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A spatial approach to statistical habitat suitability modeling: The Mt. Graham red squirrel case study

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A SPATIAL APPROACH TO STATISTICAL HABITAT SUITABILITY MODELING: THE MT. GRAHAM RED SQUIRREL CASE STUDY

by

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ABSTRACT

Multivariate statistical techniques were applied to the development of habitat suitability models for the Mt. Graham red squirrel, an endangered species. A digital map data base and a geographic information system (GIS) were used to support the analysis and provide input for two logistic multiple regression models. Squirrel presence/absence is the dichotomous dependent variable whose probability the models pretend to predict. Independent variables are a set of environmental factors in the first model, and locational variables in the second case, where a logistic trend surface was developed. Bayesian statistics were then used to integrate the models into a combined model. Potential habitat losses resulting from the development of an astronomical observatory were assessed using the environmental model and are found to represent about 3% of currently available habitat.

CHAPTER 1

INTRODUCTION

INITIAL CONSIDERATIONS

The purpose of the present study is to analyze habitat suitability for the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) in an area designated by the U.S. Forest Service as the relevant region of concern, and assess potential habitat losses due to development of an astronomical observatory proposed by the University of Arizona. The Forest Service, responsible for managing the area as a part of Coronado National Forest, must comply with federal environmental protection legislation and estimate potential impacts of development on the endangered red squirrel. Also sought is an identification of critical environmental factors determining habitat suitability and of areas where joint occurrence of desirable habitat characteristics may favor the population maintenance and growth. If these goals are accomplished, it may become possible to mitigate potential negative impacts of the observatory project, through protection of remaining high suitability areas and appropriate modification of less suitable locations. The problem will be approached from a statistical modeling perspective, with the support of a geographic information system (GIS) for data management, analysis and display. A digital data base for the Mt. Graham study area, previously unavailable, was specifically developed for this project and may be used for other research and management purposes, especially if it is complemented with additional thematic layers and periodically updated. The methodology is rooted in habitat modeling concepts and research developed during the last fifteen years, but is applied in an innovative fashion, using techniques such as logistic regression, trend surface analysis, and Bayesian classification, recently introduced to ecological management research (Jongman et al., 1988) and rarely used in conjunction with geographic information systems. It is expected that use of the familiar concept of habitat models, implemented with these sophisticated analytical methods and supported by the powerful GIS technology, will result in a product useful for planning and management of the endangered Mt. Graham red squirrel and its habitat.

ORGANIZATION OF THE STUDY

The first chapter contains an overview of some legislative and methodological antecedents of the present study. In the 1960's and 70's several legislative acts were passed reflecting growing public concerns with environmental matters, and that helped set a consistent framework for an ecological sensitive management of public lands. Briefly reviewed are the National Environmental Policy Act (NEPA) of 1969, the Endangered Species Act (ESA) of 1973, and the National Forest Management Act (NFMA) of 1976.

A theme on this legislation was an emphasis on multiple use of public lands, moving away from the previously dominating paradigm of single-resource management (Duerr et al., 1982; Dana and Fairfax, 1980). One of the issues that gained prominence in the late 60's and 70's was wildlife management, by no means a new concern but whose importance and value were certainly reinforced during this period. Also, emphasis was placed on the relationship between species and their habitats and the need to protect habitat in order to preserve the species. As a response to this legislative mandate, public land management agencies started developing methodological frameworks for habitat evaluation. A brief account of these efforts is given, but a more detailed description is left for chapter 2, where ecological background and implementation methods for habitat models are presented. The concepts of "model" and "habitat" are given formal definitions and fundamental ecological concepts underlying habitat modeling are presented. These include habitat preference, carrying capacity, niche, territoriality and selection strategy. Habitat Evaluation Procedures (HEP) and Habitat Suitability Indices (HSI) are tools developed by the Fish and Wildlife Service for habitat quality assessment when a single species is the object of concern. The basic concepts and more widely used approaches to HEP/HIS development are provided.

Chapter 3 begins with a description of the Mt. Graham study area, covering location, physiography, climate and vegetation communities. Then, the red squirrel's taxonomy, biology and ecology are presented, with emphasis on those aspects relating to habitat suitability modeling. Finally, the importance of Mt. Graham as an astronomical site and Steward Observatory's project are described.

The fourth chapter introduces the digital data base created to be used by the GIS and to provide the necessary inputs for the habitat models. Decisions regarding database design are presented and justified considering the project's goals and limitations.

Chapter 5 addresses methodological issues. Assumptions and restrictions imposed on the system of interest for the purpose of model formulation are made explicit, followed by description of sampling design, univariate analysis, and multivariate analysis. This last section is broken down into components dealing with selection of a technique, of the best environmental model, and with trend surface modeling and use of Bayesian statistics for combining independent models. Finally, impact assessment procedures are presented, based on the concept of squirrel habitat equivalents.

The study's results are presented and discussed in chapter 6, following an organization parallel to that of the previous chapter. Emphasis is placed on performance statistics, and their use for model selection and testing. Charts and maps are extensively used to synthesize the results and clarify their meaning. Maps comparing model predictions with actual observations convey the most important findings of the study. Habitat losses expected to occur as a consequence of development are then estimated, broken down by project phase and presented both in numerical and mapped form.

The final chapter summarizes the study's conclusions by raising and answering a series of questions dealing with goals achievement, strengths and weaknesses of the approach, appropriateness of various methodological decisions, model validity and reliability, and ways to improve and extend the present work in order to more effectively accomplish the objectives of long-term preservation of the endangered Mt. Graham red squirrel.

STUDY BACKGROUND

Legislative

The U. S. Forest Service's concern with the Mount Graham red squirrel population complies with legislative acts addressing environmental matters, namely the National Environmental Policy Act (NEPA) of 1969, the Endangered Species Act (ESA) of 1973, and the National Forest Management Act (NFMA) of 1976 (USFS, 1986,1988). The main principles of these three acts, products of the environmental movement of the 1960's and 1970's, are reviewed next.

