratified design. The randomization element incorporated into the NFI grid allows incorporation of some of the benefits of random sampling, such as design-based estimates of variance (Stevens 1994).

The NFI grid itself contains points separated by 5.4 km.(Figure 3.9). Our validation sampling design selected alternate NFI points, resulting in a interpoint distance of approximately 10.8 km.. This distance was selected to insure that the same individual fisher would not be detected at more than one sample unit. This assumption was most critical for a companion objective of the surveys, to test a statewide monitoring program (Zielinski and Stauffer 1996).

Systematic sampling was chosen over the alternative of random or stratified random sampling because of its superiority in estimating spatial trends. Haining (1990) states that "[a]lthough in certain cases systematic sampling may prove impractical or too costly, the theoretical evidence stresses the superiority of systematic sampling in a variety of spatial situations"(Haining 1990). Simple random sampling is rarely optimal in these types of surveys (Neave et al. 1996). Stratified random sampling may be preferable when spatial variation is highly discontinuous or periodic, allowing the area to be divided *a priori* into dissimilar regions (Haining 1990). Due to the lack of *a priori* knowledge of habitat associations, it is doubtful that this type of stratification would be optimal.

KLAMATH NF

REDWOOD NATIONAL PARK

EUREKA

SHASTA-TRINITY NF

SIX RIVERS NF

- NFI Grid Point
- NFI Point Surveyed in 1996

Extent of Retrospective Data Set
National Forest Boundary
Wilderness or Park Boundary

0   25

KM
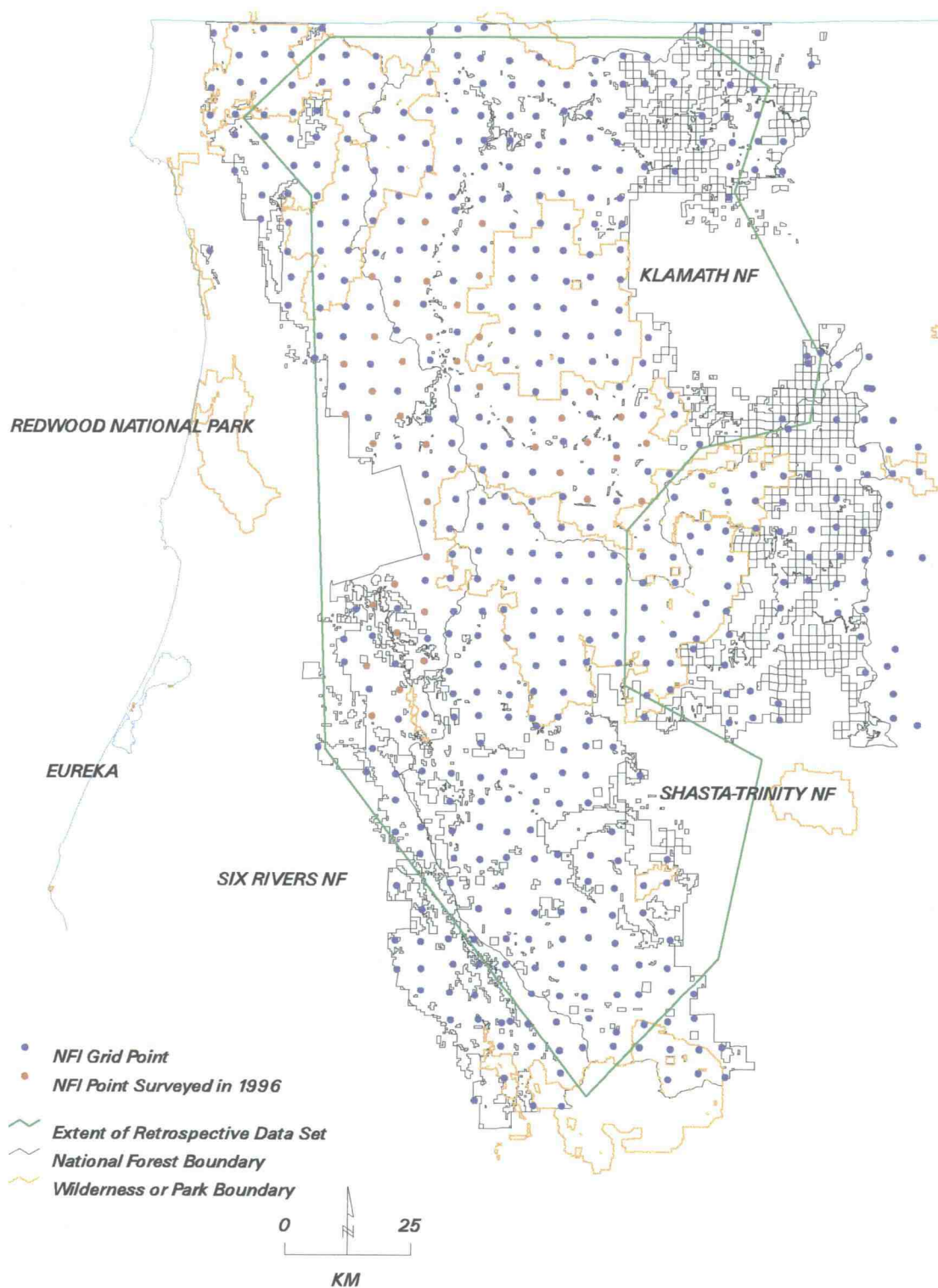
Figure 3.9 National Forest Inventory (NFI) grid sampling locations for study area.

The "gradsect" concept proposes that in order to optimize the information content of a survey, survey locations should be arrayed in a transect located along the steepest environmental gradients in the region (Austin and Heyligers 1991). These gradients are identified based on auxiliary data or the results of pilot surveys. The approach used in this study is an attempt to combine the strengths of systematic sampling with those of the gradsect approach. Although *a priori* knowledge of an optimal stratification was lacking, it was possible to identify several gradients from the retrospective analysis that could be incorporated into such a gradsect sampling design.

The gradients sampled include the decline in regional mean as one moves from the central to northern parts of the region, the coastal to inland gradient, and a mid to high elevation gradient. The latter two gradients sample a transition in forest community type, allowing investigation of how habitat associations change with floristics.

Six trackplate stations were arrayed in a regular pattern around each NFI sample unit surveyed. Five stations were arrayed at equal intervals along the perimeter of a circle with a 500 meter radius centered on the NFI point, which held the sixth station (Figure 3.10). This improved the likelihood that fishers whose home ranges contained the sample unit would not escape detection. This hierarchical sampling design also allowed the multiple-scale analysis of landscape versus plot-level habitat selection. Systematic-cluster designs such as this one are effective at detecting spatial structure when the scale of variation is not known *a priori* (Fortin et al. 1989).

A significant weakness of the retrospective analysis was the inability to analyze the importance of point or "patch"-level habitat association due to the poor fine-scale resolution of the GIS vegetation layers. This was a motivation to gather detailed vegetation data at each station location. Vegetation data collected at validation survey locations could be used to assess the significance of plot-level habitat associations, albeit with limitations caused by the smaller data set. It is also difficult to say how well data gathered at a plot scale of approximately 0.05 ha represents the characteristics of a patch, either as defined by the human observer or as perceived by the organism. This may be expected to vary between attributes (e.g. the downed log resource may be perceived at a different scale than canopy closure).

Site variables were measured at one of two scales (Table 3.2). Two perpendicular 25-meter transects were placed at a arbitrary azimuth and centered on the trackplate station (Figure 3.11). Canopy closure (measured with a densiometer) and log tally by size class were measured at this scale. DBH and condition of all snags and trees by species were measured for a variable radius plot consisting of the "in trees" recorded by a 20 factor prism (Wenger 1984). An estimate of basal area was derived from the prism count. Ocular estimates of tree and shrub cover by species, CWHR type, size class and closure class, approximate distance to water, logged areas, and roads were also recorded, as were aspect and slope. The geographic coordinates of station location were recorded either by means of a geographic positioning system (GPS) or by visual referencing to a Digital Ortho Quad (DOQ).
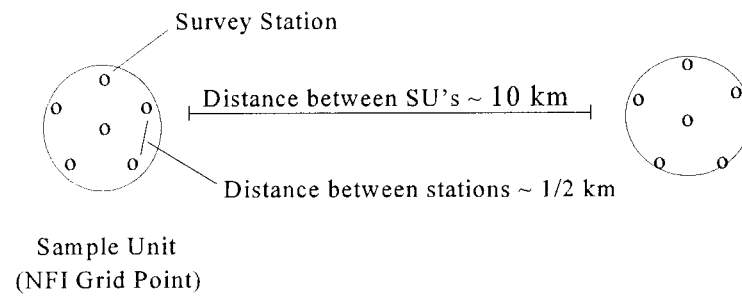
Figure 3.10 Multi-level forest carnivore sampling design.
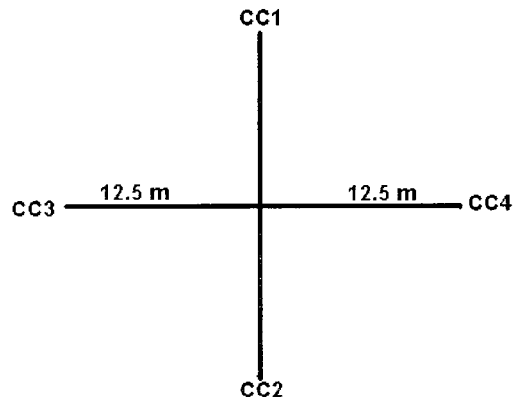
Figure 3.11 Vegetation sampling transect layout.

Table 3.2 Plot-level vegetation attributes measured in validation surveys

Attribute	Measuring device
Location	GPS or DOQ
Elevation	altimeter
Slope	clinometer
Aspect	compass
Tree composition of variable radius plot	wedge prism (20 factor American)
Tree diameter at breast height	dbh tape
Canopy closure	concave densiometer, 25m transects
Log tally	25m transects (see Figure 3.11)

Ocular Estimates of:

CWHR Type, CWHR Size Class, and CWHR Closure Class

Potential Natural Vegetation (PNV) Series/Sub-series

Micro-slope position

Canopy closure of overstory trees

Canopy closure of understory trees

Shrub cover, total and of three most abundant shrubs by species

Species, height, and condition class of trees in variable radius plot

Distance to water, road, and logged areas

The detailed plot-level data collected at the validation sites allows an assessment of the significance of plot-scale habitat association that was not possible with the TTF data used in the retrospective analysis. When comparing sites with and without detections, three types of comparison are possible. Their appropriateness depends on the nature of the question being asked.

Comparisons can be made:

1) Across all 40 sample units (SUs). This looks at whether plot-level attributes alone are useful to predict fisher presence.

2) Across the 27 SUs that received a detection at one or more station. This examines the significance of plot-level variation in predicting which stations in an occupied SU will receive detections.

3) Across the 17 SUs where lure was not applied (because they received detections before approximately the fourth visit). Long-distance attractants may obscure the effects of plot-level habitat selection. However, along with the reduction in sample size comes a loss of power to detect associations.

3.5 Prediction to the Oregon Klamath

The distributional limits of the regional population of fishers encompass both northwestern California and southwestern Oregon (Powell and Zielinski 1994, Zielinski et al. 1996). In order to understand the regional dynamics and viability of this population, an estimate of fisher distribution in Oregon is required. Although there are incidental sightings in southern Oregon, survey data of the type used in the retrospective analysis in California are lacking. Therefore distribution must be predicted based on California data. Unfortunately, the vegetation layer available for Oregon uses a different vegetation classification scheme than the California TTF layer. Therefore, although extension of the predictive model to Oregon is a valuable exercise, the accuracy of the predictions may be limited.

The categorical attributes in the Oregon vegetation layer were assigned values for the three TTF vegetation attributes (density (canopy closure), tree size class, and percent conifer) based on the mean value shown by the retrospective data falling in that class. Classes are as described in Cohen et al. (1995). For example, a pixel that belonged to the class of "closed mixed" class would receive a canopy closure value of 91.0% based on the California data (Table 3.3). FOCALMEAN's were then performed on the grids of

reclassified values. The resulting MA values were then entered into the California-based

model to derive a predictive map.

Validation of the Oregon predictions will be performed in the 1997 field season

through extension of the NFI-based sampling design to the Siskiyou National Forest

lands in coastal southwest Oregon. The results of this validation will improve our

functional understanding of the predictive model, especially the regional component, and

will strengthen efforts to manage for regional viability of forest carnivore populations in

the Klamath region as a whole.

Table3.3 Crosswalk between Oregon and TTF GIS vegetation data. Values were
assigned based on the mean value of sites in that class in the retrospective data set.
Class boundaries for the Oregon data are as described in Cohen et al. (1995).

TTF value assigned for:	Density	Tree size class	Percent conifer
Oregon vegetation class:			
Background, cloud, toposhadow	no data	no data	no data
Water	0	0	0
Open	16.8	0.86	45.6
Semi-closed	63.0	2.50	74.9
Closed mixed	91.0	2.94	60.0
Closed young conifer	90.6	2.7	94.5
Closed mature conifer	89.8	4	94.9
Closed old conifer	89.8	5	94.9

4. Results

4.1 Univariate Analysis

The data set used in the retrospective analysis consisted of data from 682 survey locations. As an initial comparison, descriptive statistics (median, mean, standard deviation) were used to compare locations with detections to those without detections (Table 4.1). These were tested for significance by means of a t-test and the non-parametric Wilcox rank sum test.

Among the vegetation variables, density (canopy closure), percent conifer, and quadratic mean diameter at breast height (QMDBH) of hardwoods showed significance at both point ("patch") and landscape scales. Among the abiotic variables, elevation and precipitation were significant. There was a significant spatial gradient represented by UTM Northing. UTM Easting was significant only in the non-parametric test.

4.2 Results of Correlation Analysis and CRH Test

A matrix of Spearman correlations between the variables was created and tested for significance with both standard and CRH modified tests (Table 4.2). As expected, moving average indices for landscapes of different sizes were highly intercorrelated, though this was not as true of their correlations with the "patch" level variate (Table 4.3). QMDBH of conifers was highly correlated with overall QMDBH. None of the other correlations between variables was greater than 0.72. However, eight combinations of variables showed correlations greater than 0.6 (table 4.4). Most of these have self-evident explanations. Density and precipitation decrease along the west-east gradient. Conifers

increase and the QMDBH of hardwoods decreases as elevation increases. Density and percent conifer are positively correlated with tree size class at the "patch" level. More interestingly, density is correlated with tree size class and hardwood QMDBH at the landscape level.

Several of the correlations between these variables are highly significant using the uncorrected sample size. However, when tested for significance using the effective sample size derived by the CRH method, many of these correlations lose their significance. Density is the only attribute that remains significantly correlated with fisher presence in the CRH test ($p = 0.05$). This is despite the fact that the magnitude of the correlation of density with fisher presence is less than that of the density or hardwood QMDBH MAs before the CRH correction. The reduction in effective sample size is greatest in the MA variables due to the effects of the spatial averaging process. This suggests caution when interpreting the significance of correlations between variables derived from the MA models. Increased correlation at coarser scales may be due to increased biological significance of landscape-level effects or to high apparent predictability (*sensu* Wiens 1989c) due to increased autocorrelation.

Table 4.1. Univariate comparisons of variables for survey locations with and without fisher detections from retrospective analysis. Medians are followed by means with standard deviations in parentheses.

Variable	Sites with detections	Sites without detections
Vegetation:		
Density (%)	76.3, 65.6 (27.7)[a,b]	63.7, 58.2, (25.5)
TTF Tree Size Class	2.00, 2.32, (1.13)	2.00, 2.30 (1.09)
Percent Conifer	67.4, 63.9, (24.9)[a,b]	74.0, 69.0 (25.9)
Quadratic Mean DBH (cm)	48.8, 49.5 (18.8)	47.8, 49.5 (17.8)
QMDBH Conifer (cm)	54.9, 56.1 (21.1)	52.8, 54.4 (19.1)
QMDBH Hardwood (cm)	18.5, 18.3 (11.7)[a,b]	13.0, 14.2 (11.2)
10 km2 MA's:		
Density MA	69.6, 66.7 (11.5)[a,b]	61.9, 60.5 (11.2)
Tree Size Class MA	2.25, 2.29 (0.34)	2.28, 2.28 (0.36)
Percent Conifer MA	64.3, 65.7 (9.6)[a,b]	67.8, 67.4 (9.6)
QMDBH Hardwood MA	18.8, 17.8 (5.6)[a,b]	16.0, 15.7 (5.3)
LMP Old Growth MA[1,2]	0.16, 0.21 (0.19)	0.15, 0.19 (0.15)
Abiotic:		
Elevation (meters)	1008, 987 (404)[a,b]	1137, 1122 (375)
Annual precipitation (mm)	1493, 1438 (424)[a,b]	1550, 1551 (517)
Road density MA[1] (km/km²)	1.99, 2.09 (0.82)	1.85, 1.93 (0.80)
UTM Easting	451510, 465592 (26664)[b]	462105, 468245 (24637)
UTM Northing	4552680, 4554976 (48386)[a,b]	4588455, 4570093 (62429)
Distance to water[1] (meters)	188, 234 (183)	242, 269 (191)
Survey duration	22, 24.4 (8.3)	24.0, 26.8 (13.0)

n = 682, 174 (25.5%) with detections
Superscripts indicate significance at 0.05 level for
a t-test, b Wilcox rank sum test
1 Data only available for locations on Forest Service lands (n = 551, 94 (17.1%) with detections)
2 Expressed as proportion of area in selected "old-growth" timber types

Table 4.2 (Following page) Correlation analyses for the sites used in the retrospective
model (*n*=682). Spearman correlation coefficients are below the diagonal, while
above it are the uncorrected significance values, followed by the values derived by
the CRH test. Values retaining significance at the 0.05 level are marked in
boldface. Effective sample size determined by the CRH test in is parentheses
below each comparison. Fifteen distance classes were used for the CRH analysis.
The upper boundaries of the classes increased in 15 km increments from 15 km to
a maximum of 225 km.

Table 4.2.

	1	2	3	4	5	6	7	8
1)Fisher presence		**0.000->0.050** (114)	0.000->0.101 (34)	0.026->0.186 (233)	0.043->0.529 (64)	0.205->0.514 (191)	0.970->0.991 (62)	0.000->0.093 (60)
2)Density	0.194		**0.000->0.000** (52)	**0.000->0.000** (444)	0.096->0.436 (162)	**0.000->0.000** (273)	**0.000->0.001** (124)	**0.000->0.003** (71)
3)Density MA	0.286	0.523		0.258->0.494 (262)	0.001->0.321 (63)	**0.000->0.017** (106)	**0.000->0.000** (41)	**0.000->0.003** (17)
4)Percent Conifer	-0.086	0.201	-0.044		**0.000->0.000** (203)	**0.000->0.000** (461)	**0.000->0.001** (243)	**0.000->0.000** (679)
5)Conifer MA	-0.079	-0.064	-0.124	0.401		**0.000->0.004** (198)	**0.000->0.000** (62)	**0.000->0.000** (148)
6)Tree size class	0.049	0.652	0.251	0.561	0.209		**0.000->0.000** (157)	**0.000->0.048** (126)
7)Size Class MA	-0.001	0.315	0.607	0.225	0.508	0.386		**0.000->0.005** (59)
8)Hardwood MA	0.217	0.372	0.708	-0.151	-0.398	0.191	0.372	

Table 4.3 Correlations (Pearson's) between vegetation variables at different scales

	Density	10km^2 MA	30km^2 MA	50km^2 MA
10km^2 MA	0.4718717			
30km^2 MA	0.4116558	0.9489205		
50km^2 MA	0.3806065	0.8975936	0.9772796	
100km^2 MA	0.3540646	0.8504375	0.9434282	0.9789827

	Tree Size Class	10km^2 MA	30km^2 MA	50km^2 MA
10km^2 MA	0.3779005			
30km^2 MA	0.3221103	0.9397629		
50km^2 MA	0.3039179	0.8704566	0.9577382	
100km^2 MA	0.2659872	0.8120712	0.9096405	0.9552665

	Percent Conifer	10km^2 MA	30km^2 MA	50km^2 MA
10km^2 MA	0.3705977			
30km^2 MA	0.3242036	0.9521109		
50km^2 MA	0.3077279	0.8943232	0.9676776	
100km^2 MA	0.2853937	0.8369026	0.9282571	0.9660954

Table 4.4. Largest correlations between model variables.

Correlation coefficient:	Spearman's	Pearson's
Density: Tree size class	0.66	0.71
Density MA: UTM Easting	-0.69	-0.68
Density MA: Tree size class MA	0.61	0.62
Density MA: QMDBHHDW MA	0.71	0.71
Percent conifer: Tree size class	0.57	0.61
Percent conifer MA: Elevation	0.68	0.70
QMDBH Hardwood MA: Elevation	-0.50	-0.58
QMDBH: QMDBH Conifer	0.96	0.96
Annual Precipitation: UTM Easting	-0.60	-0.67

4.2 Results of Mantel Test

The results of the Mantel tests indicate a strong spatial structure to the environmental data (table 4.5). All three of the distances derived from the vegetation attributes are significantly correlated with geographic distance, although this is not true of the fisher presence variable. In addition, these three variables show significant intercorrelation even after the effects of geographic distance are subtracted. Thus they show both "non-spatial" and "spatially-structured" variation in the sense of Borcard et al. (1992). Density is the only attribute whose attribute distance is significantly correlated with fisher presence, both with and without the effects of geographic distance. This confirms the results of the CRH analysis. However, the regression coefficients in a non-linear model such as multiple logistic regression (MLR) may show higher significance values than those evident in univariate correlation tests such as used above, due to the binary nature of tthe presence/absencce variable.

These results indicate that the use of more than one of the vegetation attributes in a multivariate model may create multicollinearity problems. They also indicate that spatial autocorrelation is likely to reduce the accuracy of the standard significance tests used in model fitting. Spatial structure common to the three vegetation variables increases the difficulty of isolating the cause of any correlations with fisher presence.

Table 4.5. Results of simple and partial Mantel tests on retrospective data. Simple two-matrix Mantel correlation statistics on distance matrices and associated probabilities are reported below the diagonal. Partial Mantel statistics (derived by the Smouse-Long-Sokal method (Smouse et al. 1986)) and associated probabilities are reported above the diagonal. In the partial Mantel tests the residuals from regression on the geographic distance matrix were used in order to test for correlation after accounting for the effects of geographic distance.

	Fisher presence	Density	Percent Conifer	Tree size class
1)Fisher presence		0.0539 0.002	0.0033 0.409	-0.0250 0.913
2)Density	0.0515 <0.001		0.1271 <0.001	0.3670 <0.001
3)Percent Conifer	0.0028 0.432	0.1311 <0.001		0.3004 <0.001
4)Tree size class	-0.0028 0.943	0.3551 <0.001	0.3026 <0.001	
5)Geographic Distance	-0.0142 0.875	0.1333 <0.001	0.0993 <0.001	0.0392 <0.001

4.4 MLR Model Fitting

The density MA consistently showed high statistical significance in the multivariate models. This confirms the results of the CRH and Mantel tests. After the addition of this variable, several other variables such as the QMDBH hardwood MA and elevation variables became non-significant ($p = 0.59$ and 0.48, respectively).

Seasonal effect as measured by the survey starting date was highly significant in a univariate logistic regression model. Modeled as a quadratic function, the lowest predicted probabilities of detection occurred during the summer months. The univariate seasonal model achieves a Cp reduction of 8.2% from the null model. However, when added to the multivariate model, it reduces the Cp by only 0.3-0.7%, becoming non-significant in the spatial model and marginally significant in the non-spatial model. The residual plot also shows no pattern due to season after the effects of vegetation variables are accounted for, both for the retrospective data (figure 4.1), and for the validation survey data (figure 4.2).