The National Environmental Policy Act of 1969 (Public Law 91-190) is generally considered a keystone of American environmental legislation. Thomas (1982) calls it "a seminal piece of legislation" and its role in shaping the nature of the relationship between contemporary American society and its environment is widely recognized (Dana and Fairfax, 1980; Mann, 1981; Caldwell, 1982). The stated purpose of NEPA is to reorient national environmental policy in a way that would emphasize the harmonization of man's productive efforts and environmental protection through an increased understanding of ecological and natural resources systems (Caldwell, 1982). This reorientation was needed because of the damaging impact public policies were having on the environment. NEPA requires any federally financed project to be evaluated from the standpoint of its potential environmental impacts, including those on fish and wildlife. NEPA is also considered as a point of departure for the environmental movement's participation in public decision making, for having intensified and institutionalized the public participation process. This was done through the Environmental Impact Statement (EIS) requirement of NEPA. The EIS was not only a document designed to support decisionmaking, but also a disclosure document. Moreover, the EIS forced a restructuring of the use of information in the agencies' decision process, emphasizing the role of multidisciplinary research and the consideration of intangible, hard to quantify impacts.

The Endangered Species Act (ESA) of 1973 (Public Law 93- 205) calls for conservation of endangered and threatened species and of the ecosystems that support them. The ESA also requires the identification, delineation and maintenance of critical habitats required for the survival and restoration of the species of concern. The present study can be considered as partially fulfilling these specific requirements of ESA. The major premise of the Endangered Species Act is that endangered plant and animal species have aesthetic, ecological, educational, historical, recreational, and scientific value (Dana and Fairfax, 1980). In the 1978 amendments to ESA, "critical habitat" is defined as the essential portions of a species range that require special consideration, and it is listed concurrently with the species status, making this important information available to managers (Dana and Fairfax, 1980).

The National Forest Management Act (NFMA) of 1976 was designed to increase the regulation of forest management practices. The congressional debate relating to NFMA concentrated on the issue of how much discretion administrative agencies should be allowed in the management of natural resources. The main focus of the discussion was on timber management techniques, namely on regulating the use of clear cutting, specifying adequate rotation ages, and promoting non-declining even flow as the appropriate harvest scheduling technique. The section on species diversity is the most relevant for the purposes of this study. NFMA calls for regulating forest management in a way that will provide for preservation of natural diversity according to each area's capability and suitability, and in obeyance of multiple use management principles. NFMA also emphasizes the role of interdisciplinary team work in the preparation of forest management plans, following the lead of NEPA. Forest managers are encouraged by NFMA to recognize the multidimensional character of forest resource management and to share authority with professionals from other related disciplines.

Methodological

The environmental legislation of the late 1960's and 1970's, including not only the acts referred to in the previous section, but also others such as the Forest and Rangelands Renewable Resources Planning Act of 1974 (Public Law 94-579) made very obvious the need for a structured framework for quantifying the value of wildlife and their habitats (Thomas, 1982). A large part of the available scientific research that could be useful for wildlife protection and habitat evaluation was partial, scattered, of widely varying quality and detail, and lacking a common structure, making it more difficult to meet the new legal mandates (Thomas, 1982).

By the mid 1970's efforts were initiated to develop a structured framework for habitat evaluation, especially by the U.S. Forest Service (Thomas, 1982; USFWS, 1980, 1981). Accepting Thomas' (1982) classification of wildlife management strategies into three main classes - featured species management, species richness management and combinations of the two - these efforts can be considered as complementing each other. The Fish and Wildlife Service's Habitat Evaluation Procedures (HEP) (USFWS, 1981) are specifically designed to address featured species management, that is, the production or preservation of selected species in desired numbers, at specified places (Thomas, 1982) The U.S. Forest Service procedure, designated as Wildlife and Fish Habitat Relationships (WFHR), on the other hand, are oriented towards species richness management and therefore assign primary importance to the description and analysis of ecological biotopes associated with these. The WFHR do not preclude, however the development of more detailed capability models for featured species of concern in the same way that the HEP allow for the combination of various single species models in a more complex and encompassing analysis. Both HEP and WFHR share a set of characteristics that is common to most habitat models. Therefore the main principles, assumptions, theoretical background, limitations and purpose of habitat models will be analyzed next, followed by a more detailed overview of the various kinds of Habitat Evaluation Procedures (HEP). The focus on this approach is justified by the very clear featured species orientation of the present case study.

CHAPTER 2

HABITAT MODELS

ECOLOGICAL FOUNDATIONS

In order to clearly define the concept of habitat model, it is useful to begin by explaining what is meant by both "habitat" and "model", in the present case.

Habitat is understood as the location that supports a wildlife population, including space, food, cover and other animals (Giles, 1978), and models, following McGill (1986) are abstract formal representations of a system of interest. This formalism may be expressed in either physical or mathematical terms (Jeffers, 1980) and is supposed to be useful for purposes of thinking about a problem, forecasting and decision making (Buongiorno and Giless, 1987). A habitat model is then a systematic method of relating habitat conditions to potential animal abundance (Farmer et al., 1982).

Developers of habitat models rely upon ecological theory to identify habitat dimensions expected to significantly influence animal abundance, and to quantitavely specify the nature of these relationships. Also, ecological principles are used to determine acceptable simplifications of the real system that will allow the construction of a tractable model (Clark et al., 1979).

Flather and Hoekstra (1985) and Schamberger and O'Neil (1986) identify the most relevant aspects of ecological theory underlying the conceptual development of habitat models, including two central concepts that provide the link between habitat features and animal abundance: habitat preference and carrying capacity. Pianka (1978) describes habitat as spatio-temporal mosaics of resource patches. Because of this patchiness, an individual animal's exact spatial location is often a critical determinant of its immediate fitness, or reproductive success. Natural selection favors individuals that select better habitats, thus generating a correlation between preference for a given resource patch or habitat type, and fitness within it (Pianka, 1978). Carrying capacity is the second major link between habitat and population abundance. Giles (1978) describes it as a land parameter that is measured in animal density units (number of animals/unit area), and it corresponds to the upper limit on the steady-state population size that a given environment can support (McNaughton and Wolf,1979). For a more formal definition of carrying capacity, in terms of parameters of the logistic growth curve, Pianka (1978) should be consulted.

The concept of niche is also frequently invoked in the context of habitat modeling. Hutchinson's (1957) treatment of this concept is both the most influential in contemporary ecology, and the most relevant for the purpose of this study. He defines niche as an n-dimensional hypervolume that encloses the full range of conditions under which an organism can successfully replace itself. Hutchinson's niche coordinates are non-behavioral, emphasizing the niche as a place in space. Usually two types of niche are distinguished, the fundamental and the realized niche (Hutchinson, 1957; Pianka, 1978). The first corresponds to the complete set of optimal environmental conditions under which a given organism can live and reproduce itself. It is a hypothetical and idealized representation of the niche, where the organism of interest is assumed to be free from competitors and predators, and the physical environment is optimal. The realized niche represents the actual set of conditions under which an organism exists. It is smaller or equal to the fundamental niche, due to the incorporation of the effects of competition and predation. The niche concept forms a bridge between species-habitat and inter/intraspecific relationships (Pianka, 1978), therefore becoming a useful tool for conceptualizing the relations of the model's target species with the rest of the biotic community.

Flather and Hoekstra (1985) add a couple more ecological concepts to the modeling of species-habitat relations, namely territoriality and selection strategy.

Territoriality is a complex of behavioral mechanisms that function to minimize over-exploitation of resources (Flather and Hoekstra, 1985). This is accomplished through spatial segregation, with individuals, families or small groups actively defending a certain amount of space against use by other animals (Pianka, 1978). Whenever a habitat model is meant to be spatially explicit, it must consider the resources that determine the territorial behavior; also, knowledge of average territory size is important in order to determine the spatial resolution, or scale of the data needed to develop the model, as well as to interpret potential limitations imposed by this behavior on the number of animals a given area can be expected to support.

The dynamic behavior of animal populations is frequently described as forming a continuum, between species with high maximal rates of increase, short lifespan, many small offspring, and highly fluctuating numbers, on the one end, and species with relatively stable population numbers, longer lifespans, and fewer, larger progeny, on the opposite end. The first type of selection strategy is called r-selection and the second k-selection, after the two terms in the logistic growth equation for rate of increase (r) and carrying capacity (k) (Pianka, 1978; McNaughton and Wolf, 1979).

This distinction is important, since it is usually easier to develop habitat models for k-selected species, that display a strong relationship between population abundance and resource availability (Flather and Hoekstra, 1985). Their population dynamics are primarily regulated by density-dependent factors, like availability of space and food, and their numbers usually approach the carrying capacity of a given environment. It is harder to develop habitat models for r-selected species, because the link between resource availability at a given habitat and population abundance can be weaker. The population dynamics of r-strategists is significantly influenced by density independent factors, like catastrophic climatic events (fire, hurricanes, floods) and diseases, determining large fluctuations of population size that remain, however, well below the carrying capacity level for most of the time (Pianka, 1978). Most species, of course, exhibit mixed strategies, and therefore, knowledge of their autecology is important to determine to what extent a habitat model can be successful, what other environmental factors should be considered, or whether distinct models should be developed for high and low population levels.

Although habitat models rely on the ecological concepts described above, they are of a different nature from models in other areas of ecological research, such as habitat selection, optimal foraging and carrying capacity models. Habitat models are operational, planning models, usually fairly simple, and relying on a mix of theory, empirical data and subjective knowledge. They also lack both the breadth (number of variables considered) and depth (degree of detail) of the more theoretical models mentioned above, and tend to be predominantly empirical, or correlative, while theoretical ecology models are mostly mechanistic, or explanatory.

Validity and reliability of habitat models are not as good as those of the more "scientific" models, but the goals of planning and management are different from those of science. Habitat models are usually developed under strict time and budget constraints (often limited to use of available data), with the goal of supporting decision making, and it would certainly be inappropriate to judge them by the same standards of confidence, certainty and precision as those used for scientific research models (Schamberger and O'Neil, 1986).

HABITAT EVALUATION PROCEDURES AND HABITAT SUITABILITY INDICES

The US Fish and Wildlife Service's Habitat Evaluation Procedures (HEP) previously mentioned, are a group of methods for documenting the quality and quantity of available habitat for selected wildlife species (USFWS, 1980). HEP are based on the assumption that habitat can be described by a Habitat Suitability Index (HSI), measured in a standardized 0 (lowest) to 1 (highest) interval scale, and defined as a numerical index that represents the capacity of a certain habitat to support a given wildlife species (USFWS, 1981).

All HEP methods share some common procedures and have a similar structure, the differences lying mostly in technical aspects of the numerical evaluation process. The shared features of all HEP include a statement of purposes and goals of the study, identification of relevant variables or evaluation criteria and aggregation of the individual evaluations into an overall model, according to some previously defined formal structure (USFWS, 1980, 1981). Verification and validation of the models, although some times neglected in practice (Lancia et al., 1982), are strongly emphasized by several authors as fundamental steps of modeling process (Shamberger and O'Neil, 1986;Cole and Smith, 1983; Farmer et al.,1986). The statement of objectives for an HEP/HSI model addresses issues such as the number of species of concern usually described only as single-species versus multiple-species, season of applicability of the model, specification of outputs, including units of measurement and some statement of acceptable or desirable accuracy and definition of a geographic area of concern.

The identification of relevant model variables for an HEP/HSI model should meet three criteria (USFWS, 1980):

- the variable must be related to the habitat's capacity to support the species of concern.
- there is some understanding of the nature of this relationship, namely what are desirable and undesirable levels of the variable, and how it relates to other variables.
- the variable is measurable within the study's constraints of budget, time, manpower, etc.

Variable identification is often accomplished by developing a tree-like structure that contains, at its most basic level, fundamental life requisites of species, like food , and cover, and then branch off into successively more detailed levels of description, ending with measurable model variables or evaluation criteria, for which measurement procedures and units can be specified (USFWS, 1980, 1981).

The relevance and meaning of model variables must, of course, be based on knowledge of the species' ecology, guided by the principles described in chapter 3.