The MA variables selected in final MLR model were functions of canopy closure, tree size class and percent conifer. GAM assessment suggested that regional variation should be modeled with a linear term for UTM Easting and a quadratic function for UTM Northing. An alternate model was created containing the annual precipitation variable in place of UTM Easting. This alternate model did not give as high a level of fit to the data. BIC of the alternate model was -3918 versus -3951 for the UTM Easting model. BIC of null model was -3738. However, since the substitution of a more
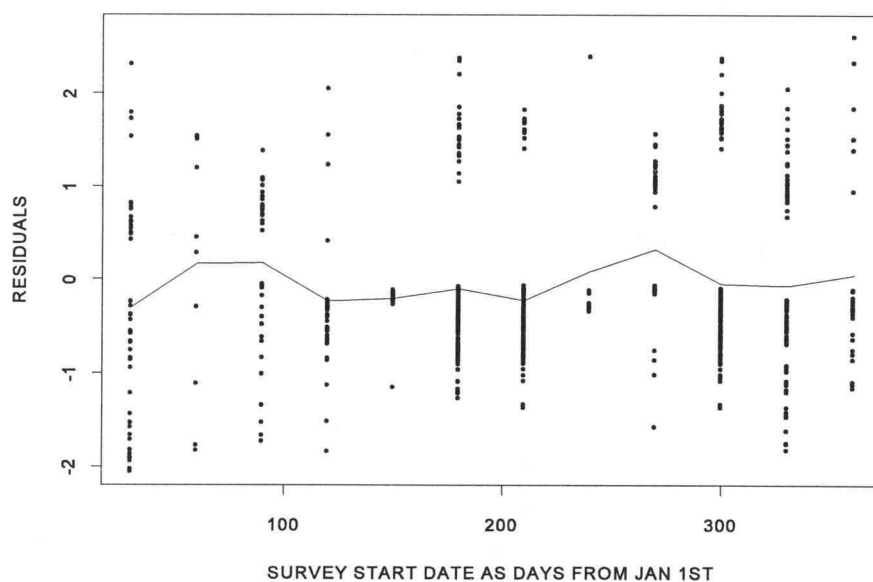
Figure 4.1 Survey start date versus residuals from MLR Model 1
(retrospective data set)
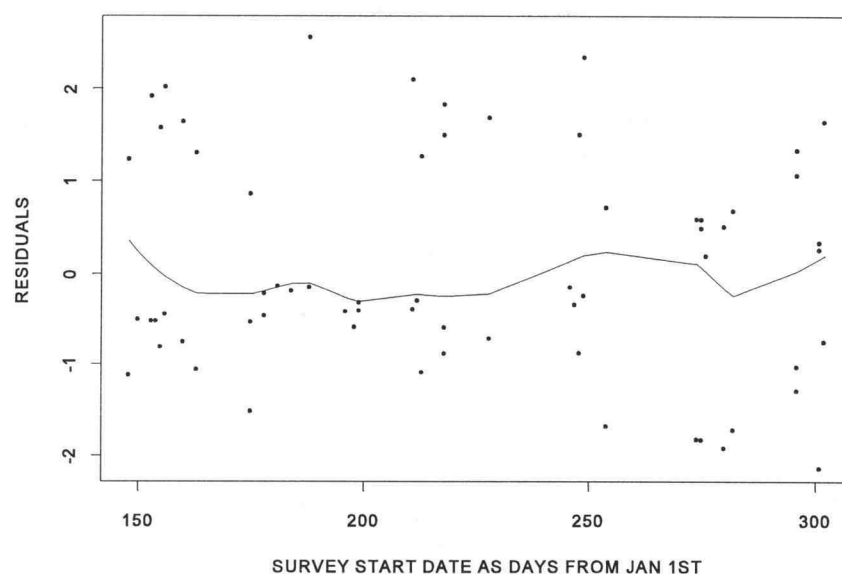
Figure 4.2 Survey start date versus residuals from validation data
(observed values - predicted values from MLR Model 1)

process-oriented variable may result in improved generality (Austin and Meyers 1996), both models were retained for further evaluation.

Two interaction terms were included in the model: canopy closure with percent conifer and tree size class with either UTM Easting or precipitation. The equations for the final models were:

Model 1: logit (p) = DENMA + SIZEMA + CONMA + UTME + UTMN + UTMN^2

+ DENMA*CONMA + SIZEMA*UTME

Model 2: logit (p) = DENMA + SIZEMA + CONMA + PRECIPANN + UTMN

+ UTMN^2 + DENMA*CONMA + SIZEMA*PRECIPANN

where DENMA = density MA, SIZEMA = tree size class MA, CONMA = percent conifer MA, and PRECIPANN = annual precipitation. Model coefficients and significance values are reported in table 4.7 and table 4.6, respectively. The probability values are then calculated from the logit value by the equation: $p = 1 / (1 + e^{-logit(p)})$.

The best fitting model (Model 1) achieves a 35% reduction in the Cp statistic.[2] Models using MA variables without the trend surface component achieved a 23% reduction. Trend surface models achieved 21 to 24% reduction, depending on the order of polynomial. Evaluation with the BIC gave a similar result, with the combined model (BIC = -3951) superior to either the MA or trend surface model alone (BIC = -3901 and -3894, respectively). BIC of the null model was -3738.

---

[2] While the C_p statistic does not give as intuitive a sense of the strength of a single model as does the R^2 statistic in linear regression, it is useful for comparisons between alternative nested models.

Table 4.6 Significance values of model coefficients derived from Chi-squared test.

	Model 1	Model 2
Density MA	0.00000000	0.00000000
Size Class MA	0.00151813	0.00151813
Conifer MA	0.05587638	0.05587638
UTM Easting	0.00000000	-
Precipitation	-	0.00000122
UTM Northing	0.01557176	0.01080693
UTM Northing^2	0.00000013	0.00930940
Density MA * Conifer MA	0.00355502	0.00016618
Size Class MA * UTM Easting	0.00000696	-
Size Class MA * Precipitation	-	0.00063786

BIC values were used for comparisons of the series of non-nested models representing different scales. The best (most negative) BIC was achieved by the combined model at the 10 km² scale (figure 4.3). The "patch"-level model had the lowest explanatory power. WHR models performed poorly at all scales when compared to the vegetation MA models.

Comparison of models at multiple scales showed density to be significant at all scales. Tree size class was only significant at landscape scales. These conclusions are tentative for "patch" scales due to the inaccuracy of the TTF vegetation data. The FOCALSTD attributes did not prove to be significant, either as main effect terms or in interaction with the FOCALMEAN variables.
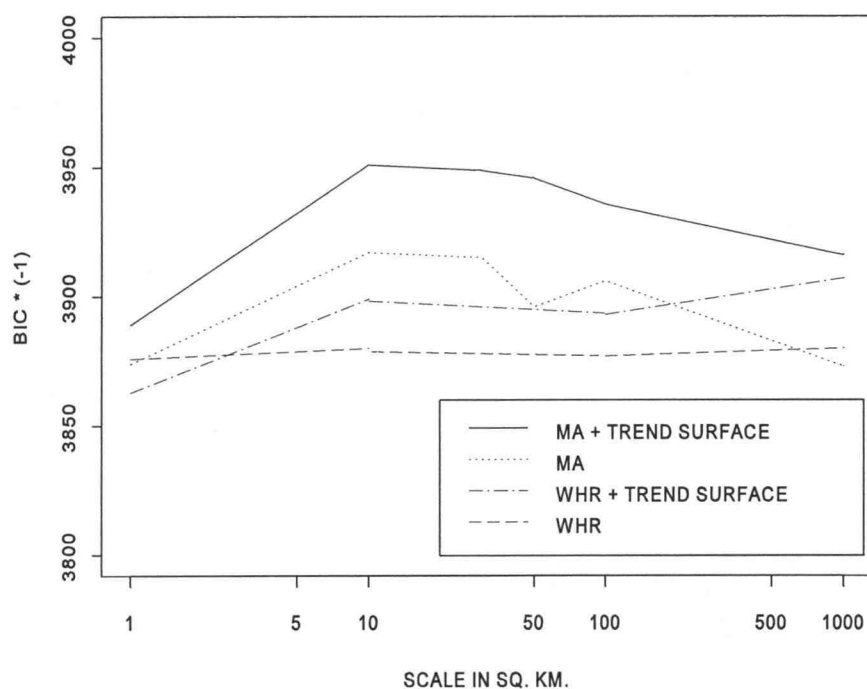
Figure 4.3 Model scale versus BIC value. Trend surface models
        include both UTM Easting (linear term) and
        UTM Northing (quadratic term).

Table 4.7. Comparison of variable coefficients of alternate models. BIC values and
validation correlations of models at both 10 km^2 and 30 km^2 are given at tthe
bottom of the table. BIC of null model = -3738. Models 1 and 2 are as in the text.
Model 1 is a MA and trend surface model, with weights, and Model 2 is similar,
but with precipitation substituted for UTM Easting. Model 1a is a version of
Model 1 without weights, whereas Model 1b is a version with weights and
without outliers. Model 3 is similar to Model 2, but without the SIZE MA
interaction term. Model 4 is a weighted model with only the MA attributes and no
trend surface variables.

Table 4.7

Model:	1	1a	1b	2	3	4
Variable						
Intercept :	-4894	-5040	-4727	-2401	-1591	-30.76
Density MA :	0.6169	0.5654	0.7539	0.6023	0.5320	0.5630
Tree Size Class MA :	44.24	51.49	39.24	-12.07	-3.992	-3.650
Percent Conifer MA :	0.4282	0.4208	0.5415	0.4911	0.4322	0.4439
Annual Precipitation:	-	-	-	-0.01307159	$-1.348*10-3$	$-1.53*10-3$
UTM Easting :	$2.972*10-4$	$3.184*10-4$	$2.789*10-4$	-	-	-
UTM Northing :	$2.089*10-3$	$2.152*10-3$	$2.014*10-3$	$1.059*10-3$	$6.946*10-4$	-
UTM Northing 2:	$-2.310*10-10$	$-2.382*10-10$	$-2.226*10-10$	$-1.176*10-10$	$-7.719*10-11$	-
Den. MA* Con. MA:	$-5.264*10-3$	$-4.761*10-3$	$-6.693*10-3$	$-6.251*10-3$	$-5.726*10-3$	$-6.161*10-3$
Size MA* UTME :	$-1.079*10-4$	$-1.228*10-4$	$-9.864*10-5$	-	-	-
Size MA* Precip.:	-	-	$5.004*10-3$	-	-	-
BIC	-3951	-3832	-3880	-3918	-3913	-3917
Correlation with validation data	0.58	0.61	0.56	0.54	0.55	0.48
<u>Version with 30km² MA's</u>:						
BIC	-3949	-3826	-3868	-3922	-3914	-3915
Correlation with validation data	0.68	0.54	0.54	0.60	0.60	0.51

Assessment of outliers was conducted using Cook's distance for the best fitting model (Hastie and Pregibon 1993). Fifteen sites with the highest leverage were identified. They were isolated points located on the eastern and northwestern edges of the data set. Removal of these points from the original data set of 682 locations increased the fit of the model. In order to assess the influence of data weighting and outlier removal, the magnitude of the coefficients in the alternate models can be compared (table 4.6).

Data weighting increased the explanatory power of the model substantially, and outlier removal did so to a lesser extent. Outlier removal generally increased the magnitude of the variable coefficients. However, the UTM northing trend surface component decreased in magnitude. All variables retain their significance in alternate models, with the exception of the percent conifer MA main effect. This variable should be retained, however, because of the significance of its interaction term.

Outlier removal may be helpful in some instances in order to generate a more robust estimation of parameters. However, it is necessary to examine the outliers to understand limitations on the generality of the model. If influential points are part of the population of interest, they may be indicating that the model poorly represents those portions of geographic or environmental space. In this case, the outliers lie on the spatial extremes of the data set. They owe their influence to non-linearities in the trend surface components of the model, especially the west/east gradient. These trends may weaken at the boundaries of the study region, and removing outliers would magnify errors in extrapolating to these boundary areas.

To measure classification accuracy for a binary response, a cutpoint predicted probability is chosen that gives the lowest errors of commission and omission (Hosmer and Lemershow 1989). A rate of correct classification can then be calculated. At an optimal cutpoint of 0.24, Model 1 and Model 2 had correct classification rates of 78.9% and 80.4%, respectively (Table 4.8)[3]. It can be seen from the table that sites predicted to have detections are more likely to be misclassified than are those predicted to be without detections. This low "positive predictive value" is an inevitable consequence of the relative rarity of the sites with detections (Sokal and Rohlf 1995).

However, this type of model diagnostic ignores the magnitude of the misclassification errors. If a station with no detections has a high predicted probability, it represents a more serious error than if it has a predicted probability just above the cutpoint. For that reason, alternate diagnostic statistics such as the Cp statistic may be more informative.

Table 4.8 Classification table showing performance results for Model 1and Model 2 (in parentheses) with retrospective data. Cutpoint = 0.24

Observed	Classified Presence	Absence	Total
Presence	102(98)	72(76)	174
Absence	72(58)	436(450)	508
Total	174(156)	508(526)	682

[3] For comparison, a random model with the observed detection ratio (0.26) would result in a 62% correct classification rate. Such a random model, however, would be expected to perform much more poorly with the validation data set, which is likely to have a different detection ratio.

Examination of the empirical variogram of the residuals showed spatial autocorrelation to a range of 11 km (figure 4.4). Nugget variance was 0.1 and sill variance was 0.2. A dropoff in the semivariance at distances beyond the range may indicate residual periodic trend or patchiness not incorporated in the model (Legendre and Fortin 1989). However, the small difference between nugget and sill variance may instead suggest that autocorrelation is not significant. An exponential model was chosen as the theoretical variogram, although no variogram model fit the empirical values well. The GIS layer of interpolated residual values shows large areas of high estimation error (Figure 4.6). This indicates that autocorrelation at the scale demonstrated in the kriging analysis, while possibly useful for fine-scale interpolation in areas with substantial survey effort, will not be useful in improving accuracy of model estimates in the large regions without any survey effort. Incorporation of the kriged residuals did not significantly improve predictive ability for the validation survey area. A plot of the kriged residuals against the observed validation residuals shows non-significant correlation (Figure 4.5) (r_s = -0.10 and -0.15 for Model 1 and Model 2, respectively). This absence of significant residual spatial autocorrelation, indicating that the spatial structure of the response variable has been satisfactorily explained by the model, has been found in other studies (e.g. Jager and Overton 1993).

4.4 Validation Results

Validation of MLR model was performed with new data from 1996 surveys, as well as more qualitatively with watershed level data from areas which lacked available

station-level survey data. The watershed level data appears qualitatively consistent with the model. For example, trackplate sample units surveyed in Redwood National Park, an area of high detection probability in our model, all received detections (Beyer and Golightly 1995). The coastal timber lands where fishers were detected by R. Klugh (unpublished data) also appear to have relatively high probability of fisher presence in our model (Figure 4.7 and Figure 5.7). Additional support is provided by trackplate surveys conducted near Trinity Lake (central eastern Klamath), which had a mean detection rate of 0.13 to 0.18 (Dark 1997). Model 2 correctly predicts a detection rate of 0.1 to 0.2 in this area. Model 1, however, assigns this area a higher probability value (> 0.7) due to extrapolation errors associated with the linear UTM Easting variable. This emphasizes the greater generality of Model 2 for regional prediction.

In the 1996 validation surveys, fishers were detected at 33.7% of the sites and at 67.5% of the sample units (Table 4.9). Average latency to first detection, including only the SUs or stations with detections, was approximately 7.0 days and 9.1 days, respectively. The histogram of latency by SU demonstrates that a 16 day survey duration is sufficient if the goal is to establish fisher presence/absence at a SU scale (Figure 4.8). Differences in detection rates between the two station types (plywood and plastic) were non-significant (Table 4.10).
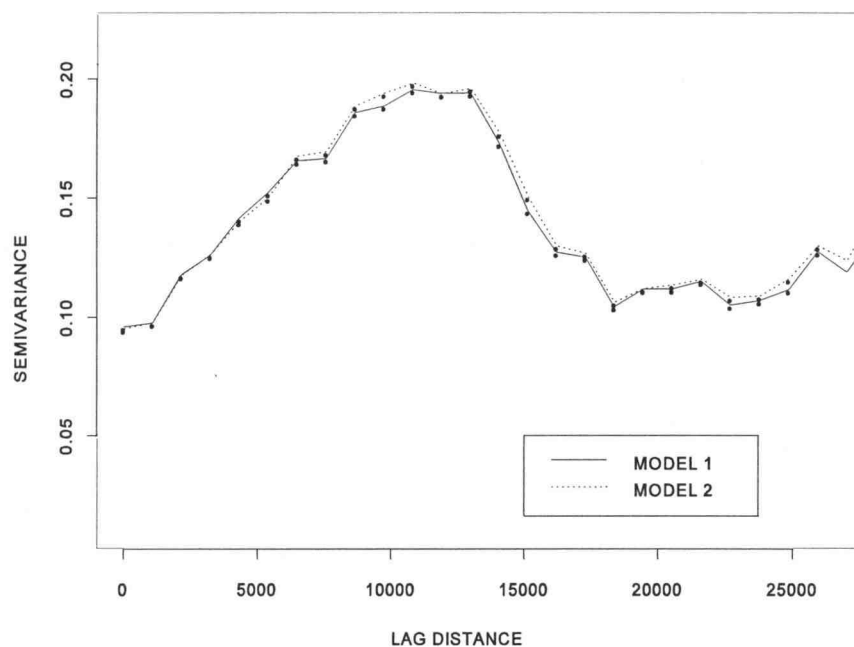
Figure 4.4 Empirical variogram of residuals from models 1 and 2
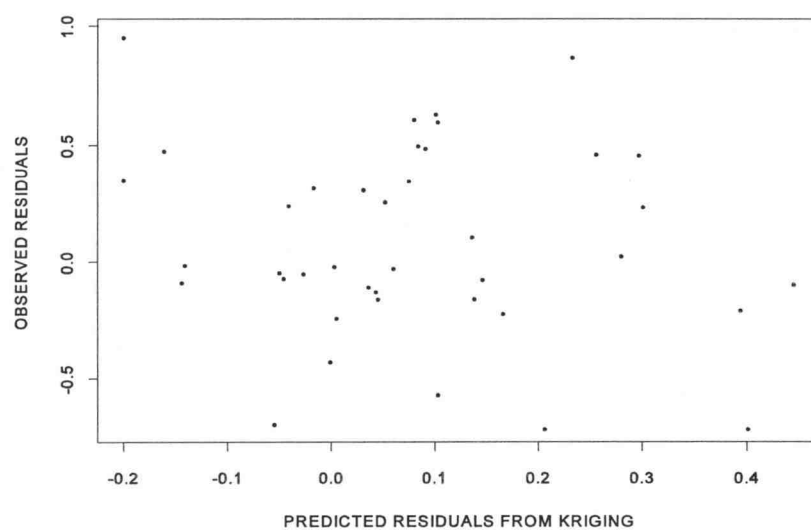
Figure 4.5 Comparison of residuals predicted from kriging with
observed residuals (Model 1)
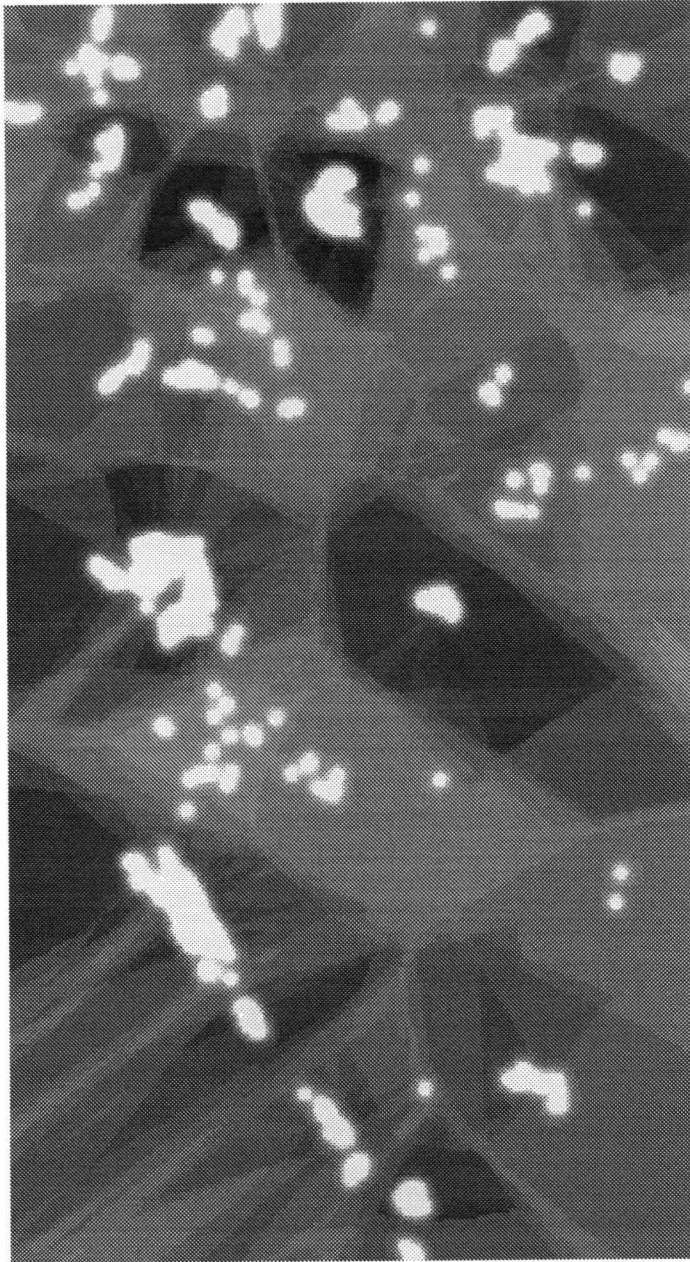
Figure 4.6 Relative level of variance in kriging analysis. Darker areas have higher levels of uncertainty.
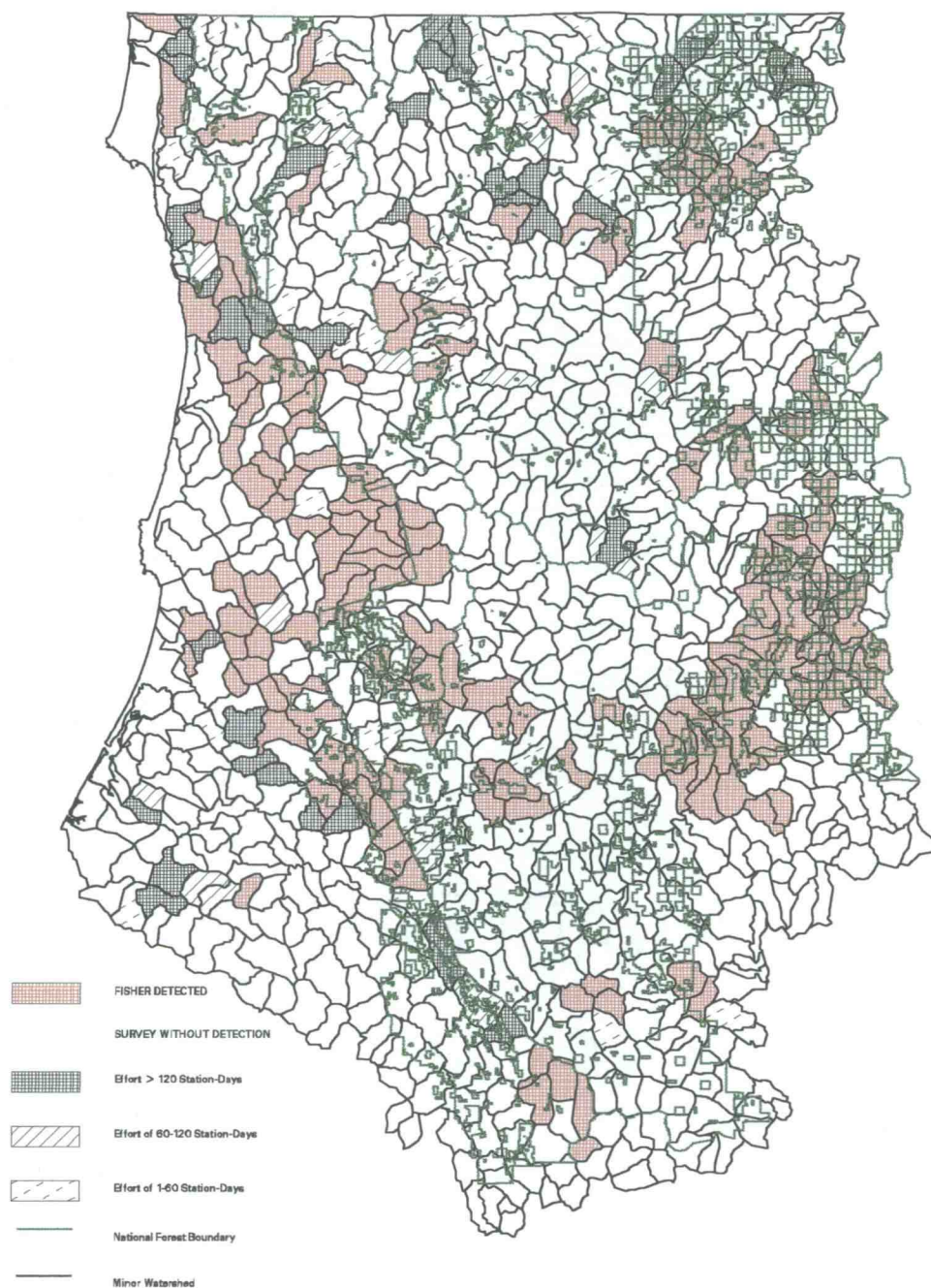
Figure 4.7 Fisher survey results by watershed. (Does not include validation survey data).
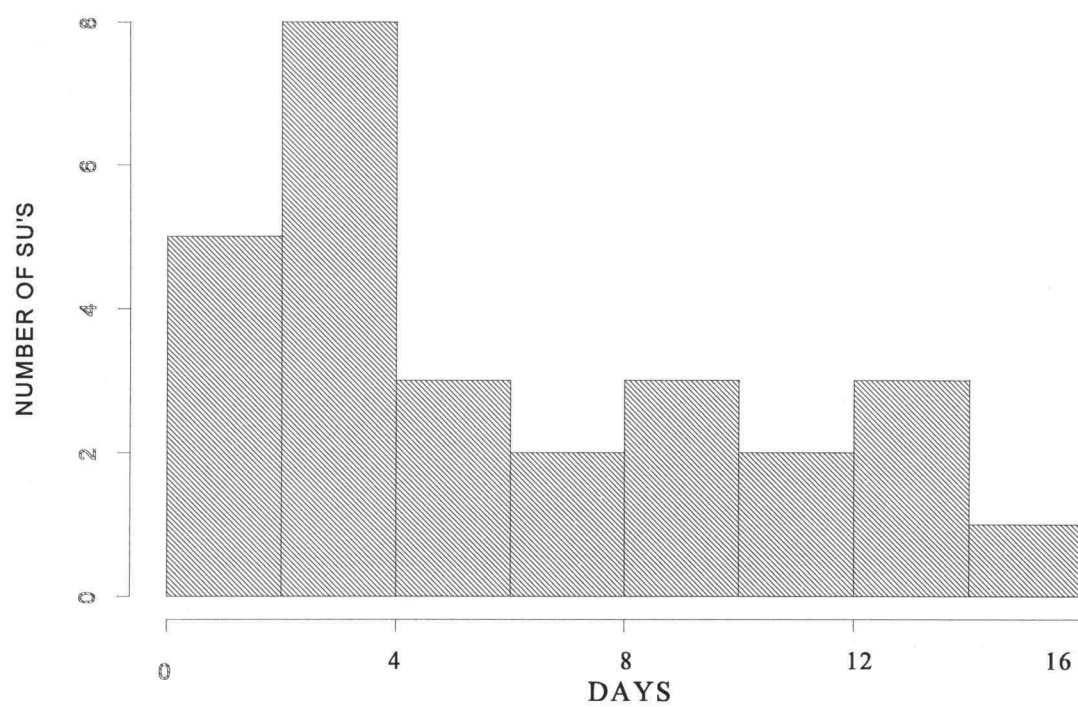
Figure 4.8 Histogram of latency to first detection of fisher by sample unit.