Model structuring is the process of aggregating the single-variable habitat evaluations into an overall evaluation, according to some pre-specified formulation. This is done by specifying relationships among the variables, in a verbal, graphical or mathematical format. Five main types of HEP/HSI models have been constructed, based on different aggregation structures: word models, mechanistic models, pattern recognition models, Bayesian probability models and multivariate statistical models (USFWS, 1981). Word models are verbal statements about the way in which variables, both individually and in combination, contribute to habitat quality of a given species. These statements usually address the direction of preferability of a variable (e.g. "the suitability of red-squirrel habitat increases with elevation") and include more precise indications of threshold levels or suitability classes (e.g. "the best red-squirrel habitat is found in forested areas with canopy closure > 70%"). The statements regarding overall (i.e. multivariable) habitat suitability vary according to whether the nature of the relationship between variables is perceived to fall, in a totally non-compensatory-fully compensatory spectrum. In the first case a given habitat is considered only as good as its value on the poorest variable, that functions as a limiting factor. At the opposite extreme we have a simple cumulative effect, where a given suitability level may be attained by any one or any combination of variables (USFWS, 1981). Verbal expressions of these two cases would be: "Habitat suitability for the red-squirrel is determined by elevation, density of cover, or food availability, whichever is the lowest", for the non-compensatory case; and "Suitable red-squirrel habitat is determined by the sum of elevation, density cover and food availability values" for the compensatory case (assuming of course in either case, that the scaling onto 0-1 interval was done at the single variable evaluation stage). Also allowed are intermediate cases, where low values on a given variable are only partially offset by high values on other variables.

The use U.S.Fish and Wildlife Service (1981) makes of the word "mechanistic" is different from the sense in which it was used previously here. The adjective mechanistic usually applies to simulation models, which are descriptive, and supposedly represent a natural process through the metaphor of a mechanism. HEP/HSI models are evaluative, normative models, that assign values to objects (habitats) described by multiple evaluation criteria. Therefore "mechanistic" in the HEP/HSI sense refers to the use of mathematical equations (functions) to assess both single variable and aggregate suitability. These models are conceptually analogous to word models but made more quantitative through the use of mathematical functions to express the contribution to habitat suitability of different levels of a single variable and again to combine them into a complete model. The compensatory versus non-compensatory continuum is present again: fully compensatory relationships are represented by additive models and totally non-compensatory models by the logical operation of minimization. Partially compensatory cases are dealt with by using arithmetic or geometric means.

Pattern recognition models are obtained by assigning values to different patterns of yes-no answers to lists of questions that concern the presence or absence of relevant environmental attributes at a given habitat. Although these models are relatively simple to build, they become impractical very quickly, as the number of variables and categories within each variable grows. A model with four questions with three categories each has 81 possible patterns (3^4). If one more question is added (3^5), 243 patterns become possible. Although they may not all actually occur, the model becomes unwieldy (USFWS, 1981).

Bayesian probability models are based on the concept of conditional probability, as expressed in Bayes' Theorem. The problem is estimating the likelihood or probability that a particular area provides suitable habitat for a given species, based on information about the area's environmental features. Bayesian habitat evaluation models are derived through a three step process (Williams et al., 1978; USFWS, 1981):

- estimation of initial ("prior" in Bayesian jargon) probabilities that some condition or set of conditions exists, based either on empirical data or subjective estimates
- collection of sample data on the variables of interest
- use the sample results to revise the sample probabilities into a final evaluation.

Williams et al. (1978) provide an hypothetical example of this technique applied to habitat evaluation of Great Plains pronghorn antelope.

The fifth and last type of HEP/HSI models is based on multivariate statistical techniques, especially regression and discriminant analysis (USFWS, 1981; Capen et al., 1986; Brenman et al., 1986; Morrison et al., 1987).Regression models of habitat suitability, are always multivariate, with a series of habitat characteristics as independent or explanatory variables and some measure of animal abundance as the dependent variable. Variations on this technique include the use of logistic regression (a non-linear technique) when only dichotomous presence-absence data is available for the dependent variable (Brenman et al., 1986) and the use of stepwise procedures, to identify the statistically more significant predictors, out of a large number of potential explanatory variables (Brenman et al., 1986; Morrison et al. 1987), and develop simpler, more parsimonious models.

In discriminant function analysis, the problem is to discriminate among previously defined groups of objects on the basis of a series of quantitative descriptors (Legendre and Legendre, 1983). In the case of wildlife habitat models, the objects or observations are sites and the groups denote abundance level of a given species. The descriptors or variables are habitat measurements at the site (Johnson, 1980; USFWS, 1981).

Verification and validation are two phases of model testing that are frequently but mistakenly taken to mean the same thing. Verification addresses the fit between model implementation and the model concept, while validation tests the correspondence between the concept and reality (Farmer et al., 1982). It is worth noting however, that since definite validation is a logical impossibility (Popper, 1959) the proper goal of this step should be an exploration of the limits of appropriateness and credibility, and not an attempt to make the model mimic reality, through some kind of matching game. The emphasis should be placed on invalidation, rather than on validation (Holling, 1978; Clark et al., 1979; Marcot et al., 1983). Lancia et al. (1982) remark that HEP/HSI models are not only often left untested but, when testing is performed, it is usually done incorrectly, i.e. using the wrong criteria. One of the most frequently used validation methods relies on experts on the species being studied, who are asked to examine model predictions and judge whether they are satisfactory. This is considered highly subjective and circular. Another popular approach is to use convergent validation, comparing several independently developed models to one another for the same species. However, Whelan et al. (1979) report widely discrepant results using this method. A similar type of testing is done by comparing model predictions of habitat suitability with independently derived density estimates for the species of concern. Lancia et al. (1982) consider all these methods as undesirable and suggest that the only acceptable tests are those obtained by comparing model predictions of habitat suitability with actual observed habitat selection data.

Schamberger and O'Neil (1986) consider that model testing serves the two main purposes of providing information about model performance and reliability in specific applications and generate data that can lead to improvement of the model. These authors also list a series of general considerations for HEP/HSI model testing, of which the following are especially relevant for the case-study to be presented in chapter 3.

-Identify model objectives and desired performance levels, before testing.

-Test models against real world response by animal (in agreement with the suggestion of Lancia et al. (1982)).

-Use long term, multi-year data for both the dependent and the independent variables.