Table 4.9. Detection data by species.

Species:	MAPE	BAAS	SPGR	URCI	URAM[1]
Total detections	212	104	106	213	412
Detections per station	2.62	2.97	2.72	3.20	2.86
Stations with detection	81	35	39	67	144
Stations per SU with detection	3.00	2.92	2.05	3.53	3.89
SUs with detection	27	12	19	19	37
Average latency by SU (days)	6.96	5.16	6.64	3.58	3.36
Average latency by station (days)	9.12	8.80	7.84	6.50	6.36

1- Includes all visits where station was rendered inoperable by animals plus visits with intact station but bear tracks on plate. Of the 412 total detections, 164 were without bear tracks, whereas 32 had tracks and an undamaged station.

MAPE = *Martes pennanti*, BAAS = *Bassariscus astutus*, SPGR = *Spilogale gracilis*, URCI = *Urocyon cinereoargenteus*, URAM = *Ursus americanus*

Table 4.10. Detection rate by station type

| | Wooden | | Plastic | |
	URCI	MAPE	URCI	MAPE
1) Stations with detection	.32	.35	.24	.32
2) Average detections/station (averaged over all stations)	.97	.90	.81	.87
3) Average detections/station (averaged over all stations with one or more detections)	3.03	2.55	3.38	2.69
4) Average latency to detection (days)	6.78	9.04	6.14	9.18

4.5.1 Model Performance

The mean probability of detection in the retrospective data set was 0.255 (174

detections out of 682 sites). The probability of receiving no detections at six randomly

selected sites from the retrospective data set would be $(1 - 0.255)^6$ or 0.171. However,

the optimal cutpoint for the validation data analyzed at the sample unit level was between

0.02 and 0.09. For a cutpoint of 0.082, the correct classification rate was 77.5% and

75.0% for Model 1 and Model 2, respectively (Table 4.11).

Table 4.11. Classification table based on validation results by sample unit.
    Results for Model 1 are followed by results for Model 2 in parentheses.
    Cutpoint = 0.082.

	Classified		
Observed	Presence	Absence	Total
Presence	22(24)	5(3)	27
Absence	4(7)	9(6)	13
Total	26(31)	14(9)	40

The original goal had been to predict presence or absence at a sample unit,

because it was thought that the retrospective model might be unable to predict the number

of stations per sample unit receiving detections. This was under the assumption that

detection probabilities within a sample unit would be highly correlated due to their spatial

proximity.

Contrary to expectations, the validation data also showed a significant

relationship between predicted probability and number of stations in a sample unit with

detections (Figures 4.9 and 4.10) A linear regression of the stations per SU with
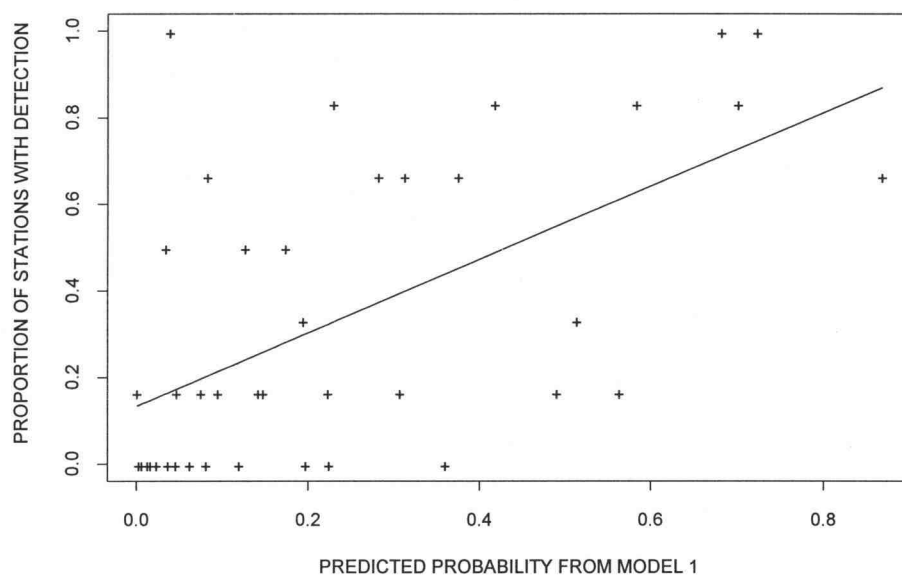
Figure 4.9 Predicted versus observed fisher detection rates (Model 1).
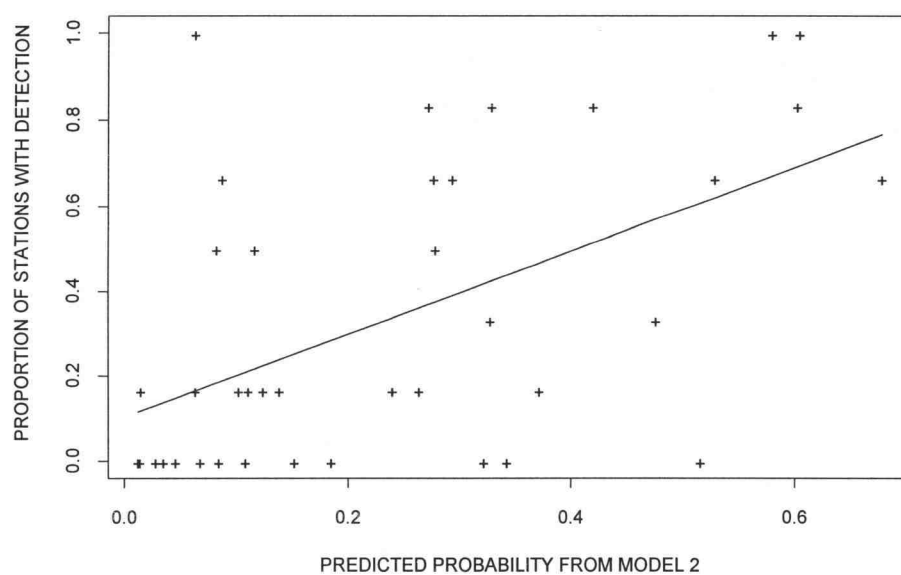
Figure 4.10 Predicted versus observed fisher detection rates (Model 2).

PREDICTED PROBABILITY (MODEL 1)

- 0 - 0.015
- 0.015 - 0.1
- 0.1 - 0.24
- 0.24 - 0.5
- 0.5 - 0.7
- 0.7 - 1.0

Fisher Detection Rate
(Out of 6 Stations per Sample Unit)

- No Detection
- 1
- 2
- 3
- 4
- 5
- 6

National Forest Boundary

0   10
KM
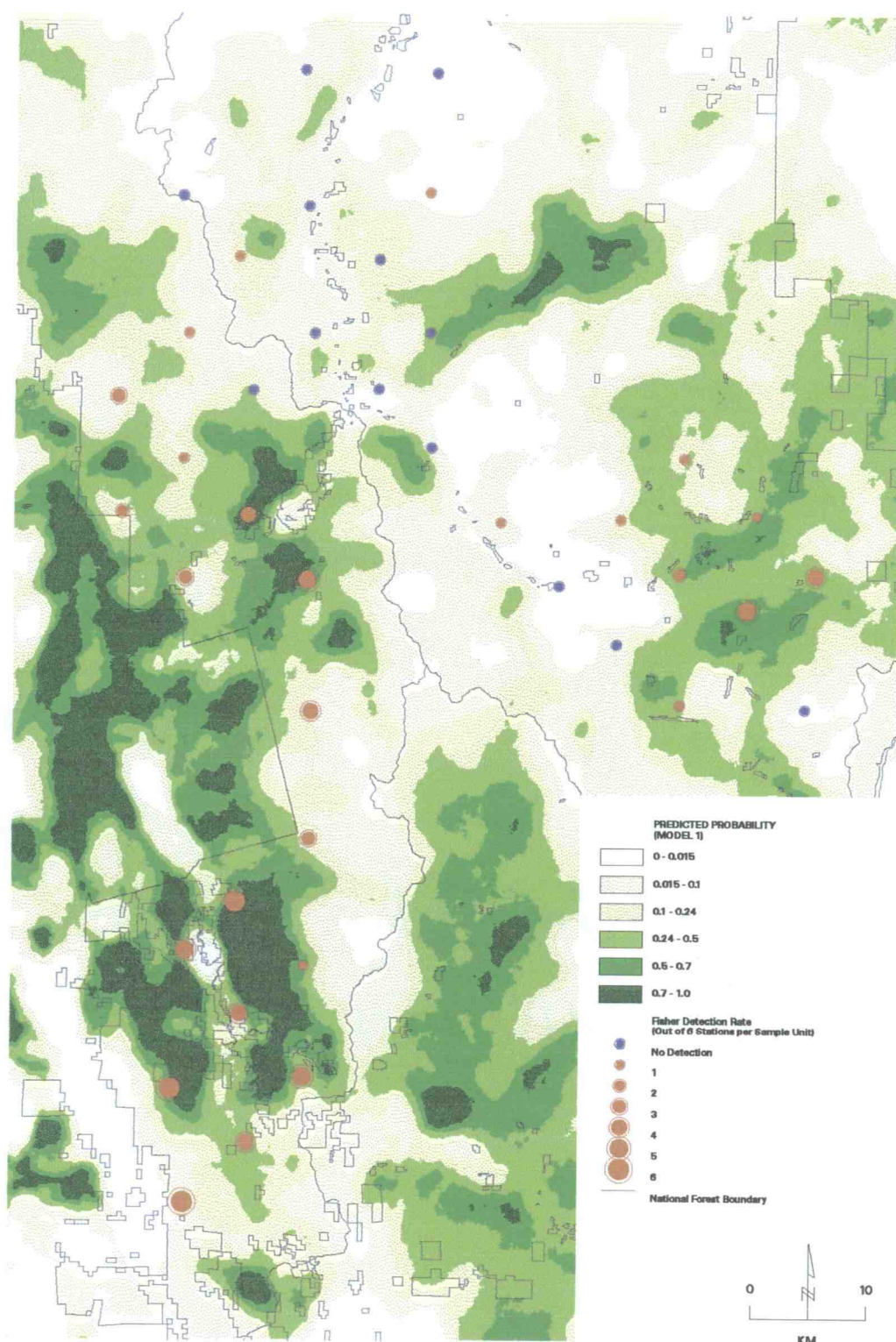
Figure 4.11 Validation survey data overlaid on predicted detection probability (Model 1)

PREDICTED PROBABILITY
(MODEL 2)

- 0 - 0.015
- 0.015 - 0.1
- 0.1 - 0.24
- 0.24 - 0.5
- 0.5 - 0.7
- 0.7 - 1.0

Fisher Detection Rate
(Out of 6 Stations per Sample Unit)
- No Detection
- 1
- 2
- 3
- 4
- 5
- 6

National Forest Boundary

0   10

KM
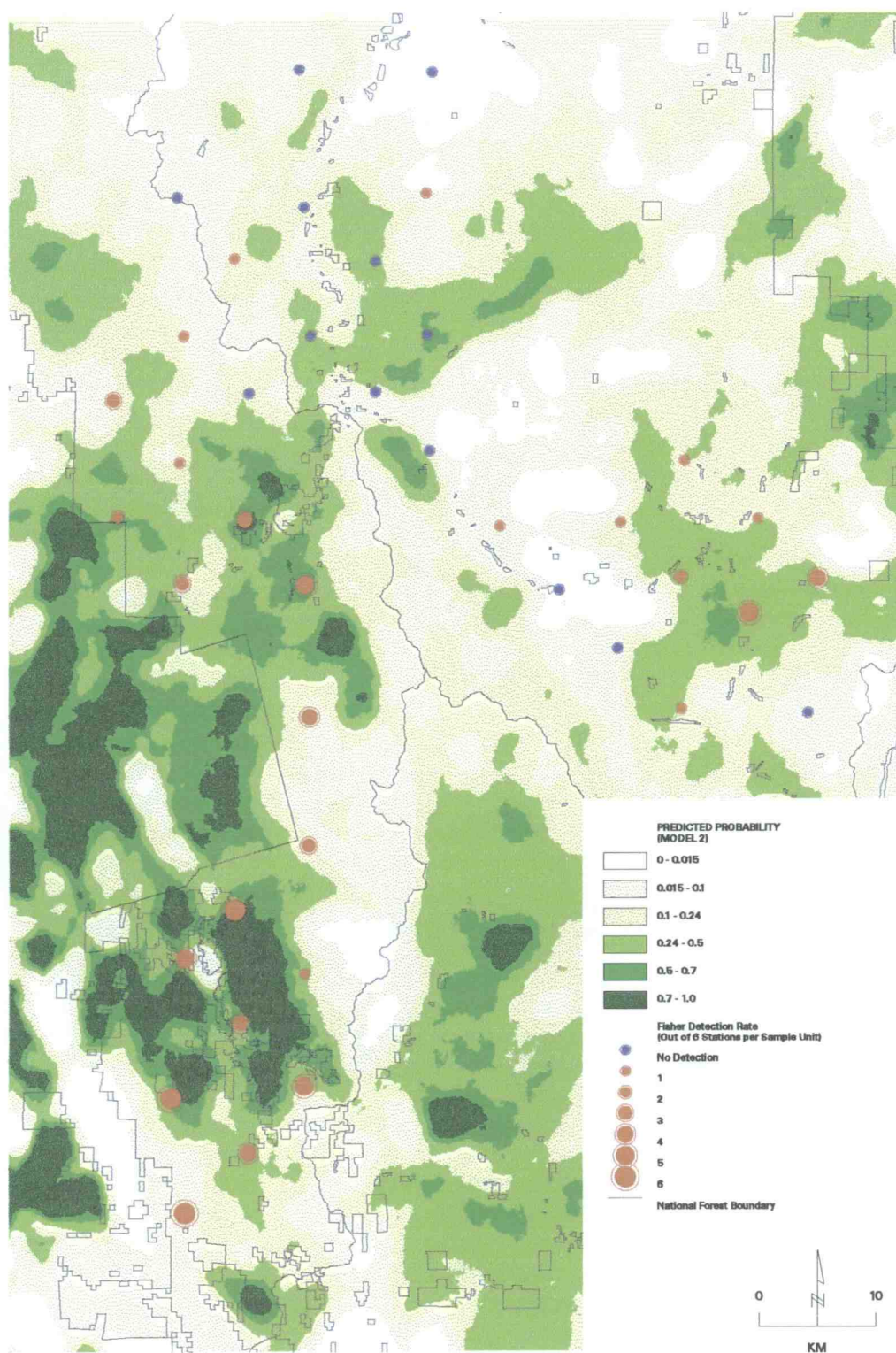
Figure 4.12 Validation survey data overlaid on predicted detection probability (Model 2)

detections on the predicted probability value was highly significant (df = 38, $p < .0001$, $R^2 = 0.33$ for Model 1 and $p = .0003$, $R^2 = 0.29$ for Model 2). When the 13 SU's with no detections are excluded from the analysis, the relationship was still significant (df = 25, $p = .0023$, $R^2 = 0.19$ for Model 1, and $p = 0.007$, $R^2 = 0.26$ for Model 2).

This effect of increasing predicted probaility on within-SU detection ratio can be also be seen in a map of the validation results overlaid on predicted probabilities (Figures 4.11 and 4.12). The binary classification accuracy of the model at the station level was similar to that in the retrospective data set. The correct classification rate at an optimal cutpoint of 0.27 was 71.3% and 70.4% for Model 1 and Model 2, respectively (Table 4.12). The cutpoint value is close to that used in the retrospective data set (0.24).

Table 4.12. Classification table based on validation results by station.
Results for Model 1 are followed by results for Model 2 in parentheses.
Cutpoint = 0.27.

Observed	Classified		
	Presence	Absence	Total
Presence	48(56)	33(25)	81
Absence	36(46)	123(113)	159
Total	84(102)	156(138)	240

. The correlation between predicted probability and observed stations per sample unit with detections is an alternate validation statistic for station level effects. Pearson's correlation coefficients for this relationship for model 1 and model 2 were 0.58 and 0.54. For alternate models incorporating the same variables averaged at a 30 km² scale, correlations were 0.68 and 0.60.

Table 4.13. Univariate comparisons of attributes of validation survey stations with and without detections of fisher. Means are followed by standard deviations in parentheses.

Detection:	*All SUs*[1]		*SUs w/detection*[2]		*SUs w/o lure*[3]	
	Yes	No	Yes	No	Yes	No
GIS attributes:						
Density MA	71.6(8.3)[a,b]	64.3(10.0)	71.6(8.3)[a,b]	67.1(9.8)	73.6(6.9)	71.1(7.4)
Percent Conifer MA	62.9(10.6)	64.1(10.0)	62.9(10.6)	65.0(8.4)	61.9(10.6)[b]	64.8(8.4)
Tree Size Class MA	2.46(0.24)[a,b]	2.29(0.35)	2.46(0.24)[a,b]	2.37(0.29)	2.49(0.23)	2.46(0.26)
Annual Precipitation (mm)	1289(208)[a,b]	1219(249)	1289(208)[a,b]	1184(200)	1354(152)[a,b]	1219(216)
Field measurements:						
Elevation (m)	863(410)	903(365)	863(410)	959(336)	786(369)[b]	922(332)
Canopy Closure	88.6(11.9)[a]	81.6(21.4)	88.6(11.9)[a]	81.5(23.7)	88.9(13.0)[a]	79.9(28.4)
Basal Area (m²/ ha)	47.6(20.0)[b]	42.6(20.4)	47.6(20.4)	42.6(19.4)	47.5(20.5)	40.8(21.8)
Percent Conifer	63.1(26.5)	60.4(30.5)	63.1(26.5)	64.1(29.1)	57.7(27.5)	54.1(31.0)
Bear damage (% of visits)	12.5(17.8)[a,b]	23.5(26.1)	12.5(17.8)	17.9(24.0)	12.9(19.1)	20.1(27.8)
Conifer Count	5.7(3.4)	5.3(4.1)	5.7(3.4)	5.8(4.1)	5.1(3.3)	4.9(4.2)
Snag Count	1.0(1.5)	1.1(1.6)	1.0(1.5)	0.9(1.4)	0.9(1.3)	0.9(1.7)
Hardwood Count	3.6(3.4)	2.8(3.3)	3.6(3.4)[b]	2.6(3.5)	4.3(3.7)	3.0(3.2)
Mean DBH (cm)	55.4(26.4)	54.9(26.6)	55.4(26.4)	57.4(26.4)	50.8(25.2)	56.1(28.2)
Conifer DBH (cm)	61.6(38.1)	66.9(41.4)	61.6(38.1)	67.1(39.4)	57.7(39.9)	69.3(45.7)
Snag DBH (cm)	33.6(45.5)	27.3(38.1)	33.6(45.5)	22.0(35.0)	37.8(48.5)	21.6(35.3)
Hardwood DBH (cm)	26.3(24.9)[a,b]	17.0(17.8)	26.3(24.9)[a,b]	14.7(16.0)	26.7(23.9)[a,b]	16.8(16.8)
Conifer QMDBH (cm)	65.5(38.9)	70.3(42.4)	65.5(38.9)	70.3(40.1)	61.7(41.1)	72.4(46.2)
Snag QMDBH (cm)	35.4(47.5)	28.3(39.1)	35.4(47.5)	23.0(36.3)	39.6(50.8)	22.6(36.8)
Hardwood QMBDH (cm)	28.1(26.2)[a,b]	18.2(19.1)	28.1(26.2)[a,b]	15.9(17.8)	28.7(25.4)[a,b]	18.5(18.8)
Log Count (Total)	3.75(3.79)[a,b]	6.37(5.77)	3.75(3.79)	4.21(3.59)	3.67(3.82)	3.61(3.08)
Log Count (15-30cm class)	2.01(2.56)[a,b]	3.56(3.77)	2.01(2.56)	2.10(2.17)	1.81(2.32)	1.63(1.70)
Log Count (30-60cm class)	1.00(1.49)[a,b]	1.66(2.07)	1.00(1.49)	1.30(1.63)	1.02(1.62)	1.05(1.55)
Log Count (60-90cm class)	0.46(0.83)	0.68(1.14)	0.46(0.83)	0.43(0.76)	0.48(0.82)	0.48(0.85)
Log Count (> 90cm class)	0.28(0.83)[b]	0.48(0.81)	0.28(0.83)	0.38(0.77)	0.36(0.95)	0.45(0.79)

1 n = 240, 81 (33.7%) with detections   2 n = 162, 81 (50.0%) with detections   3 n = 102, 58 (56.9%) with detections

a significance at 0.05 level for t-test   b significance at 0.05 level for Wilcox rank sum test

Two of the sample unit's with the lowest predicted probability each received a total of one detection at one station during the 16 day protocol. This suggests that the number of detections at a station may be useful in separating out the detection of transient from resident animals. However, this variable would show high degrees of temporal as well as spatial autocorrelation and was not analyzed here. Future re-analysis of the track data may focus on distinguishing individuals and sexes. This would improve estimates of density from the crude "number of stations visited" metric used here.

4.5.2 Station-Level Attributes

Hardwood DBH and hardwood QMDBH were significantly higher at detection sites under all three comparisons (all SUs, Sus with detections, and Sus without lure) (Table 4.13). Density was higher at detection sites under all comparisons using the parametric test for significance. Other attributes showed significant differences only when compared over all 40 SUs. Basal area was higher and bear damage and count of small logs were lower at detection sites. The lack of significance when less than 40 SUs were compared may indicate that although measured at the plot level, these attributes are correlates of landscape-scale variation. Or it may mean that the difference was too small to be significant at reduced sample sizes.

In addition to assessing plot variable significance through univariate tests, plot level MLR models were also evaluated. Bear activity and QMDBH of hardwoods were highly significant ($p < .01$). Percent conifer was significant at the $p = 0.05$ level. Other variables that were marginally significant ($.05 < p < .10$) with positive correlations were

density, QMDBH of snags, distance from road and distance from logged area. The latter two variables were recorded as categorical attributes.

CWHR canopy closure class, tree size class, and cover type were also analyzed as categorical variables. CWHR closure class was highly significant ($p < .001$) with increasing closure showing a positive correlation with detections. CWHR size class and cover type were non-significant ($p > .10$).

However, addition of these plot-level variables to the landscape-level model did not result in significant improvement in model performance. An appropriate comparison, giving that the plot-level model was elaborated after the validation surveys, is between a plot-level model and a new model containing landscape variables alone. Plot-level variables alone achieved a reduction in the Cp statistic of only 10.0%, compared to the 27.6% achieved by a new landscape-level model. BIC was -1020 for the plot-level model, -1074 for the landscape model, and -1063 for a combined plot/landscape model. BIC of tthe null model was -1002.

Addition of plot-level variables to a model containing the predicted probability value from the retrospective landscape model resulted in an additional reduction of 3.9% in the Cp statistic (from 17.0% to 20.9%). Bear damage and QMDBH of hardwoods were highly significant ($p < .01$) in both the plot-level and combined models. Density was significant in the plot-level model, but became non-significant in the combined plot-level/landscape model.

4.5.3 Data on Sympatric Carnivores

The validation surveys also provided data on sympatric carnivores. Other

mustelids were detected at a few sample units: marten at one, and weasel (*Mustela* spp.)

at four. The majority of non-target carnivore detections were of ringtail (*Bassiriscus*

astutus)(Figure 4.12), gray fox (*Urocyon cinereoargenteus*)(Figure 4.13), spotted skunk

(*Spilogale gracilis*)(Figure 4.14), and black bear (*Ursus americanus*)(Figure 4.15).

Table 4.14. Correlations (Pearson's) among carnivores of percentage of stations per SU with detections.

	MAPE	URCI	BAAS	SPGR
MAPE				
URCI	0.05457543			
BAAS	0.12539607	0.06788839		
SPGR	-0.17836687	-0.02161354	0.21953070	
URAM	-0.29556513	0.08890129	-0.04213172	-0.19038422

Table 4.15. Station attributes of sites with and without detections of ringtail.
Means are followed by standard deviations in parentheses.

	All SUs[1]		SUs w/detection[2]	
Detection:	Yes	No	Yes	No
GIS attributes:				
Density MA	69.6(8.7)	66.3(10.2)	69.6(8.7)	64.7(13.8)
Percent Conifer MA	56.0(8.6) [a,b]	65.0(9.9)	56.0(8.6)[b]	59.3(7.0)
Tree Size Class MA	2.27(0.25)	2.36(0.34)	2.27(0.25)	2.24(0.27)
Annual Precipitation (mm)	1208(176)	1248(247)	1208(176)[a,b]	1104(166)
Field measurements:				
Elevation (m)	596(371)[a,b]	939(360)	596(371)[b]	723(340)
Canopy Closure (%)	86.6(24.7)[b]	83.5(17.9)	86.6(24.7)	84.0(23.9)
Basal Area (m²/ha)	41.4(17.1)	44.8(20.9)	41.4(17.1)	40.4(19.2)
Percent Conifer	46.0(27.6)[a,b]	64.0(28.7)	46.0(27.6)	53.1(26.4)
Bear damage (% of visits)	18.9(27.9)	20.0(23.6)	18.9(27.9)	30.0(29.4)
Conifer Count	3.83(3.48)[a,b]	5.74(3.92)	3.83(3.48)	4.38(3.14)
Snag Count	0.66(1.03)	1.12(1.66)	0.66(1.03)	0.84(1.64)
Hardwood Count	4.49(3.18)[a,b]	2.83(3.32)	4.49(3.18)	3.54(2.94)
Mean DBH (cm)	49.8(19.3)	55.9(27.4)	49.8(19.3)	49.5(24.9)
Conifer DBH (cm)	57.7(42.4)	66.5(34.9)	57.7(42.4)	57.9(39.4)
Snag DBH (cm)	21.1(34.3)	31.2(41.7)	21.1(34.3)	24.1(39.9)
Hardwood DBH (cm)	31.2(18.3)[a,b]	18.3(20.8)	31.2(18.3)	25.4(23.6)
Conifer QMDBH (cm)	60.2(43.2)	70.1(40.6)	60.2(43.2)	70.0(40.9)
Snag QMDBH (cm)	21.8(35.6)	32.2(42.9)	21.8(35.6)	24.9(40.9)
Hardwood QMBDH (cm)	34.0(19.6)[a,b]	19.6(22.1)	34.0(19.6)	27.4(24.9)
Log Count (Total)	3.40(3.88)[a,b]	5.84(5.46)	3.40(3.88)	3.84(3.23)
Log Count (15-30cm class)	1.91(2.54)[a,b]	3.23(3.59)	1.91(2.54)	2.32(2.25)
Log Count (30-60cm class)	0.89(1.51)[b]	1.52(1.97)	0.89(1.51)	0.87(1.50)
Log Count (60-90cm class)	0.46(0.66)	0.63(1.09)	0.46(0.66)[a]	0.19(0.40)
Log Count (> 90cm class)	0.14(0.43)[a,b]	0.46(0.87)	0.14(0.43)	0.32(0.53)

1 n = 240, 35 (14.6%) with detections   2 n = 72, 35 (48.6%) with detections

a significance at 0.05 level for t-test b significance at 0.05 level for Wilcox rank sum test

Table 4.16. Station attributes of sites with and without detections of gray fox. Means are folllowed by standard deviations in parentheses.

Detection:	All SUs[1]		SUs w/detection[2]	
	Yes	No	Yes	No
GIS attributes:				
Density MA	68.0(9.9)	66.2(10.1)	68.0(9.9)	69.6(8.4)
Percent Conifer MA	60.6(8.7)[a,b]	64.9(10.5)	60.6(8.7)	59.9(8.1)
Tree Size Class MA	2.34(0.31)	2.34(0.34)	2.34(0.31)	2.32(0.28)
Annual Precipitation (mm)	1293(196)[a,b]	1223(250)	1293(196)	1256(189)
Field measurements:				
Elevation (m)	751(311)[a,b]	943(392)	751(311)	805(354)
Canopy Closure (%)	83.9(21.8)	84.6(17.9)	83.9(21.8)	86.6(19.2)
Basal Area (m²/ha)	44.5(21.3)	44.2(20.0)	44.5(21.3)	43.9(21.4)
Percent Conifer	47.4(27.2)[a,b]	66.8(28.1)	47.4(27.2)	55.1(28.1)
Bear damage (% of visits)	16.0(18.0)	21.2(26.1)	16.0(18.0)	19.9(23.3)
Conifer Count	4.46(3.74)[a,b]	5.84(3.92)	4.46(3.74)	5.02(3.88)
Snag Count	1.00(1.48)	1.07(1.64)	1.00(1.48)	0.81(1.21)
Hardwood Count	4.18(3.27)[a,b]	2.65(3.28)	4.18(3.27)	3.68(3.13)
Mean DBH (cm)	54.0(28.8)	55.4(25.6)	54.0(28.8)	55.1(25.3)
Conifer DBH (cm)	70.1(48.7)	63.2(36.4)	70.1(48.7)	64.6(42.0)
Snag DBH (cm)	33.5(45.5)	28.1(38.8)	33.5(45.5)	32.3(41.7)
Hardwood DBH (cm)	25.5(17.0)[a,b]	18.1(21.9)	25.5(17.0)	27.2(24.9)
Conifer QMDBH (cm)	73.1(49.7)	66.99(37.4)	73.1(49.7)	68.7(43.6)
Snag QMDBH (cm)	34.6(46.5)	29.3(40.3)	34.6(46.5)	33.4(43.6)
Hardwood QMBDH (cm)	27.1(18.1)[a,b]	19.5(23.4)	27.1(18.1)	29.5(26.7)
Log Count (Total)	5.01(4.44)	5.66(5.63)	5.01(4.44)	6.30(6.58)
Log Count (15-30cm class)	2.99(3.26)	3.06(3.58)	2.99(3.26)	3.55(4.25)
Log Count (30-60cm class)	1.04(1.52)	1.58(2.03)	1.04(1.52)	1.45(2.10)
Log Count (60-90cm class)	0.57(0.87)	0.62(1.10)	0.57(0.87)	0.83(1.39)
Log Count (> 90cm class)	0.42(0.92)	0.41(0.78)	0.42(0.92)	0.47(0.75)

1 $n = 240$, 67 (27.9%) with detections   2 $n = 114$, 67 (58.8%) with detections

a significance at 0.05 level for t-test   b significance at 0.05 level for Wilcox rank sum test

Table 4.17. Station attributes of sites with and without detections of spotted skunk. Means are followed by standard deviations in parentheses.

Detection:	All SUs[1]		SUs w/detection[2]	
	Yes	No	Yes	No
GIS attributes:				
Density MA	61.5(9.0)[a,b]	67.7(9.9)	61.5(9.0)	62.6(10.4)
Percent Conifer MA	60.5(10.6)[a,b]	64.3(10.0)	60.5(10.6)	61.4(10.8)
Tree Size Class MA	2.20(0.29)[a,b]	2.37(0.33)	2.20(0.29)	2.21(0.36)
Annual Precipitation (mm)	1132(214)[a,b]	1264(237)	1132(214)	1142(188)
Field measurements:				
Elevation (m)	802(463)[b]	906(361)	802(463)	886(413)
Canopy Closure (%)	79.6(21.6)	84.8(18.4)	79.6(21.6)	83.5(22.8)
Basal Area (m²/ha)	41.2(21.4)	44.9(20.1)	41.2(21.4)	45.7(19.5)
Percent Conifer	53.2(28.3)[b]	62.9(29.7)	53.2(28.3)	60.8(29.7)
Bear damage (% of visits)	18.6(27.3)	20.0(23.6)	18.6(27.3)	22.8(26.1)
Conifer Count	4.28(3.52)[a,b]	5.69(3.95)	4.28(3.52)	5.56(3.87)
Snag Count	0.97(1.97)	1.06(1.52)	0.97(1.97)	1.40(1.90)
Hardwood Count	3.67(3.62)	2.96(3.29)	3.67(3.62)	2.93(3.20)
Mean DBH (cm)	52.2(24.3)	5.55(2.69)	52.2(24.3)	54.6(23.8)
Conifer DBH (cm)	61.9(42.5)	65.8(39.9)	61.9(42.5)	62.7(37.4)
Snag DBH (cm)	18.5(30.1)	31.8(42.2)	18.5(30.1)	31.0(38.1)
Hardwood DBH (cm)	24.5(17.6)[b]	19.3(21.4)	24.5(17.6)	23.0(23.1)
Conifer QMDBH (cm)	64.9(44.3)	69.4(40.6)	64.9(44.3)	66.0(38.3)
Snag QMDBH (cm)	19.1(30.7)	33.0(43.6)	19.1(30.7)	32.3(39.8)
Hardwood QMBDH (cm)	26.3(18.7)[b]	20.7(22.8)	26.3(18.7)	24.5(24.3)
Log Count (Total)	5.95(4.99)	5.39(5.39)	5.95(4.99)	5.59(6.13)
Log Count (15-30cm class)	3.46(3.13)	2.96(3.55)	3.46(3.13)	3.31(4.20)
Log Count (30-60cm class)	1.72(1.92)	1.37(1.92)	1.72(1.92)	1.52(2.18)
Log Count (60-90cm class)	0.59(0.79)	0.61(1.08)	0.59(0.79)[b]	0.44(1.11)
Log Count (> 90cm class)	0.18(0.45)	0.46(0.87)	0.18(0.45)	0.32(0.60)

1 $n = 240$, 39 (16.3%) with detections   2 $n = 114$, 39 (34.2%) with detections

a significance at 0.05 level for t-test   *b* significance at 0.05 level for Wilcox rank sum test

Table 4.18. Station attributes of sites with and without detections of black bear. Means are folllowed by standard deviations in parentheses.

	All SUs [1]		SUs w/detection [2]	
Detection:	Yes	No	Yes	No
GIS attributes:				
Density MA	66.6(10.4)	67.0(9.5)	66.6(10.4)	66.5(9.2)
Percent Conifer MA	62.9(10.0)	64.8(10.4)	62.9(10.0)[a,b]	66.9(10.4)
Tree Size Class MA	2.32(0.35)	2.38(0.30)	2.32(0.35)	2.39(0.31)
Annual Precipitation (mm)	1239(245)	1248(229)	1239(245)	1200(224)
Field measurements:				
Elevation (m)	863(361)	930(406)	863(361)[a,b]	1008(391)
Canopy Closure (%)	86.3(17.0)[a,b]	80.3(21.2)	86.3(17.0)[a,b]	80.2(21.5)
Basal Area (m²/ha)	44.9(20.5)	43.4(20.2)	44.9(20.5)	42.3(20.9)
Percent Conifer	60.8(28.7)	62.2(29.9)	60.8(28.7)	65.7(30.7)
Bear damage (% of visits)	33.0(23.2)	----	33.0(23.2)	----
Conifer Count	5.38(3.81)	5.57(4.07)	5.38(3.81)	5.81(4.17)
Snag Count	0.97(1.42)	1.18(1.82)	0.97(1.42)	1.23(1.96)
Hardwood Count	3.37(3.36)	2.64(3.29)	3.37(3.36)[a,b]	2.12(2.97)
Mean DBH (cm)	53.3(26.6)	57.5(26.3)	53.3(26.6)	57.2(26.9)
Conifer DBH (cm)	63.7(39.7)	67.2(41.1)	63.7(39.7)	63.4(38.6)
Snag DBH (cm)	26.9(39.3)	33.7(42.8)	26.9(39.3)	33.2(41.6)
Hardwood DBH (cm)	21.8(21.0)	17.8(20.5)	21.8(21.0)[a,b]	15.4(20.8)
Conifer QMDBH (cm)	67.3(40.9)	70.7(41.6)	67.3(40.9)	67.1(39.2)
Snag QMDBH (cm)	28.1(40.9)	34.8(43.7)	28.1(40.9)	34.3(42.7)
Hardwood QMBDH (cm)	23.2(22.3)	19.2(22.0)	23.2(22.3)[a,b]	16.4(22.2)
Log Count (Total)	5.76(5.29)	5.06(5.36)	5.76(5.29)	5.17(5.45)
Log Count (15-30cm class)	3.18(3.42)	2.82(3.59)	3.18(3.42)	2.77(3.53)
Log Count (30-60cm class)	1.48(2.04)	1.35(1.73)	1.48(2.04)	1.38(1.77)
Log Count (60-90cm class)	0.65(1.09)	0.54(0.95)	0.65(1.09)	0.60(1.01)
Log Count (> 90cm class)	0.46(0.86)	0.34(0.77)	0.46(0.86)	0.41(0.83)

1 n = 240, 144 (60.0%) with detections   2 n = 222, 144 (64.9%) with detections

a significance at 0.05 level for t-test   b significance at 0.05 level for Wilcox rank sum test

Ringtail Detection Rate
(Out of 6 Stations per Sample Unit)

- No Detection
- 1
- 2
- 3
- 4
- 5
- 6

National Forest Boundary

0   10

KM

Universal Transverse Mercator, Zone 10
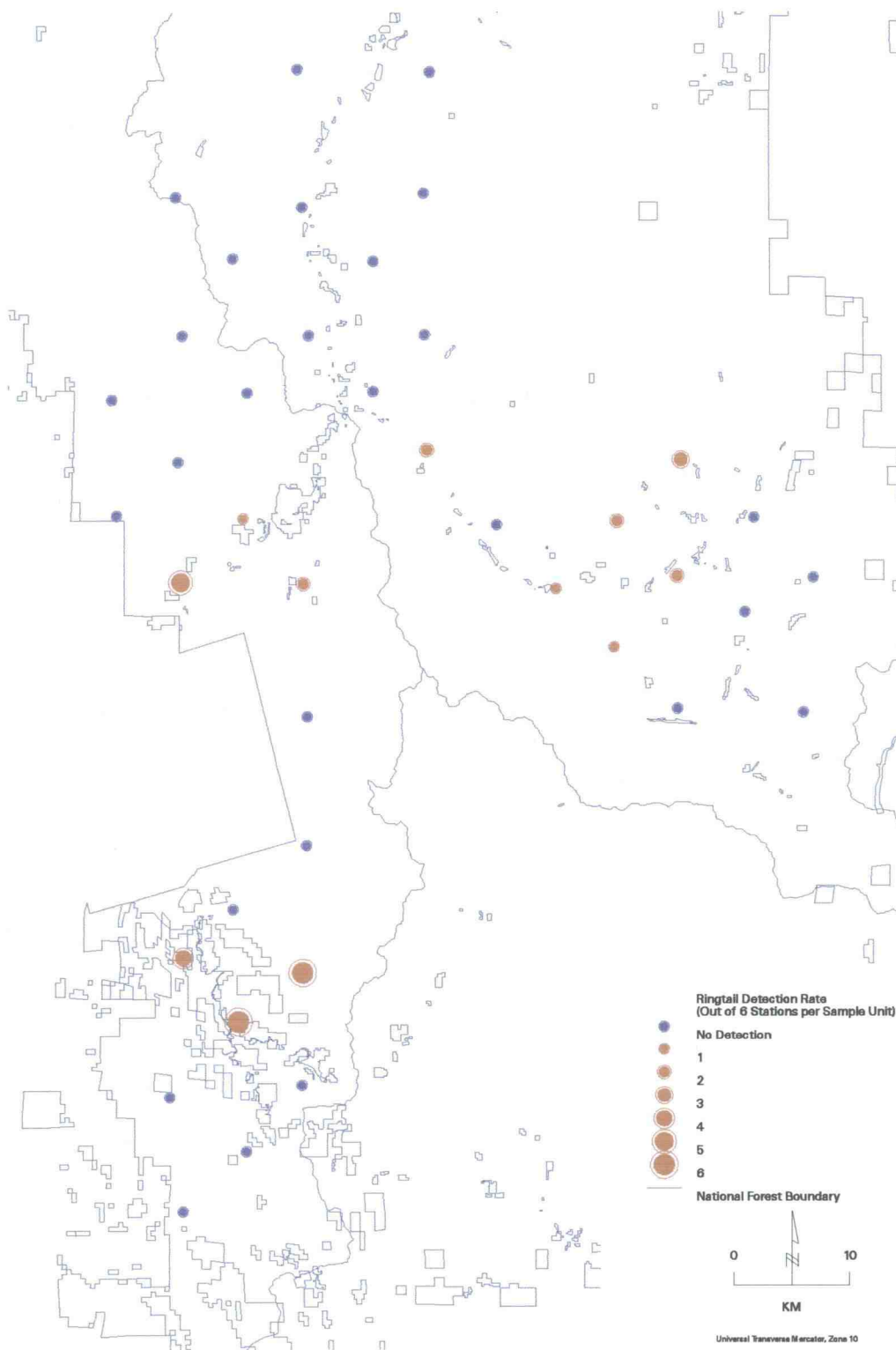
Figure 4.13 Detections of ringtail by sample unit.
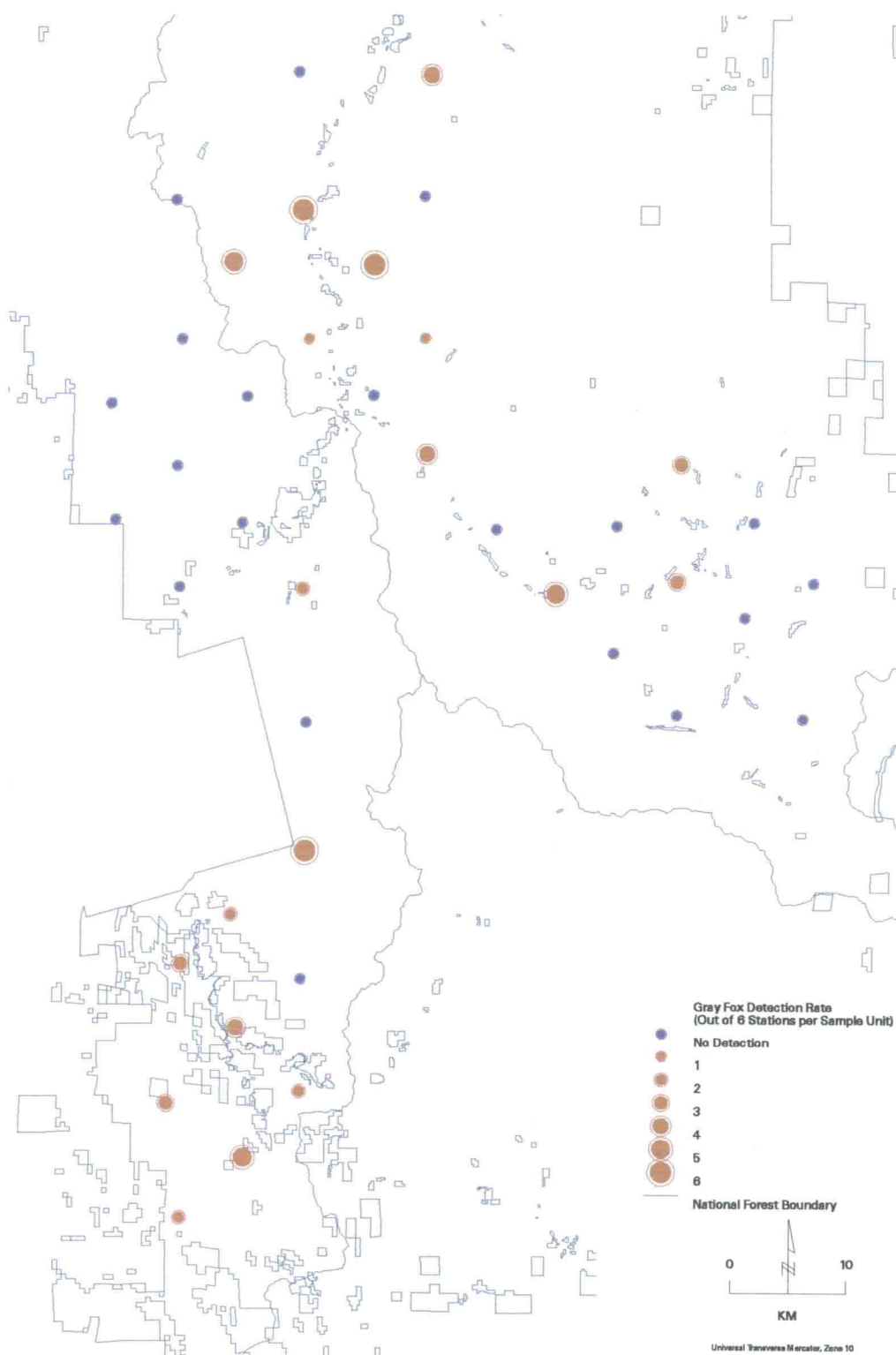
Figure 4.14 Detections of gray fox by sample unit.