-Test against data sets not used for model development.

-Test for validity of individual variables before proceeding with global model testing.

-Use large sample sizes.

-Use test sites covering the entire range of habitat quality.

As it will be described below, most of these recommendations where followed in the Mount Graham red-squirrel habitat model. Those that were not, mostly due to lack of data, will be highlighted, in order to clarify potential limitations of the model.

CHAPTER 3

MOUNT GRAHAM, THE RED SQUIRREL AND THE OBSERVATORY PROJECT

The description of Mount Graham's physical and biotic environment that follows is far from exhaustive, for two reasons. First, other literature sources provide much of this information (Shreve, 1919; Moir and Ludwig, 1979; Pase and Brown, 1982a, b; Office of Arid Land Studies, 1985; USDA, 1976, 1986, 1988; Johnson, 1988), and second, the goal of this study is restricted to modeling the relationships between the Mount Graham red squirrel and its habitat. Consequently, special attention is paid to those environmental factors expected to better predict the squirrel's habitat choice, including vegetation type and structure, and topographic elements, such as elevation, slope and aspect (USDA, 1988). The present site description is therefore, biased towards these environmental factors and doesn't cover others, like geology, soils, or hydrology, which are mentioned only to the extent they relate to the potentially more relevant ones. Also not discussed is other Mount Graham fauna, known to be remarkably diverse and to include rare endemics, some of which are subject to special protection measures (Office of Arid Lands, 1985; USDA, 1986). This omission is, again justified by the two reasons mentioned above, especially the second, since habitat suitability models commonly exclude predation and competition, due to difficulties in data gathering and analysis (Schamberger and O'Neil, 1986). In the red squirrel's case, the potentially more significant population interaction may be interspecific competition with the introduced Abert squirrel (Office of Arid Lands Studies, 1985; USDA, 1986). However, experts believe that the niches of these two species are clearly separate, minimizing the importance of competition. There is also some evidence suggesting that, when competition occurs, the red squirrel may frequently predominate, especially in groves that include mature and old growth spruce fir and/or douglas-fir (USDA, 1988).

MOUNT GRAHAM AND ITS ENVIRONMENT

Location and Physiography.

Mount Graham is located in the Pinaleno Mountains of Graham County, Arizona, 125 miles NE of Tucson, and 8 miles south of Safford (figure 1). The Pinalenos are part of the Basin and Range physiographic province, and Mount Graham (maximum elevation 10720 feet, at High Peak) is the third highest mountain in Arizona, after the San Francisco Peaks and Mount Baldy, in the White Mountains. Mt. Graham is

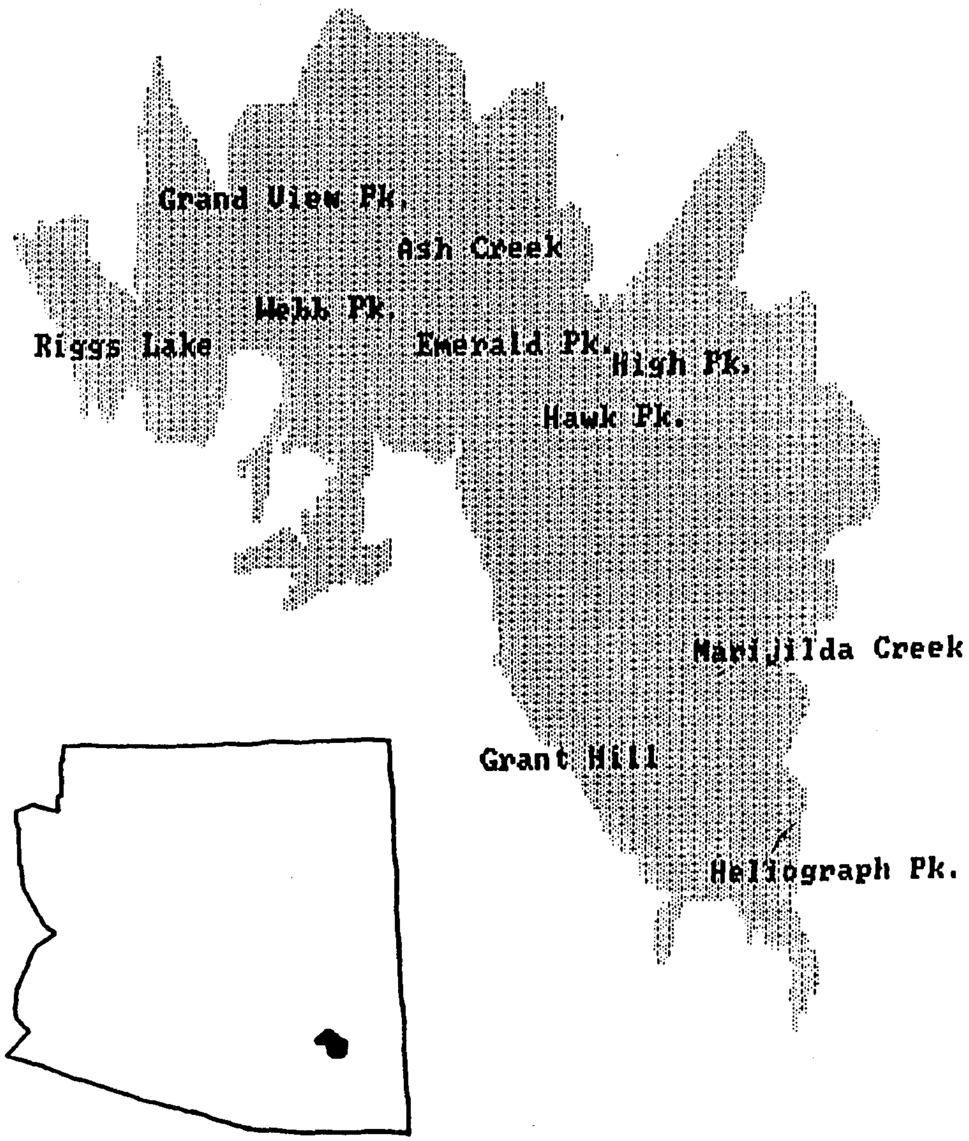


Figure 1. Mt. Graham location and study area.

surrounded on the south and west by the Sulphur Springs Valley and Aravaipa Canyon, the San Simon Valley on the east and the Gila Valley on the north (Office of Arid Lands Studies, 1985). The study area outlined by the Forest Service for this study covers 6460 hectares, ranging in elevation from 6520 feet, to the top of High Peak.