Spotted Skunk Detection Rate
(Out of 6 Stations per Sample Unit)

- No Detection
- 1
- 2
- 3
- 4
- 5
- 6

National Forest Boundary

0 — 10

KM

Universal Transverse Mercator, Zone 10
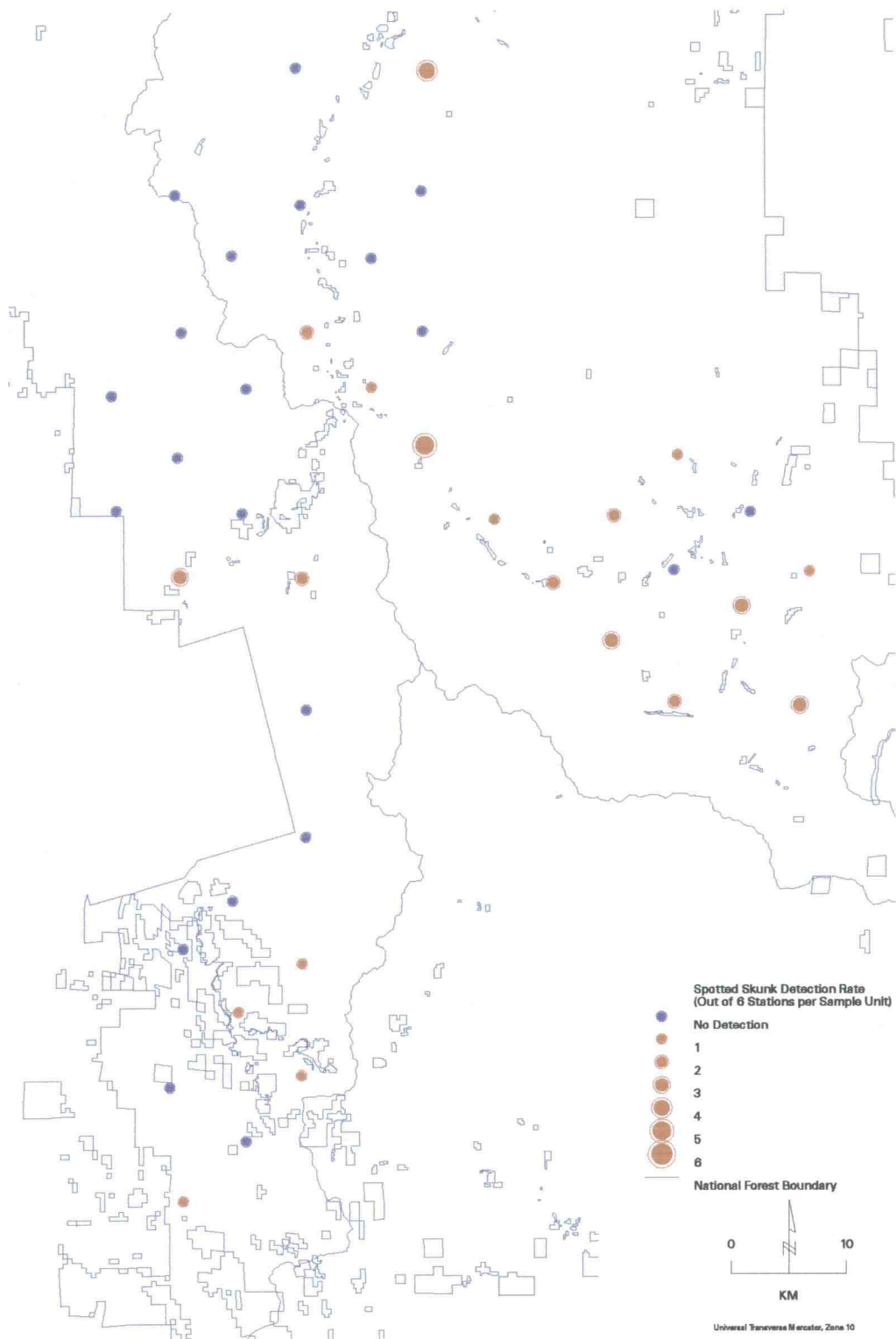
Figure 4.15 Detections of spotted skunk by sample unit.
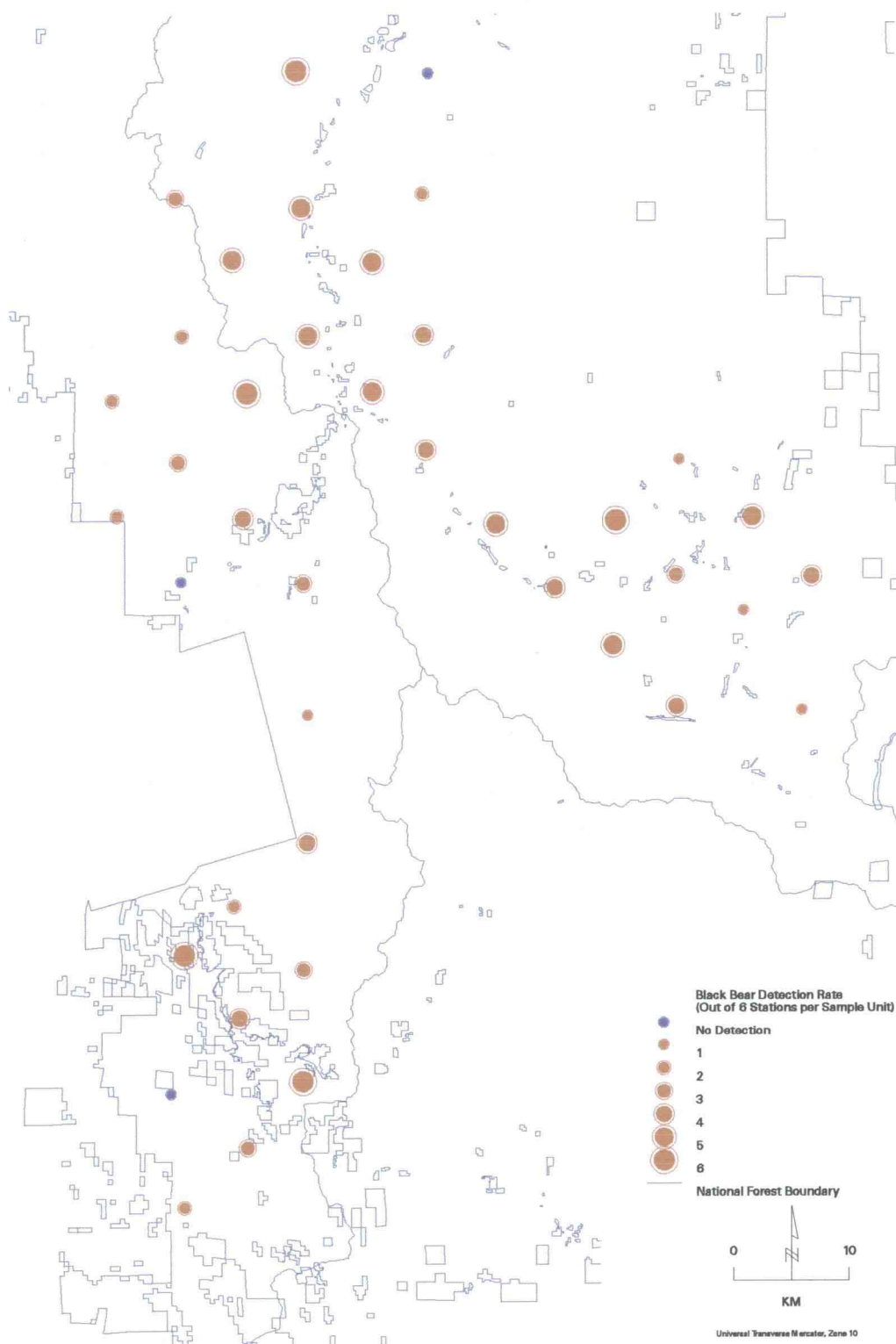
Figure 4.16 Detections of black bear by sample unit.

5. Discussion

5.1 Spatial Dynamics of the Klamath Fisher Population

Inferences drawn from a correlative approach such as used in this study have limitations when compared with those drawn from an experimental study (Wiens 1989a). It is important to explicitly recognize the limitations both on prediction and on the functional interpretations given to observed patterns. The resulting conclusions may only be an artifact of the power of multivariate methods to detect pattern in chance associations in the data set (James and McCulloch 1990). Validation results may lend added support to pattern hypotheses. However, any process interpretations must continue to be framed as hypotheses until alternate processes are rejected by other methods.

Prior knowledge of subject theory may be critical in distinguishing among competing models, as is recognized explicitly in Bayesian statistics. However, this may expose the analysis to criticisms of subjectivity. As Haining (1990) concludes, "good data analysis seeks a balance between being theoretically informed and letting the data speak. Balance is essential in order to avoid the twin problems of on the one hand using data analysis merely to confirm existing prejudices and on the other reporting ambiguous data patterns".

Limitations on prediction may stem from the complex nature of the observed spatial structure, which is only crudely approximated by the models used. In addition, extrapolation of spatial trends beyond the extent of the data set is based on the assumption that the spatial trends continue into adjacent regions. This assumption is

problematic without a good functional understanding of the processes responsible for the trend. An additional source of uncertainty is the untested relationship between fisher distribution and habitat suitability as expressed in individual survival and reproduction. However, if conducted in the spirit of exploratory data analysis, this type of spatial modeling may be a fruitful source of hypotheses that can then be explored by more intensive methods.

5.1.1 "Patch"-Scale Dynamics

Although plot-level variables in general show low significance, variables measuring the size of hardwoods consistently show high significance in all comparisons. They show similar significance in the retrospective data set. Recent studies of other taxa have emphasized the role of large hardwoods in promoting complex structure in western forests. They may form a reservoir of biodiversity in young managed forests for taxa such as lichens (Neitlich and McCune 1997). The general importance to carnivores of hardwood habitat resources is evident from the data on sympatric carnivores, all of which show significant associations with hardwoods.

Two plausible hypotheses are apparent to explain the positive correlation of fisher detection with large hardwoods. Older hardwoods provide a much greater volume of mast in the form of nuts and fruits. This may lead to increased abundance of fisher prey. The prey/hardwood interaction is the most plausible explanation for strong associations at the plot scale. At the landscape scale, large hardwoods also provide structure in the form of cavities for resting and denning. Telemetry studies in both the Klamath region and the

southern Sierras have shown that hardwood cavities are frequently used for these purposes by fishers (W. Zielinski, unpublished data). Because cavities have little value below a certain size, the habitat value of hardwoods for fishers may increase non-linearly, with high resource value only occurring after a certain size threshold.

Bear damage is significant for the obvious reason that it reduces the possibility of fishers being detected by rendering the station inoperative. This effect operates at the landscape scale due to the generalist nature of habitat use by foraging bears. The negative correlation with small log count also seems to operate at the landscape scale. Small log count is negatively correlated with the tree size class moving average (MA) (r_p = -0.25) but may also reflect a history of disturbance by fire, logging, or thinning.

Percent conifer is significant in the univariate analysis. It shows moderate correlation (R = 0.45) with the landscape level conifer MA, and is not significant in the multiple scale model. Plot-level canopy closure also loses significance in a multiple scale model. This may be due to correlations with both the density MA and quadratic mean diameter at breast height (QMDBH) of hardwoods (R = 0.28 and 0.34, respectively).

The low explanatory power of the plot-level model when compared with landscape model supports the hypothesis that fishers select habitat more strongly at the landscape scale. It is encouraging that detailed plot-level vegetation or prey data may not be necessary for predicting fisher distribution. If this were not the case, conservation planning for forest carnivores on a regional scale would be difficult. However, data on fine-scale habitat selection will still be useful both for ruling out the effects of other plot-level habitat variables and for obtaining a functional understanding of the processes

driving landscape-level associations. The challenge is learning how to scale up from patch to landscape levels, and from individual to population-level responses.

5.1.2 Landscape-Scale Dynamics

The explanatory power of the three vegetation MA variables supports the hypothesis that fishers select habitat based on perceptions of landscape-level habitat quality as represented by vegetation structure or its correlates. While somewhat correlated, the three vegetation variates quantify substantially distinct elements of vegetation structure. The density MA shows the highest significance and the clearest biological interpretation. Landscapes with higher density and overhead cover provide increased protection from predation and lower the energetic costs of traveling between foraging sites. High density provides a cooler microclimate in summer and more favorable snow conditions in winter. Abundance or vulnerability of preferred prey species may be higher in areas with higher canopy closure (Buskirk and Powell 1994).

The percent conifer MA is only marginally significant in its main effect, but retains significance through its interaction term. Given the importance of hardwoods, it might seem contradictory that the percent conifer MA is an increasing function. In fact, in the retrospective data set, univariate comparisons show that detection sites have significantly lower percent conifer. However, in the multivariate model the effect becomes complex through the negative interaction with the density MA. This suggests that the effect of increasing density is more positive in mixed hardwood/conifer landscapes than in purely conifer landscapes. Dense conifer landscapes are often

composed of homogeneous young or early mature forests. Dense mixed landscapes,

however, typically owe their canopy closure to the hardwood component and may include

late seral stands.

The tree size class MA has the most complex and difficult to interpret correlations

of the three vegetation variables. This attribute shows a higher level of measurement error

than other vegetation attributes (Cal. Timberland Task Force 1993). Detection of changes

in tree size with remote sensing imagery is inherently challenging (Cohen et al. 1995). A

univariate GAM plot of the tree size class MA in the retrospective data shows an

increasing cubic function (Figure 5.1). However, a multivariate model incorporating the

size class MA as a cubic function is not significantly better fitting than one using a

decreasing linear function. The fact that most values fall near the "dip" of the cubic curve

at values of 1.7 to 2.7 raises suspicions about the generality of the cubic curve. However,

if this curve is not an artifact of factors such as selection bias in the retrospective data set,

it suggests that mustelids show a threshold response to decreasing percentages of large

trees in the landscape, as has been proposed (Bissonette et al. 1989) but not demonstrated

in a field study (Hargis and Bissonette in press).

Univariate analysis of the validation data set lends some support to the existence

of such a threshold. The validation survey data shows a highly significant positive

correlation between tree size class MA and fisher detection (p = .0001). A GAM plot of

the validation data shows a curve similar to that in the retrospective data (Figure 5.2).

These types of curves are difficult to model accurately with generalized linear models
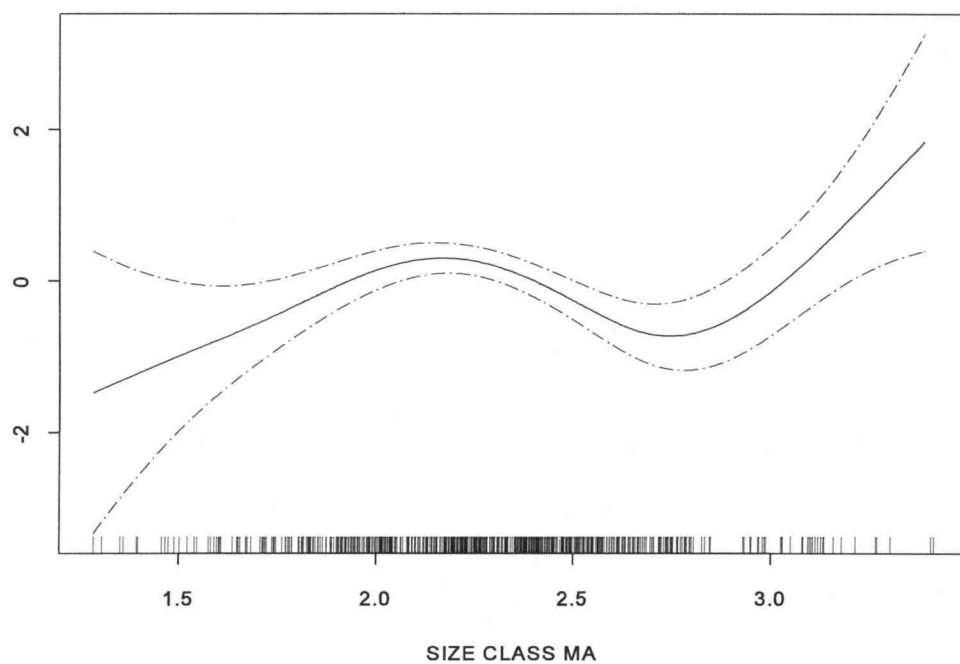
Figure 5.1 Tree size class MA versus GAM function (univariate model)
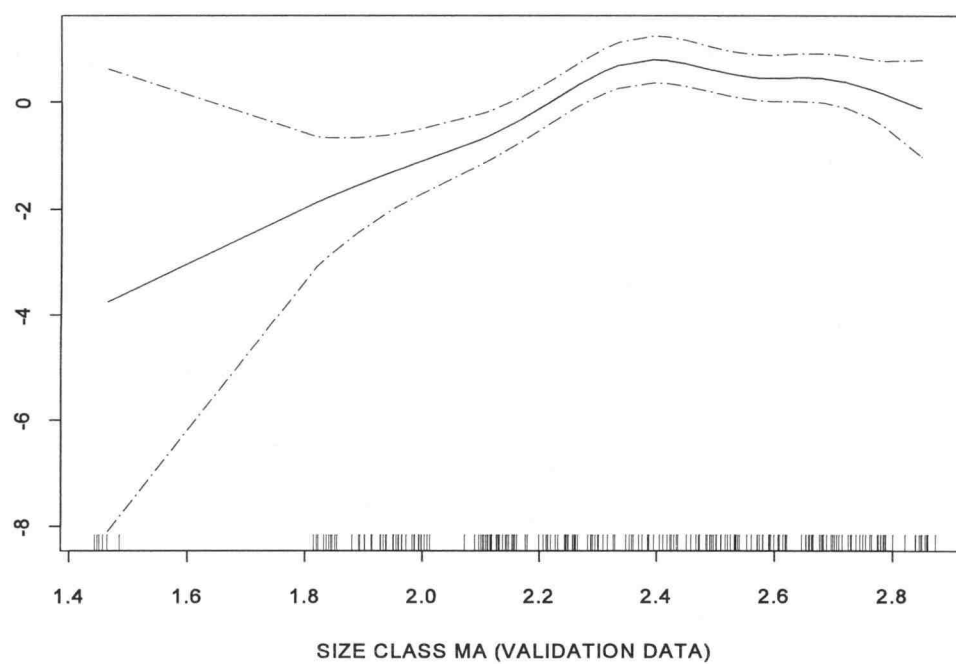
Figure 5.2 Tree size class MA versus GAM function in univariate model
for validation data

(Hastie 1993), and, in general, the analysis of thresholds and limiting factors is a challenge to traditional statistical analysis (Thomson et al. 1996).

In the final model selection, a negative interaction of the size class MA with UTM Easting was chosen as a better fitting alternative over the cubic function of size class. The interaction term of size class MA and UTM Easting is highly significant in multivariate models and its addition results in a lower Bayesian Information Criterion (BIC) (-3951 versus -3880 for the cubic model). This would suggest a pronounced regional gradient in habitat association patterns. The cubic curve of the size class MA disappears when the interaction of the size class MA and UTM Easting is incorporated in the model.

A bivariate plot of size class versus UTM Easting for the retrospective data set shows detections in a range of size class MA values (Figure 5.3). Size class of all sites generally declines from west to east in the retrospective data. This may represent selection bias, as this trend is not evident in the systematic validation surveys (Figure 5.4). The positive coefficient of the size class MA main effect combines with the negative interaction to result in a net positive predicted correlation of detections with size class anywhere west of UTM Easting 410000.

In the alternate model incorporating precipitation, the tree size class MA main effect has a negative coefficient. The interaction term with precipitation is positive, resulting in a positive predicted correlation of detections with size class where precipitation is greater than 2400 mm.
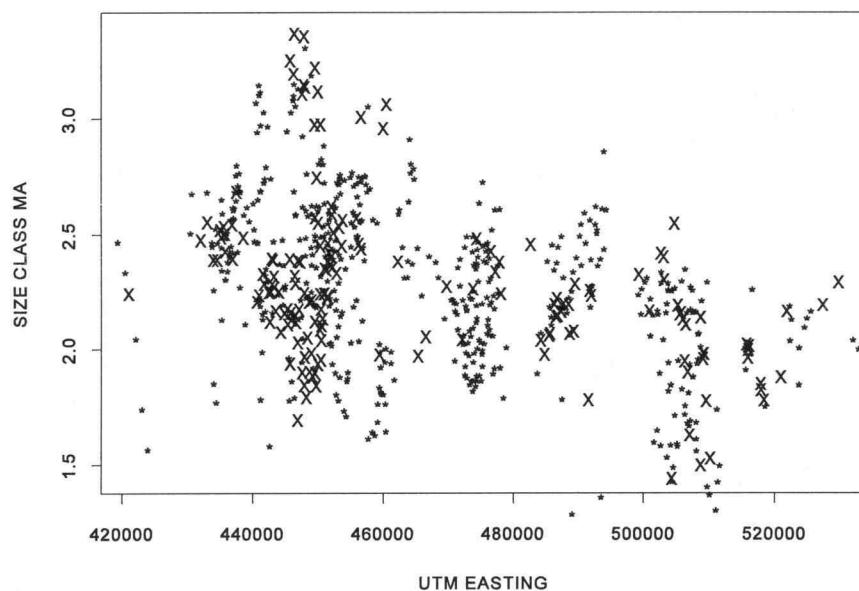
Figure 5.3 Plot of tree size class MA and UTM Easting versus fisher detection (retrospective data). X's represent sites with detections, while *'s represent sites without detections.
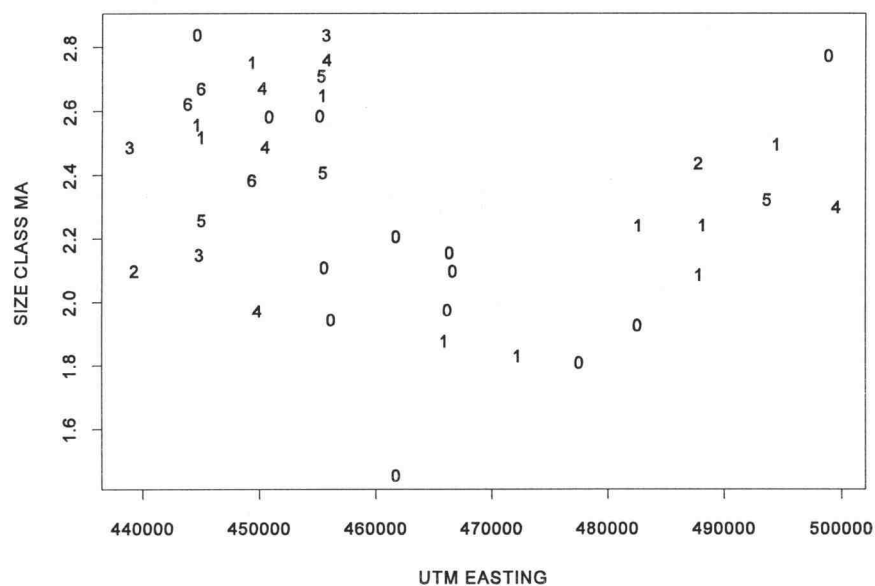
Figure 5.4 Plot of tree size class MA and UTM Easting versus fisher detection for validation data. Numbers represent the number of stations in a sample unit receiving detections.

The generally negative net contribution of size class in the multivariate model is misleading if interpreted as if it were a univariate effect. An increase in other covariates such as density in older stands may actually result in a quite different univariate correlation. The relatively high correlation of the size class MA with the density and percent conifer MA's (r_p = 0.63 and 0.55, respectively) strongly suggest that multicollinearity effects may be limiting the interpretability of the coefficients. This is supported by the decrease in magnitude of the coefficients of the other MA's when the size class MA variable is removed from the model. The less rich model may be more interpretable, but it has a higher BIC (-3922 versus -3951). This argues for the retention of the size class MA in the model.

Since the most westerly site in the retrospective or validation data set has an UTM Easting of 419000, it can be seen that the positive correlation of detection with size class predicted in coastal areas is based on extrapolation. This is one of the reasons for focusing validation surveys in coastal areas during the 1997 field season.

Extrapolation of the size class MA - UTM Easting interaction term to areas east of the extent of the retrospective data set increases the magnitude of the interaction effect to a biologically implausible extent. The model incorporating precipitation gives much more plausible extrapolated values due to the fact that precipitation does not decrease linearly across the region. Incorporation of the UTM Easting variable and its interaction term provides a better fit to the data within the study area. Its poor performance outside the extent of the retrospective data set highlights the difficulty of extrapolating complex spatial trends (Haining 1990).

In summary, it appears that landscape-level tree size class has a positive correlation with fisher detection in the more mesic forests of the Douglas-fir/mixed evergreen zone, at least up to a certain threshold. The relationship between tree size and fisher distribution in the more xeric pine and oak forests of the eastern Klamath is uncertain. This has interesting parallels with the findings of habitat studies of the northern spotted owl, which have revealed stronger selection for large diameter stands in more coastal areas (Noon and McKelvey 1996b).

The lack of significance of the FOCALSTD attributes indicates that variance in habitat value at the landscape scale is not significantly correlated with fisher distribition in this data set. Public forest lands in this region may show similar levels of habitat contrast (e.g. between late-successional forest and clearcut) and pattern (e.g. 16 ha dispersed cutblocks) due to similar management practices and planning guidelines on all National Forests. This conclusion might not hold if a fisher data from a wider range of land-use categories (e.g. private timber land, wilderness areas) were available for analysis.

Variables not found to be significant in the multivariate model include elevation and road density. Elevation is correlated with the vegetation variables, particularly percent conifer. The fact that vegetation has more explanatory power than elevation suggests that the often noted correlation of fisher distribution with elevation may be due to the effects of vegetation, either directly or as a mediator of snow condition. This will aid in the generalization of the model to areas such as the Sierra Nevada where the median elevation of fisher habitat differ from that in the Klamath region.

Road density at the landscape level was not significant in either univariate or multivariate analyses. Direct human persecution of fishers is low in the Klamath due to low trapping intensity (C. Carroll, pers.obs.). Therefore, road density could be expected to have an effect on fisher distribution primarily through a correlation with habitat alteration through logging. In fact, sites in the retrospective data set on public forest lands show a significant negative correlation (R = - 0.33, r_s = - 0.26) between road density andlate-successional forest at the landscape level. However, the correlation between the "old-growth" MA attribute and fisher presence, like that between the road density MA and fisher presence, is non-significant in this data set.

Although little broad-scale comparitive data are available, there is evidence tthat public lands in the Klamath have not experienced the magnitude of logging that has occurred in other parts of the Pacific Northwest. For example, the amount of northern spotted owl habitat may be a useful analogue to the amount of late-successional forest in a region. It is apparent from Figure 5.5 (Noon and McKelvey 1996b) that the Oregon Cascades and Coast Ranges have lost between 65 and 70% of this habitat type in the last four decades, whereas the Klamath region has lost 35 to 40%.

Because of this, "natural" gradients in habitat quality due to regional gradients in forest structure and productivity may be as significant as the effects of human impact. This is, of course, one of the explanations proposed for the survival of fishers in the region. Analysis of data from a wider range of road densities such as found on private lands or wilderness areas might reveal correlations that are not evident in our study. It seems likely, however, that fishers are better indicators of "landscape integrity" in the
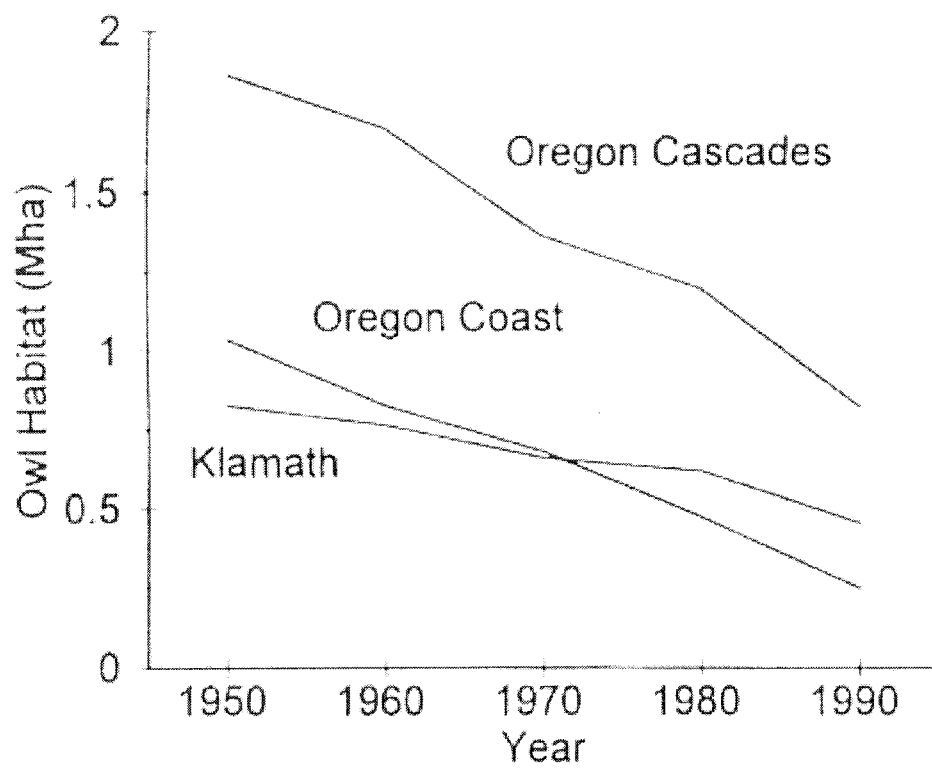
Figure 5.5 Decline in habitat of northern spotted owl in the Pacific
Northwest (from Noon and McKelvey 1996b)

MEAN ROAD DENSITY

LOW

MEDIUM

HIGH

National Forest Boundary

Streams

Watershed Boundaries

0   25

KM

1:300,000

Universal Transverse Mercator, Zone 10
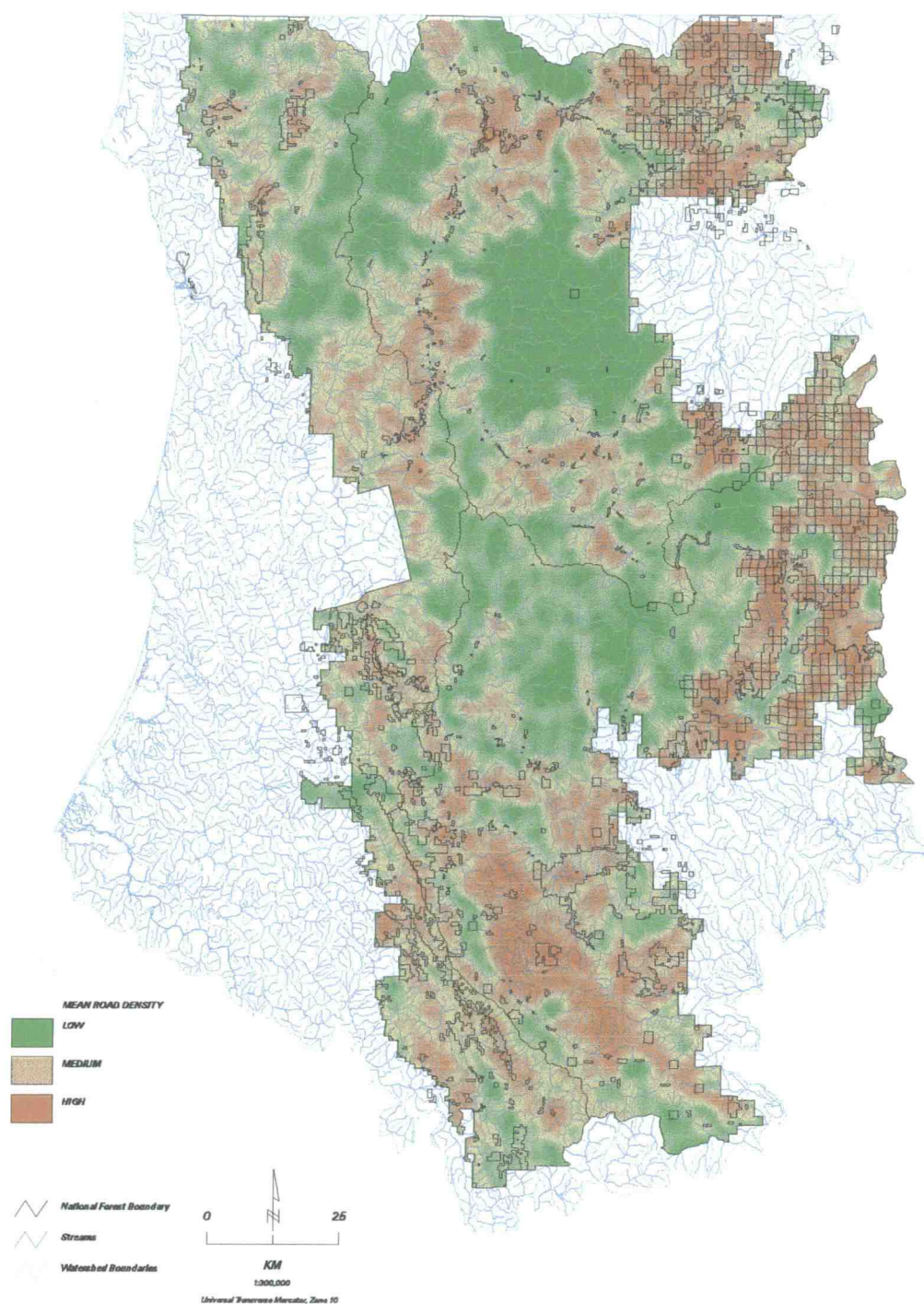
Figure 5.6 Mean road density on public forest lands in northwestern California.

form of forest composition than in the form of "wildness". For that purpose, species

sensitive to human presence (e.g. wolverines or grizzly bears (*Ursus arctos*)) or directly

persecuted by man (e.g. wolves (*Canis lupus*) or black bears) may be better candidates

(Mladenoff et al. 1995). Legal and illegal hunting pressure on black bears is high in the

region (C. Carroll, pers. obs.). Their high densities in the Klamath region (Table 4.9) may

be related to the existence of large roadless areas (Figure 5.6), as has been found in other

regions (Powell et al. 1996).

5.1.3 Regional-Scale Dynamics

The trend surface component of the model shows high levels of statistical

significance. However, interpretation of its biological significance is more difficult than

with the vegetation variables. The UTM Easting variable, which is modeled as increasing

linearly from west to east, corresponds in the Klamath to a coastal to inland gradient. The

climatic gradients in precipitation and temperature associated with this transect are, along

with elevation, the most influential abiotic factors controlling the distribution of the

region's diverse flora. These floristic changes can be expected to change the relationship

of forest structure to fisher distribution. Although early studies of niche partitioning

emphasized the importance of structure, it is now evident that both structure and floristics

play a role in affecting the composition of animal communities (Wiens 1989a).

Floristic changes can be expected to influence prey species composition. The

west/east climatic gradient may also influence vegetation structure variables unmeasured

in this study, such as shrub cover. Fisher were detected more frequently than predicted at

validation sites with low tree canopy closure but high cover percentages of the shrubby

huckleberry oak (*Quercus vaccinifolia*).

The alternate model which substituted precipitation for the UTM Easting variable

showed less explanatory power (BIC of -3918 versus -3951). The correlation between

these two variables is high (R = -0.67, r_s = -0.60), and the addition of one of the terms to

the model rendered the other non-significant. Multiple climatic factors may be

responsible for the correlation of fisher detection with UTM Easting. In addition to

annual precipitation, these might include temperature and less aggregated variables such

as summer precipitation.

However, comparison of model predictions for the watershed data (Figure 4.7)(R.

Klugh and R. Golightly, unpublished) and for sightings data from Oregon (Siskiyou

National Forest, unpublished data) suggests that the precipitation model may have greater

generality. For this reason, it will be used to evaluate fisher distribution on a regional

level in order to reduce the magnitude of extrapolation errors. Differences between the

maps created by the two models may give a general idea of the degree of uncertainty in

the model predictions (Figures 5.7 and 5.8).

The quadratic function of UTM Northing lacks a plausible abiotic interpretation,

as gradients in climate and floristics are much less evident from north to south than from

west to east within the Klamath region. Lack of data from Oregon or Mendocino County

make it uncertain how well this trend extrapolates to the northern and southern margins of

the region. Gates et al. (1994) noted the high significance of trend surface variables in

their MLR models of the distribution of British bird species. They attributed this to the

persistence of historical effects due to poor recolonizing ability. In the case of the fisher, this effect might be attributed to the existence of dispersal barriers. Periera and Itami (1991) proposed that the trend surface component of their model of the distribution of the Mt. Graham red squirrel was due to intraspecific interactions that caused aggregation of occupied sites beyond that predicted by the environmental variates.

In the case of fishers, this aggregation may be due to population-level processes such as source-sink effects. Fishers may disperse from large regional concentrations of favorable source habitat to occupy adjacent sink areas. Smaller concentrations of potentially suitable habitat may remain unoccupied due to isolation. Detection of fishers in a wide range of landscapes in the validation surveys indicates that they will travel through habitat that may be unable to support long-term survival. Therefore, barriers to dispersal may be less significant than source-sink processes on the intra-regional scale.

Testing of the source-sink hypothesis against alternate explanations (such as a purely climatic or floristic gradient or the effects of dispersal barriers) is difficult due to the inherently non-replicable nature of regional-scale biogeographic processes. The most persuasive evidence would come from intensive studies of dispersal, as well as survivorship and reproduction. An alternative would be to collect survey data from the same locations over time to determine if sink areas could be identified by high temporal variability in detection. If source-sink effects are important in determining fisher distribution, regional-scale conservation planning may be necessary to insure the continued viability of the Klamath fisher population.
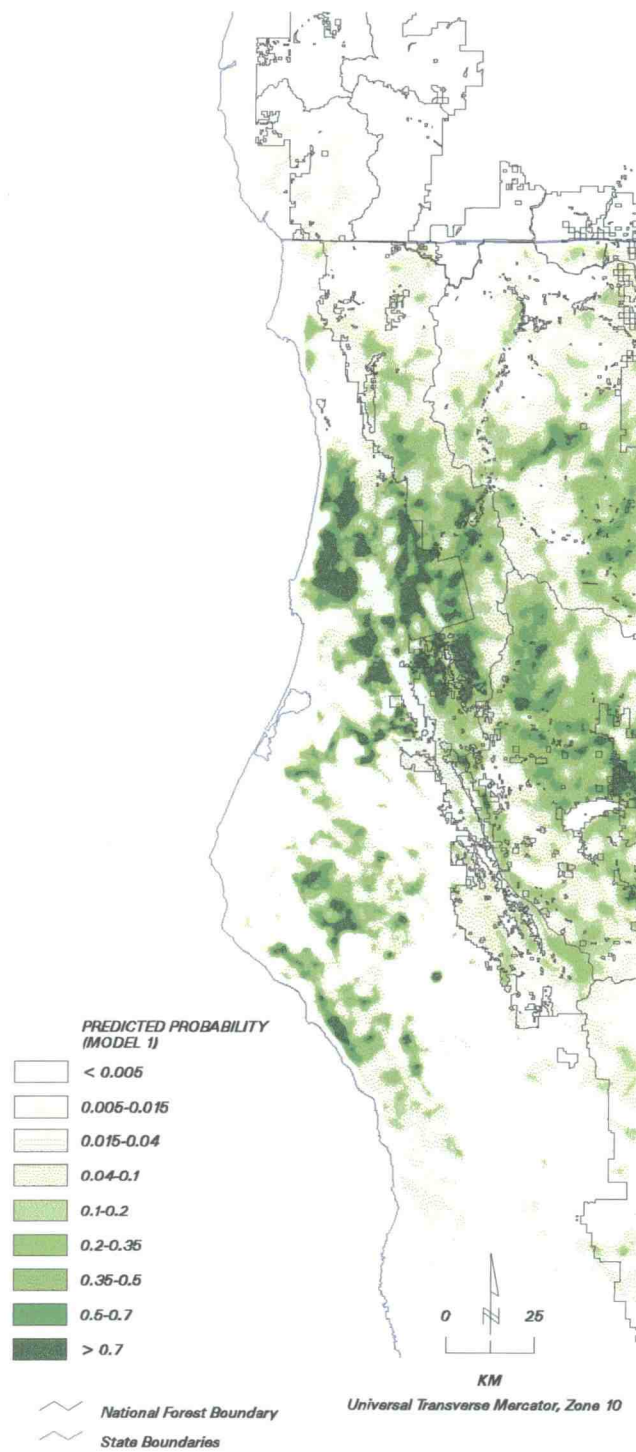
Figure 5.7 Map of predicted probability of fisher detection (Model 1).

Figure 5.8 Map of predicted probability of fisher detection (Model 2) (following page).

PROBABILITY

< 0.015

0.015-0.1

0.1-0.24

0.24-0.5

0.5-0.7

> 0.7

National Forest Boundary

State Boundaries

0   25

KM
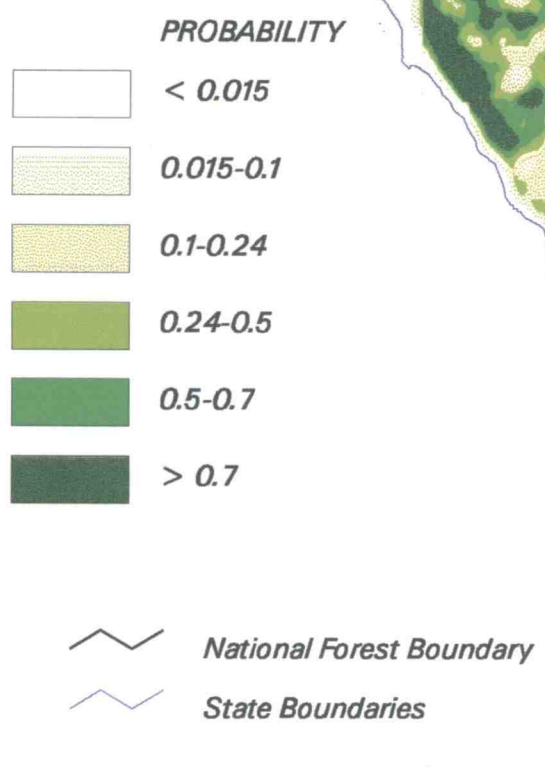
Universal Transverse Mercator, Zone 10

Without a functional understanding of the factors driving the trend surface component of the model, it is difficult to extrapolate these variables to adjacent regions. It might be expected that the Oregon Klamath would experience a coastal to interior climatic gradient similar, although not identical to, the California Klamath. This provides support for the extrapolation of the effects of climatic factors such as precipitation, as well as the UTM Easting component. The quadratic UTM northing component was more difficult to extrapolate to Oregon. It is possible that regional source-sink dynamics show different spatial structure in Oregon due to aggregations of habitat in areas such as the Grassy Knob and Kalmiopsis Wilderness Areas.

5.2 Comparisons of Predicted and Observed Distribution

This study demonstrates that conclusions drawn from habitat selection studies may be highly dependent on the scale at which selection is measured. Whereas a plot-level analysis of our validation data might indicate that there is no significant association between fishers and tree size class, a landscape level analysis reaches the opposite conclusion. Analysis at multiple scales may be especially critical for understanding the distribution of wide-ranging carnivores such as the fisher.

Although the level of agreement between model and data is encouraging, it is likely that the complexity of fisher distributional dynamics is only crudely approximated by the trend surface and moving average components. The non-systematic nature of the retrospective data inevitably leads to regions with large estimation error. Spatial trends must be extrapolated to areas without survey effort. These areas are highlighted on a map

of kriging error structure (Figure 4.6). Private lands and the southeastern Klamath region

(Shasta-Trinity National Forest) have the highest levels of kriging error.

In addition, poorly sampled portions of attribute space are evident. For example,

few surveys have been conducted in areas of low road density due to logistical

constraints. This results in poor sampling of high-elevation areas and their characteristic

forest types (e.g. red fir (*Abies magnifica shastensis*)).

Comparison of the probability maps produced under alternate models can serve as

a type of "sensitivity analysis" of the robustness of predictions to variations in model

structure. A comparison of the MLR model map with that produced by a landscape

version of the CWHR model shows that the CWHR model underemphasizes areas in the

eastern part of the region (Figure 5.9). In addition, CWHR models without the UTM

Northing component do not accurately predict detection probability in the northern part of

the region. CWHR modeling is usually conducted with patch-level information, which

further weakens its accuracy.

The model incorporating 30 km^2 scale MA variables has slightly less explanatory

power than the 10 km^2 scale model in the retrospective analysis (BIC of -3949 and -3951,

respectively). However, it gives significantly better predictions for the validation data set

($r = 0.68$ rather than 0.58). A coarser-scale model may be less sensitive to fine-scale error

and variability in the main data set and thus may have greater generality. The 30 km^2

scale model cannot be considered to have been validated by the 1996 surveys since it was

elaborated after examining the validation survey data. Its predictions will be compared

with the results off the 1997 surveys.

The explanatory and predictive power of the model is high for landscape-scale models using retrospective data (Austin and Meyers 1996, Neave et al. 1996). However, approximately two thirds of the variance remains unexplained in both retrospective and validation data sets. Various possible sources of unexplained variance exist. Measurement error in the GIS vegetation layer is known to range from 60-80% for categorical attributes (Cal. Timberland Task Force 1993). The effect of this fine-scale error is reduced, but not eliminated, by the MA modeling. The nature of the GIS data available for the entire region limited the choice of landscape-scale variables. This may mean that some important landscape-level variates are not included in the model.

Other sources of variance include effects at scales not incorporated in the model. The plot-level vegetation variables I examined had little explanatory power, but other fine-scale variation such as spatial and temporal variation in prey abundance may be important. Prey abundance may not be directly correlated with the forest structure variables measured in this study. The randomization incorporated into the NFI grid sampling design insures that validation stations will not necessarily be placed in the "best" habitat as in previous surveys. This will increase the amount of unexplained variation.