General descriptive information on Mount Graham's physiography is scarce. Searches of the University of Arizona's subject index catalog, Quicksearch computer system, and Special Collections catalog led to no relevant references. Existing studies address very specific, highly technical topics, like paleontology, geomagnetism and geochemistry, but an overview of the mountain's physiography and geomorphology doesn't seem to be available. The best references turn out to be introdutory sections of studies whose primary emphasis is on vegetation (Shreve, 1919; Johnson, 1988) and road construction impact assessment (USDA, 1976).

Both Shreve and Johnson consider that the most remarkable features of the Pinalenos are the abundance of perennial streams, and the large elevational range of 6720 feet on the NE slope. The mountain rises abruptly, 60% and steeper slopes being fairly common. Shreve (1919) describes the Pinalenos as a series of rolling areas surrounded on all sides by steep ridges and narrow canyons. He emphasizes the drop in elevation to the Gila drainage at 2600 feet, on the NE side, opposed to a much less dramatic descent on the SW slopes, down to the Sulphur Springs Valley, at the elevation of 5000 feet. The large difference in basal topography between these two exposures is attributed in great part to the presence of the strong Gila drainage on one side and that of a much weaker one -Arivaipa- on the other (Shreve, 1919).

The Pinalenos are separated from the Santa Teresa Mountains, on the NW, by a pass, at 4500 feet and from the Greasewood Mountains, to the SE by Stockton Pass (elevation 5600 feet). The general orientation of the range is WNW-ESE and topographically two sections can be identified, a small one on the NW, dominated by Blue Jay Peak (elevation 8840 feet) and a much larger one to the SE. Taylor Pass, at 7150 feet separates the two (Johnson, 1988). The bulk of the range lies on the second section, and this is also where the red squirrel habitat study area is located. The topography is very rugged and many canyons in this part of the mountain have permanent streams, creating sharp contrasts between the vegetation communities of lower-to-mid altitude slopes and canyons (USDA, 1976). The evergreen oak woodlands and scrub are carried up high on very steep, highly insolated south facing slopes, while mesophytic vegetation descends down the mountain along permanent streams running in narrow canyons. This interdigitation pattern is typical of "sky-island" desert mountains, but is especially evident in the Pinalenos (Shreve, 1919).

The Pinalenos are crested by a series of peaks, of which the most remarkable are Heliograph Peak (10022 feet) on the SE side, High Peak (10720 feet) Hawk Peak (10640 feet) and Emerald Peak (10471 feet), on the central part of the SE section, and Webb Peak in the western third of this same section. Blue Jay Peak, already mentioned, lies outside the area of interest for this study. Also significant topographic features are three impoundments: Riggs Flat Lake (8760 feet) on the NW edge of the study area, Snow Flat (8776 feet), more to the east, closer to Webb Peak, and Frye Mesa Reservoir (4800 feet) outside of our area of interest (Johnson 1988). Access to this section of the mountain is provided primarily by Swift Trail (State Route 366), paved up to Shannon Campground Turnoff (USDA, 1976).

Climate.

Climatic conditions at Mount Graham are characterized by large contrasts. The altitude gradient from the desert floor to the top of the mountain is very steep and at the elevation where most of the study area is located, low density, dry air favors rapid radiant heating during the day and fast cooling during the night. Because of its location, Mount Graham is less cloudy than coastal mountains of equivalent elevation, and less or equally windy than comparable more continental mountains, such as Mt. Hopkins or Kitt Peak (Office of Arid Lands Studies, 1985). Most Artic-Pacific cyclonic winter storms pass to the north of the mountain, and the summer monsoons lose most of their moisture over the desert before reaching Mount Graham. Precipitation patterns of the higher altitude areas of the Pinalenos differ quantitatively from data recorded for Fort Grant and Safford, where the two nearest meteorological stations are located. Nevertheless, the seasonality is the same. Johnson (1988) estimates the precipitation at 2135 m (7000 ft.) on Mt. Graham to approximate 30 cm (12 in.) in summer and 15 cm (6 in.) in winter. Snow levels at any elevation and relationships between elevation and precipitation above 2135 m (7000 ft.) are unknown. Temperature data for the Pinalenos are obtained through the same extrapolation method. Johnson (1988) suggests that average monthly temperatures at High Peak are between 33°F and 44°F less than those recorded at Fort Grant. This would result on average temperature between 1°F and 12°F for the coldest month (January) and between 35°F and 46°F for the warmest month (July). Actual temperatures anywhere in the mountain will obviously be modified by microclimatic influences.

Vegetation.

The major vegetation types found within the study area are spruce-fir, mixed conifer, ponderosa pine, aspen, meadows, cienegas, and rock outcrop communities (USDA, 1988). This section will rely on detailed descriptions provided by Moir and Ludwig (1979), Pase and Brown (1982), Hendrickson and Minckley (1984), Johnson (1988) and on the overviews of the Office of Arid Lands Studies (1985) and USDA (1986).

Spruce-fir forest predominates at the top of Mount Graham. It is dominated by Picea engelmanii (Engelmann spruce) and Abies lasiocarpa var. arizonica (Corkbark fir) and is the southernmost subalpine conifer forest in North America (Office of Arid Lands Studies, 1985; Pase and Brown, 1982). Moir and Ludwig (1988) identify four distinct habitat types within the spruce-fir forest. The first is the Picea engelmannii/Moss habitat type, where Engelmann spruce of all age classes are present, together with strong regeneration of corkbark fir. Understory vegetation is poor, mostly mosses and lichens, with very sparse herbs and shrubs. This community grows in dry high altitude sites, on excessively drained skeletal soils, typical of ridges, upper slopes with southern exposures, and saddles above 10000 feet of elevation. Populus tremuloides (Aspen) is the main species of early successional stages, although both Engelmann spruce and corkbark fir can be their own predecessors, especially in very poor soils.