Landscape pattern (e.g. habitat fragmentation) may also have an effect on fisher distribution that is additive to the effects of habitat area alone (Hargis and Bissonette in press). Variance in habitat quality (analyzed by means of the FOCALSTD function) proved to be non-significant, but other aspects of landscape structure were not incorporated into the model. These include metrics such as patch area or habitat

MEAN SUITABILITY
(CWHR MODEL)

	< 1 (LOW)
	1 - 1.5
	1.5 - 1.7
	1.7 - 1.9
	1.9 - 2.1
	2.1 - 2.3
	2.3 - 2.5
	2.5 - 2.6
	2.6 - 2.7
	> 2.7 (HIGH)

National Forest Boundary

State Boundary

0   25

KM

Universal Transverse Mercator, Zone 10
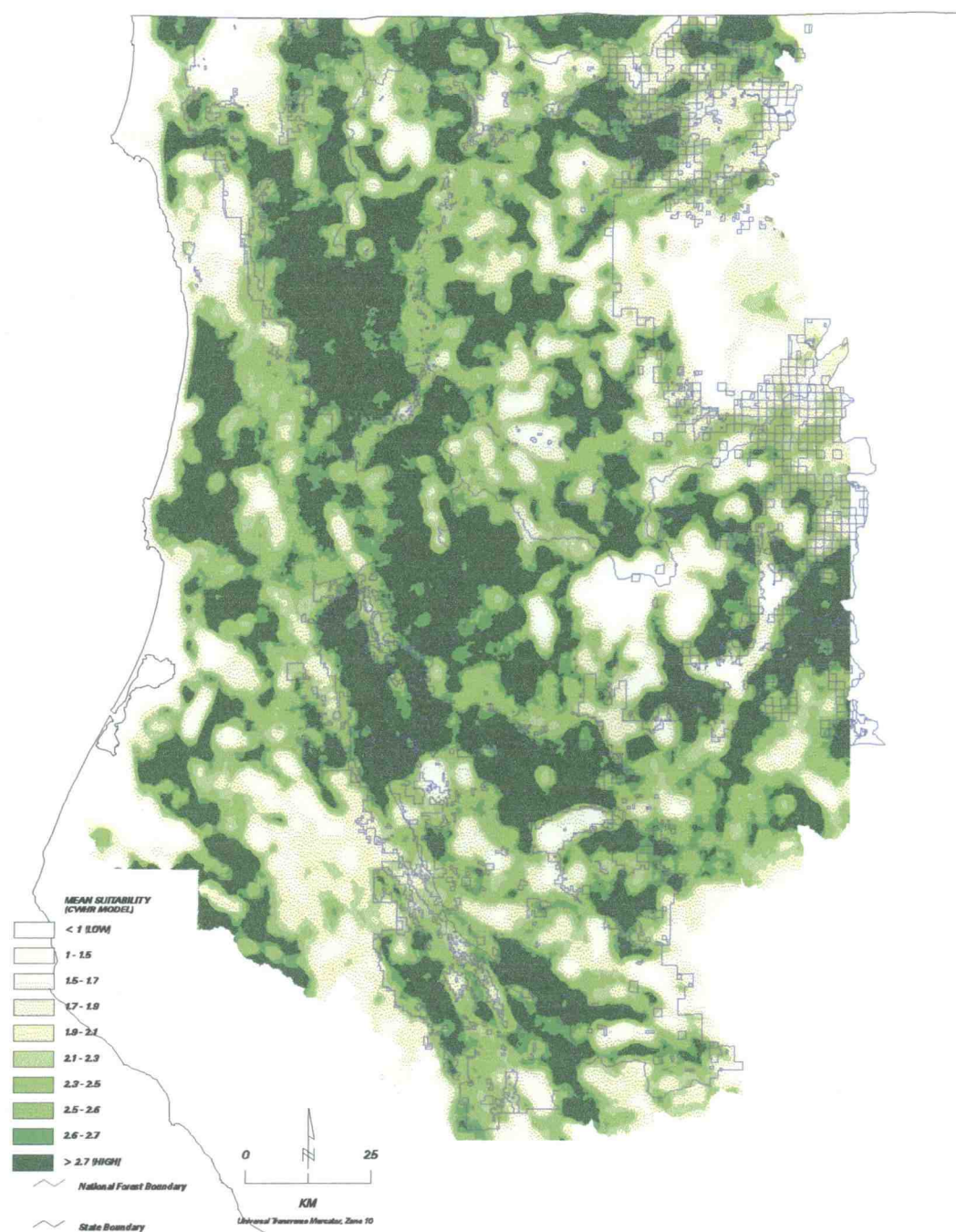
Figure 5.9 Map of habitat suitability for fishers predicted from landscape-level adaptation of CWHR model.

contagion. which can be measured by landscape analysis programs such as FRAGSTATS (McGarigal and Marks 1995). However, the computationally-intensive nature of these programs prevent their incorporation into a moving-window analysis.

Stochastic variability in habitat occupancy due to events such as the death of resident animal and temporal shifts in home range boundaries adds an additional component of unexplained variance. However, the degree of explanatory power achieved demonstrate that, at least for wide ranging carnivores such as the fisher, spatial habitat modeling can be a useful tool for increasing our understanding of the factors influencing distribution.

5.3 Sympatric Carnivore Data

Correlations among carnivores of percentage of stations per SU with detections show low values (Table 4.14). However, correlation coefficients will not reveal non-linear relationships between species or between species and environmental variables. The strongest correlation (between bear and fisher) can be attributed in part to the fact that bears often render the station unable to detect other carnivores (until the next station check) by rolling or collapsing the station. The low correlation strengths suggest that the various carnivores are using different habitat resources or scales of selection. The differences between the species in latency to first detection and stations per sample unit with detections also suggest differences in grain response. Gray fox was detected at fewer SUs than was fisher, but at those SUs was detected earlier and at more of the stations. This is in agreement with the smaller home range size of gray fox (Zeiner et al. 1988).

Comparisons of environmental variables at detection and non-detection sites also support the hypothesis that the different species select resources at different scales. As was the case in the fisher data, significant comparisons across all sites may reflect landscape-level association, whereas significant comparisons between stations in occupied sample units may indicate patch-level association.

Habitat generalists should select at a fine scale because they can locate preferred microscale resources in a variety of landscapes (Pedlar et al. 1997). Black bears show significant station-level association with patches of mixed forest with large hardwoods. Unlike the other carnivore species, they show less evidence of landscape-scale association, at least at the 10 km² scale (Table 4.18). Ringtails and gray fox show significant association with mid-elevation mixed hardwood/conifer landscapes with large hardwoods (Tables 4.15 and 4.16). Spotted skunk also associates with mixed hardwood/conifer landscapes, but these are the drier and more open conifer/deciduous oak forests of the eastern Klamath (Table 4.17). No species other than fisher show a significant positive association with landscape-level tree size class. Spotted skunk show a negative association with this variate that may be due to their abundance in the smaller forests of the eastern Klamath.

5.4 Future Uses of the Model

Future uses of the model include prediction of habitat suitability in other regions such as the Sierra Nevada. The distribution of fishers in the Sierra Nevada is presently limited to the southern portion of the range (Zielinski et al. 1996). Comparisons with

historical trapping records show that this represents a fairly recent range contraction. It is not known whether the extirpation of fishers from the northern Sierra Nevada resulted from habitat alteration, direct human impacts such as trapping, or a combination of factors. Predictive modeling of fisher distribution in the Sierra Nevada using the model developed in the Klamath would help determine whether habitat is significantly poorer in the northern Sierra than in the southern part of the range. This information would be useful in planning recovery efforts such as reintroduction.

Extrapolation of the model to other regions will encounter several difficulties. It is necessary to use models without trend surface variables. Precipitation is a acceptable substitute for UTM Easting, but modeling fisher distribution in the Sierra Nevada without incorporating substitutes for the UTM Northing variable will lower prediction accuracy.

Floristic differences between the Klamath and Sierras are also likely to complicate modeling. Douglas-fir, the most abundant conifer in the Klamath, is absent from the southern Sierra, and deciduous hardwoods are more prevalent than evergreen species. The north-south orientation of the Sierra range produces a strong west/east orographic effect on precipitation, as well as distinct elevational zonation of plant communities. This may create barriers to dispersal not encountered in the more topographically complex Klamath ranges. Differences in historical human impact, such as the prevalence of selective logging in the Sierra Nevada, present additional challenges to model extrapolation.

The development of multi-species models through spatial habitat modeling is another promising avenue for research. Individual models can be developed for each of the forest carnivore species commonly detected at survey stations. Comparisons of the

predictions of these models with those of a multi-species model may help separate the effects of habitat alone from the effects of forest carnivore community interactions.

5.5 Research Implications

5.5.1 Tools Required for Regional Spatial Analyses

Analysis of regional spatial data sets requires data sources and analytical tools distinct from those traditionally used in wildlife research. The use of remote sensing data allows analysis and planning on a similar scale to that of the anthropogenic stressors which affect plant and animal distributions. Multitemporal analyses of such data sets are useful in detecting such large-scale trends, especially if other data such as wildlife surveys are incorporated. The GIS and data storage capability needed for these analyses is becoming more widely available, allowing its use by groups outside of government and academia.

Geostatistical software is increasingly available to supplement traditional non-spatial statistical analysis. The analysis used here has the advantage of incorporating functions such as MA and kriging that are already available in some GIS packages. These functions represent the first steps in the increased integration of GIS and spatial statistical software (Bailey 1993). As this type of analysis becomes more common, it is hoped that a wider variety of spatial modeling methods will be incorporated into GIS software.

Coordination of the design of field surveys is needed to allow data from many areas to be analyzed in common for multiple purposes. For example, ground-based vegetation surveys on public lands could be designed to gather additional information

useful for monitoring forest health trends. The National Forest Inventory (NFI) program of the U.S. Forest Service represents an initial step towards broadening the utility of traditional Forest Inventory and Analysis (FIA) plots. The fact that the surveys incorporate a systematic sampling design also enhances their usefulness in detecting spatial trends. Linkage of wildlife surveys to such a systematic sampling design, such as was used in this study will also improve coordination of data collection.

5.5.2 Applications to Monitoring

The relevance of this type of spatial analysis to monitoring efforts is high. The cost of a extensive monitoring program makes the choice of a optimal sampling design critical. Analysis of spatial correlation structure of pilot survey data may provide direction as to the optimal distance between sampling sites (Haining 1990).

Spatial analysis can also aid in the identification of the areas where regional environmental gradients are steepest. A gradsect sampling approach has recently been used to design a long-term study to detect responses of vegetation to climate change in forests of the Rocky Mountains (Stohlgren and Bachand 1997). Areas of highest estimation error for both spatial and environmental variates (i.e. "holes" in current data) can also be identified and targeted for survey effort.

Spatial analysis of retrospective or pilot survey data may also help in the selection of candidates for indicator species based on the concept of grain response (McGarigal 1993). Habitat alteration and fragmentation at a particular spatial scale is expected to affect strongly only those species that sample the landscape at that scale. Species tend to

group into a limited number of locations along the continuum of possible scales due to interactions between morphological constraints and the spatial structure of the environment (Holling 1992). Monitoring of habitat change at multiple scales is facilitated by selecting representative species from among these spatial "guilds".

Designing an optimal multi-species monitoring program using spatial analysis presents challenges due to the variety of scales at which focal species respond to environmental change. An interpenetrating grid sampling design such as is used in the NFI program can incorporate multiple scales of sampling (Stevens 1994). Sampling sites at the coarsest scale would cover the whole region. The sites would be "densified" in areas identified by spatial analysis in order to improve trend detection for species responding to fine scale processes (Noss 1990). The existence of coarse-scale data for these species throughout the region would facilitate scaling up from the fine-scale data.

In an effort to avoid the regulatory "train wrecks" brought about by the listing of endangered species, a shift from species to "ecosystem management" has been advocated (Grumbine 1994). In this context, it may seem more efficient to monitor aggregate indicators of ecosystem "health" or functional integrity rather than continuing to monitor individual species. However, well-selected focal species or groups of species may serve as sensitive "bioindicators" of landscape change at scales not evident to the human observer (Karr 1981, Noss 1990). If focal species are to fulfill this role, monitoring programs must be carefully designed. In the past, monitoring programs have been implemented without a clear understanding of scale, statistical power, and other sampling design issues (Noss 1990, NRC 1995). Increasingly, these considerations are being

incorporated into the planning stages of monitoring programs. However, the need to

revisit these questions after initial monitoring data has been collected is not often

recognized. Although it is important to maintain consistency of effort over time, it should

be possible to refine sampling programs based on spatial and temporal trends detected in

the course of pilot monitoring programs (Legendre et al. 1989). This "adaptive

monitoring" could play an important role in "adaptive management" strategies.

5.6 Conservation Implications

5.6.1 Regional Characteristics and Fisher Population Dynamics

The persistence of fishers in the Klamath region focuses attention on regional-

scale patterns that distinguish this region from other parts of the western U.S. from which

fishers have been extirpated. The ecology and land-use patterns of the Klamath region

may help explain current patterns of fisher distribution. The sprouting ability of both

evergreen hardwoods and redwoods helps these forests recover canopy closure more

rapidly after disturbance, making their habitat resources more resilient to logging. This

would make these landscapes more similar to eastern forests than to other western forests

and might help explain the persistence of fishers in both the eastern U.S. and in this

region.

The Klamath region can be seen as representing a continental-scale "ecotone"

between the evergreen hardwood forests of the Madrean flora to the south and the

coniferous forests to the north (Whittaker 1961, Sawyer et al. 1977). The late seral

Douglas-fir/mixed evergreen hardwood forests of the region may produce landscapes

with an optimal combination of habitat resources for fishers: high levels of canopy closure, large wood provided by the conifers and mast provided by the hardwoods.

Due to its steep topography, the Klamath region has also lost less of itslate-successional forest than have forest lands in the Oregon Coast and Cascades (Figure 5.5). The late-successional forest that remains in the region is predominantly on public lands. This means that late-successional forest in low-elevation forest types is scarce. This has disproportionately impacted coastal taxa such as the Humboldt marten. However, the predominantly early seral character of coastal forests may create landscape connectivity problems for other taxa, especially if current trends towards shorter harvest rotations continue.

While high-elevation forest types are well represented in protected areas, mid-elevation types are not. Our results suggest that these mid-elevation Douglas-fir/mixed evergreen types are among the most valuable fisher habitat in the region. Recent designation of Late-Successional Reserves (LSRs) has improved representation of these types, albeit in a semi-protected management category.

5.6.2 Spatial Distribution of Fisher Habitat

The distribution of habitat predicted by the final model incorporating precipitation provides a coarse evaluation of the representation of fisher habitat in various mannagement categories (Table 5.1). Although the mean probability values vary between Model 1 and 2, the relative rankings of the landuse categories is similar. It can be seen from the table and the associated map (Figure 5.10) that existing reserves provide

relatively poor representation of fisher habitat. Although the redwood parks are an exception, most protected areas are dominated by high-elevation forests. Late-Successional Reserves provide significantly better representation of fisher habitat, which is not suprising given that were designed to protect another late-seral associated species, the northern spotted owl (McKelvey et al. 1993). However, the spatial structure of fisher distribution is more aggregated than the distribution of LSRs. This means that some LSRs in the margins of the region have low probability of being used by fishers, while other non-LSR areas close to the central "mainland" of fisher distribution are likely to be important habitat. Protection of fisher viability in this mainland area may require higher levels of representation in protected or semi-protected categories.

These conclusions also call attention to the need to supplement traditional conservation goals with an awareness of the biological importance of non-wilderness lands. Many of the areas highlighted as predicted habitat are biologically productive low to mid-elevation forests that have experienced some degree of human impact. Species-rich low to mid-elevation forests where logging began earlier may retain only highly fragmented LSOG habitat. However, these patches may be more valuable as nuclei for biodiversity reserves than their size or connectivity would indicate (Franklin 1993, Spies et al. 1994).

In the past, the "non-pristine" nature of these areas would have made them unlikely to gain the public support necessary for their protection. In the past decade, conservationists have increasingly become aware of the role of these areas in sustaining

PREDICTED PROBABILITY (MODEL 2)

- [ ] 0 - 0.015
- [ ] 0.015 - 0.1
- [ ] 0.1 - 0.24
- [ ] 0.24 - 0.5
- [ ] 0.5 - 0.7
- [ ] 0.7 - 1.0

~ National Forest Boundary
~ Wilderness or Park Boundary
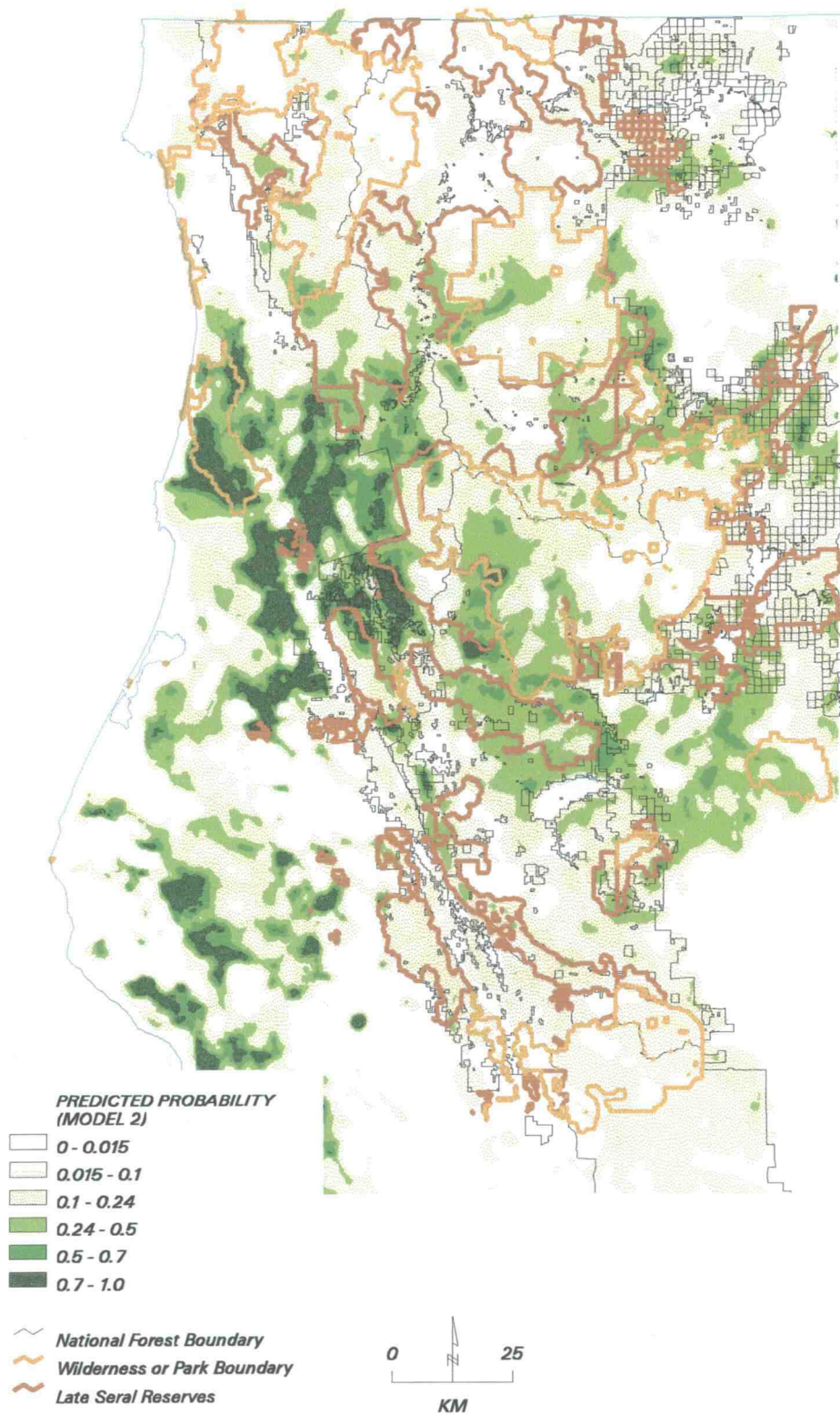~ Late Seral Reserves

0 ——— 25
KM

Figure 5.10 Predicted probability of fisher detection (Model 2) as compared to landuse category.

biodiversity. However, the somewhat artificial dichotomy between "wildness" and

"biodiversity" continues to be a source of conflicting priorities in the face of limited

resources for conservation.

Table 5.1. Mean predicted probability value vs. ownership and management category.
Values for Model 1 are followed by values for Model 2 in parentheses.

Overall	0.185 (0.148)
All Forest Service land	0.202 (0.147)
Matrix	0.206 (0.145)
Late-Successional Reserves	0.242 (0.176)
Forest Service reserves (wilderness)	0.146 (0.119)
Non-Forest Service reserves (parks)	0.361 (0.231)
Private land	0.213 (0.179)

5.6.3 Implications for Population Viability

This study further documents the discontinuous distribution of fishers in the

Pacific coastal states that has become evident from previous work in California (Zielinski

et al. 1996), Oregon (Aubry 1997) and Washington (Aubry and Houston 1992). The

nearest neighboring fishers to the Klamath population are the small reintroduced

population near Crater Lake in Oregon and the southern Sierran population (Aubry 1997,

Zielinski et al. 1996). Dispersal between the Klamath and these populations is likely to be

infrequent in the former case and non-existent in the latter. This poses concerns for

population viability in the face of environmental and genetic stochasticity that need to be

adequately addressed in the future conservation planning for the species.

These concerns apply equally, if not more strongly, to the coastal population of

marten in these states, which belong to the subspecies *Martes americana humboldtensis*

and *M. a. caurina* (Clark et al. 1987). Marten in coastal California were once widespread

throughout the redwood zone north of Santa Rosa (Grinnell et al. 1937, Zielinski and

Golightly 1996). The single detection of marten in the course of our study represents the

only confirmed detection of marten in the range of *M. a. humboldtensis* since the 1940's

(Slauson et al. 1996). Marten are more frequently detected in coastal Oregon (L. Webb,

pers. comm.). Marten detections in coastal Oregon have been primarily in areas identified

as fisher habitat in a version of our model that does not include the north/south spatial

trend variables. This is not surprising, since martens have been found to be linked to

forest structure to an even greater extent than fishers (Thompson 1991, Buskirk 1992,

Buskirk and Ruggiero 1994, Thompson and Harestad 1994). Present data, while

incomplete, suggest that coastal marten may be relatively common in the region only in

the northern and central Siskiyou National Forest, with remnant populations occurring

south into California. If this is the case, the results of our study should raise concerns

over the viability of the coastal marten populations in both states.

5.6.4 Suggested Conservation Strategy

The clearest lesson to be drawn from the present study is the importance of

planning on a regional scale. This reinforces the conclusions of the conservation planning

process for another umbrella species, the northern spotted owl. The population modeling

studies that formed part of the reserve design process for the Northwest Forest Plan

emphasized the parallels between the processes that occur within a population (births and

deaths) and those that occur between populations in a metapopulation (immigration and

emigration)(Noon and McKelvey 1996a). Lande's (1987) model had predicted the existence of extinction thresholds as the proportion of suitable habitat in an area declined. A population inhabiting an area below the threshold level could be on an extinction trajectory even if habitat degradation was halted. Similarly, the regional metapopulation might show non-linear responses to the size and spacing of habitat clusters. If these clusters were too small or isolated, the imbalance between immigration and emigration might limit long-term viability despite the presence of suitable habitat (McKelvey et al. 1993, Noon and McKelvey 1996a). The decline in distribution of the fisher in the western U.S. may be due to similar regional-level dynamics. Existing land management planning processes are poorly adapted to decision making across administrative boundaries. The survival of the fisher, like that of other wide-ranging carnivores such as the timber wolf, may depend on multi-ownership cooperative management at the regional scale (Mladenoff et al. 1995).

Designing regional conservation networks for forest carnivores is difficult without data on the distribution of source and sink habitat. If core refugia are expected to be a source of recolonizers that maintain metapopulation viability, the reserves need to be located primarily in source habitat (the exception being areas designed to enhance connectivity). Reserves must be spatially distributed in such a way as to insure connectivity with populations needing recolonization (Buskirk 1995). Although distribution is used as a surrogate for habitat quality in this study, future research is needed to explore the relationship between distribution and fitness. Initial reserve designs arising from exploratory studies such as this one may be expected to be modified as more

information becomes available. In the context of adaptive management, these reserve designs become testable hypotheses in an iterative process of refinement by future studies (Holling 1978, Murphy and Noon 1992, McKelvey et al. 1993).

Concerns over the viability of the Klamath fisher population arise from specific aspects of the spatial distribution of predicted habitat. The Klamath population may conform to a "mainland-island" metapopulation because of the concentration of habitat in the Trinity River area. Maintenance of the mainland area as a robust source of dispersers is the highest priority in these situations. This study has also called increased attention to areas of eastern Klamath, such as the Trinity and Whiskeytown Lake areas, as potential habitat. These more xeric forests had not been classified as highly suitable by existing habitat models such as CWHR.

The Klamath population may conform to a "patchy" metapopulation due to the long-range dispersal ability of fishers (Stith et al. 1996). Well-defined dispersal barriers such as agricultural lands on the margins of the region may limit recolonization of adjacent regions. Within the region, however, habitat threshold effects that are not identified with dispersal barriers may be driving the reduction in distribution. That this reduction is ongoing is suggested by the existence of large portions of the validation area where fishers were not detected (Figure 4.10).

Real-world metapopulations may resemble more than one type of metapopulation model. In such a "mixed" metapopulation, "central patches are united by dispersal into a single population, slightly more isolated ones undergo extinction and recolonization, and still more isolated patches are usually vacant" (Harrison and Taylor 1997).

Connectivity between the central "mainland" areas and outlying populations is necessary if the reduction in distribution is to be reversed. Connectivity between Redwood National Park and the Hoopa Indian Reservation and Six Rivers National Forest may be further impacted in the future due to the lack of public land in this area. Maintenance and restoration of habitat linkages between the central Klamath and remnant coastal habitat in the Kings Range and Headwaters Forest area may be critical for persistence of fishers in these areas. The near extirpation of fishers from the middle Klamath River corridor above the confluence with the Salmon River poses problems for dispersal to the Oregon Klamath region. Fires and subsequent salvage logging also seem to have extirpated fisher from much of the lower Salmon River watershed. Restoration of habitat connectivity in the northeastern Klamath would help recreate regional-scale habitat linkages to the Cascades and Sierra Nevadas. This would facilitate natural recolonization of these areas.