The Abies lasiocarpa/Vaccinium scoparium habitat type is characterized by corkbark fir dominance, with moderate to heavy regeneration of both Engelmann spruce and corkbark fir. Sometimes mature Pseudotsuga menziesii (Douglas fir) trees are present.

The main understory species are Vaccinium sp. (Blueberry). This community is associated with a wide range of topographic conditions, from gentle to steep uplands slopes, canyon side slopes, ridges, and valley bottoms, generally at elevations above 9800 feet. Aspen is again the prevalent early seral species on clearings due to natural or man-made disturbances.

Small areas at elevations higher than 10200 feet, usually with cobbly, skeletal soils, are covered by the Picea engelmanii/Carex foenea. When clearings occur in this community, Carex foenea (a species of sedge) takes over, since the intense solar radiation makes it hard for spruce to regenerate.

Moir and Ludwig (1979) describe four mixed conifer habitat types present at the Pinaleno Mountains: Abies concolor-Pseudotsuga menziesii/Acer grandidentateum, and Pseudotsuga menziesii-Pinus strobiformis/Muhlenbergia vireceus. The first of these habitat types is characterized by the dominance of either or both White fir and Douglas fir. A low shrub layer dominated by Holodiscus dumosus (shrubby cream brush) distinguishes the Mount Graham phase. It occurs primarily in moderate to steep canyon side slopes, with E and NW exposures, between 7900 feet and 9500 feet, but can follow stream channels down to 6800 feet, and climb southern exposures with deep, well drained soils up to 10000 feet. At the higher elevations, this habitat type forms an ecotone with the spruce-fir forest and, in warmer sites with White fir-Douglas fir habitat types. Aspen is, once more, the most important post fire seral species, although this role may also belong to Douglas fir or Ponderosa pine, in the case of more severe fires.

The Abies concolor-Pseudotsuga menziesii (sparse understory) habitat type has all size classes of these two species, although crown dominance may be shared with Ponderosa pine and White pine (Pinus strobiformis).

Understory is very sparse and dominated by Robinia neomexicana (New Mexican locust). This type of forest favors cool, dry sites, moderate to steep slopes, with northern to eastern aspects and elevations between 8000 and 9200 feet, sometimes higher in warmer exposures. It forms ecotones with White fir-Douglas fir/Gambel oak (Quercus gambelii), in warmer sites, and with spruce-fir, at the highest, coolest boundary, and has a somewhat distinctive early successional vegetation pattern, in that neither aspen nor Gambel oak are important post-fire pioneers, especially if the fire is severe. Forest clearings of this origin are quickly covered by an herbaceous layer, where conifers soon re-establish. White fir dominates the regeneration of the Abies concolor/Acer gradidentatum habitat type, where Douglas fir plays a minor role. The understory is clearly dominated by Acer grandidentatum var. grandidentatum (Big tooth maple). This habitat type prefers northern drainages with gentle slopes, between 7500 and 8000 feet, often down to 7000 feet, along streams. Early successional communities are diverse, with Douglas fir, Ponderosa pine, aspen and Gambel oak.

Douglas fir and White pine are the dominant species of the Pseudotsuga menziesii-Pinus strobifomis/Mulenbergia virescens habitat type, although Ponderosa pine of all sizes is also present. Douglas fir regeneration is usually denser than that of White pine, shrub vegetation is scarce, and the herbaceous layer is dominated by Muhlenbergia virescens (screwleaf muhly). Ridges and dry mid to upper slopes, gentler to steep, with south and west aspects, and elevation between 7600 and 9200 feet are the characteristic topographic conditions. This habitat type forms ecotones with the Pine-oak woodlands, on drier exposures. It is the driest and warmest of the mixed conifer habitat types that can be found at Mount Graham.

Two other mixed conifer habitat types that can be found in the Pinalenos are mentioned by Ludwig and Moir (1979) and Johnson (1988). Dominated by Abies concolor/Carex foena, and by Pseudotsuga menziesii/Quercus bypoleucoides (silver leaf oak) are the dominant species. The first shows similarities with the Abies concolor/Acer grandidentatum type and is present at around 9100 feet, while the second forms ecotones with the Pseudotsuga menziesii-Pinus strobiformis/Muhlenbergia Viscerens, on cool, wet sites. Due to their very restricted distribution, little additional information is provided.

Ponderosa pine (Pinus ponderosa var.arizonica) forest doesn't cover as large an area of the Pinalenos as it might be expected, because extreme slope steepness and rocky terrain prevail at the altitudes this species would otherwise prefer (Shreve, 1919). Nevertheless, existing stands of old growth are park like with scattered trees intermixed with groups of younger trees. Where regeneration is scarce, the understory is grassy or herbaceous (Pase and Brown, 1982). Ponderosa pine is found at lowest elevations (down to 6000) feet- on the northeast face of Mount Graham than on the southwest slopes, where it rarely grows below 7600 feet. This is due not only to the influence of aspect but also because of the effect elevation of the basal plain or valley has on the vertical distribution of vegetation (Shreve, 1919). Gambel oak and New Mexican locust are often present in the Ponderosa pine forest, at lower and rockier sites, while white fir is a common understory species at higher elevations. White pine and Douglas fir are associate species of the higher altitude stands.

Populus tremuloides (aspen) is the last arboreal vegetation type of significance within the study area. Its role as a pioneer species, colonizing open patches generated by natural or man-made disturbances was described above. This species covers a very small area of Mount Graham, but its stands support rich wildlife communities, providing food and cover for several mammal and bird species (Pase and Brown, 1982).

The remaining habitat types identified in the Mount

Graham Red Squirrel Biological Impact Assessment (USDA, 1988) are cienegas, mountain meadows, and rock outcrops and other denuded areas.

Hendrickson and Minckley (1984) define cienegas as wetlands characterized by permanently saturated, highly organic soils and poorly diversified flora, dominated by low sedges. The high elevation (above 6600 feet) cienegas, like those at Mount Graham, are marshy to bog-like and, besides the usual sedges, semi-aquatic and terrestrial grasses (family Gramineae) and cold resistant rushes (family Juncaceae) are characteristic. Cienegas may also support low woody shrubs such as alder (Alnus tenifolia), currant (Ribes sp.) and willows (Salix sp.). These communities are frost inhibited or lie beneath snow for a large part of the year, with surface water undergoing successive stages of freezing and thawing in winter, and frequently drying out over the summer(Hendrickson and Minckley, 1984).