The study data also highlight the role of large hardwoods as a keystone resource in the forests of the region. Forest management has traditionally seen hardwoods as competitors with timber producing conifers and has sought to eliminate them. Their role in maintaining soil productivity (Perry et al. 1989), biodiversity (Neitlich and McCune 1997), as well as wildlife habitat resources, suggests that the largest hardwoods on a site should be retained after logging.

This study forms part of a larger research effort to develop a Klamath/Siskiyou Biodiversity Conservation Plan (Vance-Borland et al.1996). This project is a regional assessment of conservation needs based on analysis of physical habitat diversity,

assessment of representation of vegetation types, mapping of the distribution of rare species' habitats and other biological "hotspots", analysis of aquatic habitats, and habitat modeling of forest carnivores. The goal is to use species-level and ecosystem-level research in a complementary fashion to determine conservation priorities for the region. Although this goal is widely held, few examples currently exist of the successful integration of the results of habitat modeling of umbrella species with other planning priorities such as ecosystem representation. The methods used in this study should be widely applicable in addressing reserve design questions in other regions.

Bibliography

Agee, J. K. 1993. Fire ecology of Pacific northwest forests. Island Press, Washington, D.C.

Agee, J. K., S. C. F. Stitt, M. Nyquist, and R. Root. 1989. A geographic analysis of historical grizzly bear sightings in the North Cascades. Photogrammetric Engineering and Remote Sensing 55:1637-1642.

Akcakaya, H. R. 1994. RAMAS/GIS: Linking landscape data with population viability analysis (version 1.0). Applied Biomathematics, Setauket, NY.

Allen, T. F. H., R. V. O'Neill, and T. W. Hoekstra. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110, Rocky Mtn. Forest and Range Experiment station, Fort Collins, CO. 11 pp.

Aspinall, R., and N. Veitch. 1993. Habitat mapping from satellite imagery and wildlife survey data using a Bayesian modeling procedure in a GIS. Photogrammetric Engineering and Remote Sensing 59:537-543.

Aubry, K. B. 1996. Ecological characteristics of fishers in southwestern Oregon; progress report: February 1997. Unpaged.

Aubry, K.B., and D.B. Houston. 1992. Distribution and status of the fisher in Washington. Northwestern Naturalist 73:69-79.

Austin, M. 1985. Continuum concept, ordination methods, and niche theory. Annual Review of Ecology and Systematics 16:39-61.

Austin, M., and P. C. Heyligers. 1991. New approach to vegetation survey design: gradsect sampling. Pages 31-36 in C. R. Margules and M. P. Austin, editors. Nature conservation: cost effective biological surveys and data analysis. CSIRO, Melbourne, Australia.

Austin, M., and J. A. Meyers. 1996. Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. Forest Ecology and Management 85:95-106.

Bailey, T. C. 1993. A review of statistical spatial analysis in geographic information systems. Pages 13-44 in S. Fotheringham and P. Rogerson, editors. Spatial analysis and GIS. Taylor and Francis, Bristol, PA.

Bailey, T. C. and A. C. Gatrell. 1995. Interactive spatial data analysis. Addison-Wesley, NY.

Baker, B.W., B.S. Cade, W.L. Mangus, J.L. McMillen. 1995. Spatial analysis of sandhill crane habitat. Journal of Wildlife Management 59: 752-758.

Banci, V. 1989. A fisher management strategy for British Columbia. Wildlife Bulletin No. B-63. B.C. Ministry of the Environment, Lands and Parks, Wildlife Branch. Victoria, B.C.

Beardsley, D. And R. Warbington. 1996. Old growth in northwestern California National Forests. Res. Pap. PNW-RP-491. USDA Forest Service Pacific Northwest Research Station, Portland, OR. 47 pp.

Beyer, K.M., and R.T. Golightly. 1995. Distribution of Pacific fisher and other forest carnivores in coastal northwestern California. Unpublished report. 23 pp.

Bissonette, J.A., R.J. Frederickson, and B.J. Tucker. 1989. Pine marten: a case for landscape level management. Pages 89-101 in Transactions of the North American Wildlife and Natural Resources Conference. Wildlife Management Institute, Washington, D.C.

Bojorquez-Tapia, L. A., I. Azuara, and E. Ezcurra. 1995. Identifying conservation priorities in Mexico throough geographic information systems and modeling. Ecoological Applications 5:215-231.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045-1055.

Boyce, M.S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23: 481-506.

Brainerd, S.M. 1990. The pine marten and forest fragmentation: a review and general hypothesis. Pages 421-434 in Transactions of the 19th IUGB Congress, Trondheim, Norway.

Burgman, M.A., S. Ferson, and H.R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman and Hall. London, England.

Buskirk, S.W. 1992. Conserving circumboreal forests for martens and fishers. Conservation Biology 6:318-320.

Buskirk, S. W. 1995. The refugium concept and the conservation of forest carnivores. Pages 242-245 in Transactions of the 21st IUGB Congress, Halifax, Canada.

Buskirk, S.W. In prep. Mesocarnivores of Yellowstone.

Buskirk, S.W., A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. 1994. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American Martens. Pages 283-296 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Buskirk, S.W. and L.F. Ruggiero. 1994. American Marten. Pages 7-37 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Ft.Collins, CO. 184 pp.

California Timberland Task Force. 1993. The report of the California Timberland Task Force. California Department of Forestry and Fire Protection, Sacramento, CA. 78 pp.

Carlton, J. 1995. Rare fisher threatened: petition filed for endangered species act protection. Predator Project Newsletter. Winter 1995.

Carpenter, S. R. 1990. Large-scale perturbations: opportunities for innovation. Ecology 71:2038-2043.

Clark, L. A., and D. Pregibon. 1993. Tree-based models. Pages 377-420 in J. M. Chambers and T.J. Hastie. 1993. Statistical Models in S. Chapman and Hall, New York, NY.

Clark, T.W., E. Anderson, C. Douglas, and M. Strickland. 1987. *Martes americana*. Mammalian Species Number 289. American Society of Mammalogists. 8 pp.

Cliford, P., S. Richardson, and D. Hemon. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45:123-134.

Cohen, W. B., T. A. Spies, and M. Fiorella. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. International Journal of Remote Sensing 16:721-746.

Conroy, M. J., and B. R. Noon. 1996. Mapping species richness for conservation of biological diversity: conceptual and methodological issues. Ecological Applications 6:763-773.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33: 140-158.

Dark, S. J. 1997. A landscape-scale analysis of mammalian carnivore distribution and habitat use by fisher. M.S. thesis, Humboldt State University, Arcata, CA.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

Dutilleul, P. and P. Legendre. 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. Oikos 66:152-171.

ESRI, Inc. 1996. Arc-Info, version 7.0. Environmental Systems Research Institute, Inc. Redlands, CA.

Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology to test hypotheses abbout large-scale abundance patterns in migratory birds. Ecology 77:28-35.

Fortin, M.-J., P. Drapeau, and P. Legendre. 1989. Spatial autocorrelation and sampling design in plant ecology. Vegetatio 83:209-222.

Fortin, M.-J., and J. Gurevitch. 1993. Mantel tests: spatial structure in field experiments. Pages 342-359 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of field experiments. Chapman and Hall, NY.

Fox, L. 1989. A classification, map, and volume estimate for the coast redwood forest in California. Forest and Rangeland Assessment Program, Calif. Dept. of Forestry and Fire Protection, Sacramento, CA. Unpublished report, 37 pp.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications 3:202-205.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Gen.Tech. Rep. PNW-8. USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Freel, M. 1991. A literature review for management of the marten and fisher on national forests in California. USDA Forest Service Pacific Southwest Region, San Francisco, CA. Unpaged.

Gates, S., D. W. Gibbons, P. C. Lack, and R. J. Fuller. 1994. Declining farmland bird species: modelling geographical patterns of abundance in Britain. Pages 153-177 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Science, Cambridge, UK.

Gibilisco, C.J. 1994. Distributional dynamics of modern *Martes* in North America. Pages 59-71 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, Sables, and Fishers: Biology and Conservation. Cornell Press, Ithaca. 484 pp.

Gosz, J. R. 1993. Ecotone hierarchies. Ecological Applications 3:369-376.

Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1937. Furbearing mammals of California. Vol. I. University of California Press, Berkeley, CA. 375 pp.

Grumbine, R. E. 1994. What is ecosystem management? Conservation Biology 8:27-38.

Gutierrez, R., and S. Harrison. 1996. Applying metapopulation theory to spotted owl management: a history and critique. Pages 167-185 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Wahington, D.C.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University Press, Cambridge, UK.

Hanski, I. 1996. Metapopulation ecology. Pages 13-44 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, IL.

Hanski, I., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Hargis, C.D., and J.A. Bissonette. In press. Effects of forest fragmentation on populations of American marten in the intermountain west. Proc. 2nd International *Martes* Symp., Edmonton, Canada.

Harrison, S. 1994. Metapopulations and conservation. Pages 111-128 in P.J. Edwards, R.M. May, and N.R. Webb, editors. Large-Scale Ecology and Conservation Biology. Blackwell Scientific Publications, Cambridge, MA.

Harrison, S., A. Stahl, and D. Doak. 1993. Spatial models and spotted owls: exploring some biological issues behind recent events. Conservation Biology 7:950-953.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27-42 in I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Hastie, T. J. 1993. Generalized additive models. Pages 249-308 in J. M. Chambers and T.J. Hastie. Statistical Models in S. Chapman and Hall, New York, NY.

Hastie, T. J., and D. Pregibon. 1993. Generalized linear models. Pages 195-248 in J. M. Chambers and T.J. Hastie. Statistical Models in S. Chapman and Hall, New York, NY.

Hastings, A. and S. Harrison. 1994. Metapopulation dynamics and genetics. Annual Review of Ecology and Systematics 25:167-188.

Heinemeyer, K.S. 1993. Temporal dynamics in the movements, habitat use, activity, and spacing of reintroduced fishers in northwestern Montana. Missoula, MT: University of Montana. M.S. thesis. 158 pp.

Heinemeyer, K.S., and J.L. Jones. 1994. Fisher biology and management in the western United States: a literature review and adaptive management strategy. USDA Forest Service Northern Region, Missoula, MT. 108 pp.

Holling, C.S. 1978. Adaptive Environmental Assessment and Management. Wiley, New York, NY.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447-502.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, NY. 307 pp.

Hurlbert, S. H. 1984. Psuedoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Irwin, L.L. 1994. A process for improving wildlife habitat models for assessing forest ecosystem health. Journal of Sustainable Forestry 2: 293-306.

Jager, H. I., and W. S. Overton. 1993. Pages 422-431 in M. F.Goodchild, B. O. Parks, and L. T. Steyaert, editors. Environmental modeling with GIS. Oxford University Press, NY.

James, F. C., C. A. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecological Applications 7:118-129.

James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annual Review of Ecology and Systematics 21:129-66.

Johnson, D. H. 1989. An empirical Bayes approach to analyzing recurring animal surveys. Ecology 70:945-952.

Karieva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299-302.

Karieva, P., D. Skelly, and M. Ruckelshaus. 1996. Reevaluating the use of models to predict the consequences of habitat loss and fragmentation. Pages 156-166 in S. T. A. Pickett, R.S. Ostfeld, M. Schachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York, NY.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Kolasa, J. and D. C. Rollo. 1991. The heterogeneity of heterogenneity: a glossary. Pages 1-23 in J. Kolasa and S. T. Pickett, editors. Ecological heterogeneity. Springer-Verlag, NY, NY.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Lacy, R. C. 1993. VORTEX: a computer simulation model for population viability analysis. Wildlife Research 20:45-65.

Lacy, R.C., and T.W. Clark. 1993. Simulation modeling of american marten (*Martes americana*) populations: vulnerability to extinction. Great Basin Naturalist 53:282-292.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130:624-635.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659-1673.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107-138.

Legendre, P., and M. Troussellier. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnol. Oceanogr. 33: 1055-1067.

Legendre, P., M. Troussellier, V. Jarry, and M.-J. Fortin. 1989. Design for simultaneous sampling of ecological variables: from concepts to numerical solutions. Oikos 55:30-42.

Lehmkuhl, J.F., and M.G. Raphael. 1993. Habitat pattern around northern spotted owl locations on the Olympic peninsula, Washington. Journal of Wildlife Management 57: 302-315.

Levins, R. 1970. Extinction. Pages 77-107 in M. Gerstenhaber, editor. Some mathematical questions in biology. Am. Math. Soc., Providence, RI.

Link, W. A., and D. C. Hahn. 1991. Empirical Bayes estimation of proportions with application to cowbird parasitism rates. Ecology 77:2528-2537.

Majure, J. J., N. Cressie, D. Cook, and J. Symanzik. In press. GIS, spatial statistical graphics, and forest health. Proc. 3rd Conference on GIS Modeling, Albuquerque, NM.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York, NY.

Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals. Chapman and Hall, New York, NY.

Mathsoft. 1996. S+SPATIALSTATS User's manual, version 1.0. MathSoft, Inc. Seattle, WA.

May, R. 1994. The effects of spatial scale on ecological questions and answers. Pages 1-18 in P. J. Edwards, R. M. May, And N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Science, Cambridge, MA.

McGarigal, K., and B.J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. USDA Forest Service Pacific Northwest Research Station, Portland, OR. 122 pp.

McGarigal, K. 1993. Relationships between landscape structure and breeding birds in the Oregon coast range. Doctoral thesis, Oregon State University, Corvalllis, OR.

McGarigal, K., and W.C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs 65: 235-260.

McKelvey, K., B.R. Noon, and R.H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. pp. 424-450 in P.M. Kareiva, J.G. Kingsolver, and R.B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA.

Meyer, K. E., and W. F. Laudenslayer, Jr. 1988. A guide to wildlife habitats of California. Ca. Dept. of Forestry and Fire Protection, Sacremento, CA. 166 pp.

Milne, B. T., K. M. Johnston, and R. T. T. Forman. 1989. Scale-dependent proximity of wildlife habitat in a spatially-nuetral Bayesian model. Landscape Ecology 2:101-110.

Minta, S.C., and P.M. Kareiva. 1994. A conservation science perspective: conceptual and experimental improvements. Pages 275-304 in T.W. Clark, R.P. Reading, and A. Clarke, editors. Endangered Species Recovery. Island Press, Washington, DC.

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

Murphy, D.D., and B.R. Noon. 1992. Integrating scientific methods with habitat planning: reserve design for northern spotted owls. Ecological Applications 2: 3-17.

Neave, H. M., R. B. Cunnningham, T. W. Norton, and H. A. Nix. 1996. Biological inventory for conservation evaluation III. Relationships between birds, vegetation and environmental attributes in southern Australia. Forest Ecology and Management 85:197-218.

Neitlich, P. N., and B. McCune. 1997. Hotspots of epiphytic lichen diversity in two youung managed forests. Conservattion Biology 11:172-182.

Noon, B. R. and K. S. McKelvey. 1996a. A common framework for conservation planning: linking individual and metapopulation models. Pages 139-165 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Wahington, D.C.

Noon, B. R. and K. S. McKelvey. 1996b. Management of the spotted owl: a case history in conservation biology. Annual Review of Ecology and Systematics 27:135-62.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4:355-364.

Noss, R.F., and A.Y. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press. Washington, D.C.

Noss, R.F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949-63.

NRC (National Research Council). 1995. Review of EPA's environmental monitoring and assessment progrram: overall evaluation. National Academy Press. Washington, D.C.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102-112.

Periera, J.M., and R.M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression - a study of the Mt. Graham red squirrel. Photogrammetric Engineering and Remote Sensing 57: 1475-1486.

Perry, D., M. P. Amarannthus, and J. G. Borchers. 1989. Bootstrapping in ecosystems. Bioscience 39:230-237.

Powell, R.A. 1994a. Declaration on fishers and habitat management in the Sierra Nevada mountains. Appendix C: Expert Declarations in S. Yassa and D.B.Edelson. Petition with request for stay. NRDC. San Francisco, CA.

Powell, R.A. 1994b. Structure and spacing of *Martes* populations. Pages 101-121 in S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Martens, sables and fishers: biology and conservation. Cornell University Press, Ithaca, NY.

Powell, R.A. and W.J. Zielinski. 1994. Fisher. Pages 38-73 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mtn. Forest and Range Experiment Station, Ft. Collins, CO.

Powell, R. A., J. W. Zimmerman, D. E. Seaman, J. F. Gilliam. 1996. Demographic analysis of a hunted back bear population with access to a refuge. Conservation Biology 10:224-234.

Pulliam, R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652- 661.

Pulliam, R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45-69 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, IL.

Raftery, A. E. 1995. Bayesian model selection in social research. In P. V. Marsden, editor. Sociological Methodology 1995. Blackwell Science, Cambridge, MA.

Ramsey, F.L., M. McCracken, J.A. Crawford, M.S. Drut, and W.J. Ripple. 1994. Habitat association studies of the northern spotted owl, sage grouse, and flammulated owl. Pages 189-209 in N. Lange, L. Ryan, and L. Billard, D. Brillinger, L. Conquest, and J. Greenhouse, editors. Case studies in Biometry. John Wiley & Sons, New York, NY.

Raphael, M.G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in douglas-fir forests of northwester California. Pages 23-31 in Management of amphibians, reptiles, and small mammals in North America. Gen.Tech. Report RM-166. USDA Forest Service Rocky Mtn. Forest and Range Experiment Station, Ft. Collins, CO.

Raphael, M.G., J.A. Young, B.M. Galleher. 1995. A landscape-level analysis of marbled murrelet habitat in western Washington. Pages 177-189 in C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael, J.F. Piatt, editors. Ecology and conservation of the marbled murrelet. Gen. Tech. Rep. PSW-GTR-152. USDA Forest Service PSW Research Station, Albany, CA.

Rosenberg, K.V. and R.G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263-272 in J. Verner, M. L. Morrison, and C.J. Ralph, editors. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Rossi, R. E., D. J. Mulla, A. G. Journell, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62:277-314.

Ruggiero, L.F., K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, technical editors. 1994. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. Gen. Tech. Rep. RM-254. USDA Forest Service Rocky Mtn. Forest and Range Experiment Station, Ft. Collins, CO. 184 pp.

Sawyer, J. O., and D. A. Thornburgh. 1977. Montane and subalpine vegetation of tthe Klamath mountains. Pages 699-732 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Cal. Native Plant Soc. Special Pub. No. 9.

Sawyer, J. O., D. A. Thornburgh, and J. R. Griffin. 1977. Mixed evergreen forest. Pages 359-382 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Cal. Native Plant Soc. Special Pub. No. 9.

Schneider, R.R. and P.Yodzis. 1994. Extinction dynamics in the american marten (*Martes americana*). Conservation Biology 8:1058-1068.

Schumaker, N. 1996. Using landscape indices to predict habitat conectivity. Ecology 77:1210-1225.

Sierra Audubon Society. 1990. Petition to list tthe Pacific coast fisher as endangered. 26 pp. unpublished.

Slauson, K. C. Carroll, and B. Zielinski. 1996. Don't count the Humboldt marten out yet. The Marten 1(2):1-4. Newsletter of the Humboldt Chapter of the Wildlife Society.

Smouse, P. E., C. J. Long, and R. R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systematic Zoology 35:727-32.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman, New York, NY.

Species Analysis Team. 1994. Results of additional species analysis: appendix J2 to the FSEIS on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. Goverment Printing Office, Washington, DC. 486 pp.

Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555-568.

Stevens. D. L. 1994. Implementation of a national monitoring program. Journal of Environmental Management 42:1-29.

Statistical Sciences. Inc. 1995. S-PLUS, version 3.3. MathSoft, Inc. Seattle, WA.

Stith, B. M., J. W. Fitzpatrick, G. E. Woolfenden, and B. Pranty. 1996. Classification and conservation of metapopulations: a case study of the Florida scrub jay. Pages 187-215 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press. Wahington, D.C.

Stohlgren, T. J., and R. R. Bachand. 1997. Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado. U.S.A. Ecology 78:632-641.

Thompson. I.D. 1991. Could marten become the spotted owl of Canada? Forestry Chronicle 67:136-140.

Thompson, I.D. and A.S. Harestad. 1994. Effects of logging on American martens with models for habitat management. Pages 355-367 in S. W. Buskirk, A.S. Harestad. M.G. Raphael, and R.A. Powell, editors. Martens, Sables, and Fishers: Biology and Conservation. Cornell Press, Ithaca, NY. 484 pp.

Thomson, J. D., and G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, andd rocks. Ecology 77:1698-1715.

Trexler, J.C., and J. Travis. 1993. Nontraditional regression analyses. Ecology 74: 1629-1637.

Tukey, J. W. 1977. Exploratory data analysis. Addison-Wesley, Reading, MA.

USDI Fish and Wildlife Service. 1996. 90-day finding for a petition to list the fisher in the western United States as threatened. Federal Register 61:8016.

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

Vance-Borland, K., R. Noss, J. Strittholt, P. Frost, C. Carroll, R. Nawa. 1995. A biodiversity conservation plan for the Klamath/Siskiyou region: a progress report on a case study for bioregional conservation. Wild Earth 5:52-59.

Ver Hoef, J. M. and N. Cressie. 1993. Spatial statistics: analysis of field experiments. Pages 319-341 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of field experiments. Chapman and Hall. NY.

Wallin, D. O., F. J. Swanson, B. Marks, J. H. Cissel, J. Kertis. 1996. Comparison of managed and pre-settlement landscape dynamics in forests of the Pacific Northwest, USA. Forest Ecology and Management 85:291-309.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060-2068.

Weaver, J. 1993. Lynx, wolverine, and fisher in the western United States: research assessment and agenda. USDA Forest Service Intermountain Research Station. Missoula, MT. 132 pp.

Wenger, K. F. 1984. Forestry handbook. 2nd edition. John Wiley and Sons, NY.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Wiens, J. A. 1989a. The ecology of bird communities. Vol. I. Foundations and Patterns. Cambridge University Press, New York, NY.

Wiens, J. A. 1989b. The ecology of bird communities. Vol. II. Processes and Variations. Cambridge University Press, New York, NY.

Wiens, J. A. 1989c. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wiens, J.A. 1995. Habitat fragmentation: island vs. landscape perspectives on bird conservation. Ibis 137: S97-S104.

Wiens, J. A. 1996. The emerging role of patchiness in conservation biology. Pages 93-107 in S. T. A. Pickett, R.S. Ostfeld, M. Schachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York.

Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

Yassa, S. and D.B. Edelson. 1994. Petition with request for stay. Natural Resources Defense Council. San Francisco, CA. 32 pp.

Zeiner, D. C., W. F. Laudenslayer, Jr., K. E. Mayer, and M. White. 1988. California's wildlife: Volume III. Mammals. Cal. Dept. of Fish and Game. Sacramento, CA.

Zielinski, W.J. and R.T. Golightly. 1996. The status of marten in redwoods: Is the Humboldt marten extinct?. Proc. Conference on Coast Redwood Forest Ecology and Management, June 18-20,1996, Humboldt State Univ., Arcata, CA.

Zielinski, W.J. and T.E. Kucera. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. Gen. Tech. Rep. PSW-GTR-157. USDA Forest Service Pacific Southwest Research Station, Albany, CA. 163 pp.

Zielinski, W. J. 1991. A survey protocol to monitor forest carnivores in proposed management activity areas. USDA Forest Service PSW Research Station, Arcata, CA. 18 pp.

Zielinski, W.J., T.E. Kucera, and R.H. Barrett. 1996.The current distribution of fishers (*Martes pennanti*) in California. California Fish and Game 81:104-112.

Zielinski, W.J. and H.B. Stauffer. 1996. Monitoring *Martes* populations in California: survey design and power analysis. Ecological Applications 6:1254-1267.

Zielinski, W. J., R. L. Truex, C. V. Ogan, and K. Busse. In press. Detection surveys for fishers and martens in California, 1989-1994: summary and interpretations. Proc. 2nd International *Martes* Symp., Edmonton, Canada.

Zinke, P. J. 1977. The redwood forest and associated north coast forests. Pages 679-698 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Cal. Native Plant Soc. Special Pub. No. 9.