The subalpine meadows occurring at Mount Graham, between 8000 and 10000 feet of altitude are the only grassland communities in the study area and are very important as wildlife habitat, as well as floristically diverse. Johnson (1988) mentions 14 taxa of herbs and grasses growing on this habitat.

Isolated rock outcrops are present throughout the entire mountain. Stressful soil and water conditions determine reduced species diversity (Johnson, 1988) although some of the rarest plant species occurring at Mount Graham can be found here (Office of Arid Lands Studies, 1985). Other areas of bare ground were grouped with rock outcrops in the Red Squirrel Biological Impact Assessment (USDA, 1988). They are patches resulting from either natural disturbances, like fire and windthrows, or man-made, such as clear cuts, road corridors and fuelbreaks. While most tend to be quickly recolonized by vegetation, they are hostile habitat for wildlife.

The description of Mount Graham's physical and biotic environment just presented is one of the basic pieces of information required for setting up the problem of developing a habitat suitability model for the Mount Graham red squirrel. The other part is, obviously the squirrel itself, and some information regarding the species' taxonomy, biology and ecology are provided next.

THE MOUNT GRAHAM RED SQUIRREL

Taxonomy.

Hoffmeister (1986) and USDA (1988) are the main sources for this section and should be consulted if more detailed information is sought.

The Mount Graham red squirrel's scientific name is Tamiasciurus hudsonicus grahamensis. The first name identifies the genus, together with the second they define the species, while the third name applies only to the subspecies endemic to Mount Graham, that is the main object of the analysis in this study. At higher taxonomic levels, the Mount Graham red squirrel belongs to the order Rodentia, family Sciuridae.

Tamiasciurus are tree squirrels with big eyes and bushy tails. They are small sized and have reddish to grayish brown dorsum, separated from the whitish venter by a black stripe. White stripes are present both above and below the eyes. The tail is darker and shorter than the body. Red squirrels lack the pronounced tufts of hair on ears characteristic of other squirrel species. In dorsal profile, the rounded shape of the skull is evident (Hoffmeister, 1986).

The Mount Graham red squirrel is a small sized subspecies (ca. 8 inches) of T. hudsonicus. It has a shorter body and longer tail than other subspecies and the dorsum often shows yellowish or reddish-yellowish interspersed specks. The color of the back extends over the upper side of the tail, and the lateral dark stripe varies in width between individuals. The post-orbital part of the skull is narrower than in the other subspecies (Heffmeister, 1986).

Biology.

The Mount Graham red squirrel weighs about 140 grams (5 ounces) for an average body length of 196 mm (8 inches) and has a high metabolism for its body weight, at about 175% the basal metabolic rate. Adult females have one or two litters per year, with an average size of 3 to 5 offspring, varying between 2 and 8. Mating occurs in February to early April, and the gestation period lasts 35 to 40 days (USDA, 1988). Females first reproduce after their first winter, when they are between 8 and 12 months old. After the second winter all squirrels are considered adults. Both the proportion of breeding adult females, and the proportion of those that have two litters vary widely from year to year. This leads to the type of "boom and bust" population dynamics, very common in small mammals, especially rodents. Although based on limited evidence, it is generally believed that T. hudsonicus suffers very high mortality between weaning and first reproduction, low mortality during the adult stage and higher again in the later years. The maximum age red squirrels reach, in the wild, is estimated at seven years (USDA, 1988).

Ecology.

The relationships between the Mount Graham red squirrel and its environment are primarily shaped by its need to find appropriate food sources and cover conditions. Conifer seeds from closed cones are the most important food and closed cone seed crop explains more of the red squirrel's demography than any other single variable (USDA, 1988). The importance of conifer cones in the red squirrel diet is shared by most other subspecies of T. hudsonicus (Smith, 1970; Rothwell, 1979; Gurnel, 1983) although it has been demonstrated that their diet may include several other foods that have seasonal importance. Flyger and Gates (1982) mention winter terminal buds of evergreens, mushrooms and other fungi, bones, young birds, hazelnuts, and insects, to which USDA (1988) adds pollen from conifer cones and buds, cambium of spruce and fir twigs, berries and seeds from hardwood trees and shrubs. The Mount Graham red squirrel diet is not well known, except for the importance of conifer cones and limited evidence indicating that at least eight species of mushrooms are also consumed. The seed productivity of conifer trees present at Mount Graham has been ranked by Jones (1974), with Douglas-fir as the most productive species, followed by Engleman spruce, corkbark fir and lastly Ponderosa and White pine. Engleman spruce is considered to be the main supplier of food to the Mount Graham red squirrel, followed by corkbark fir. Presence of the first of this species is considered the main contributor to good quality squirrel habitat.

Red squirrels are territorial animals, very aggressive towards both conspecifics and other species of tree squirrels (Flyger and Gates, 1982). Size estimates for home range and territories differ somewhat between authors. Flyger and Gates (1982) mention home range sites of 1.3 to 1.5 hectares and territories of 0.2 and 1.2 ha. Gurnell (1984) states that actively defended areas vary between 0.5 and 3 ha, and USDA (1988) indicates that the average activity area (concept equivalent to home range) in other North America habitats varies between 0.1 and 2.5 ha, with average values of 0.5 to 1 ha.

The territoriality of red squirrels is expressed in their food caching habits as central place foraging behavior, meaning that they carry harvested cones to a central place in their territories, where they are piled up or buried for winter and next year's supply (USDA, 1988). Hurly and Robertson (1986) remark that this type of behavior is absent from the squirrels of the genus Sciurus and indicate that it is advantageous for Tamiasciurus sp. because of the high ratio of woody tissue to seed in conifer cones, that makes them unprofitable as a food source for large mammals. Also, the territorial nature of red squirrels prevents theft by small mammals, including other squirrels. These cone caches, or middens may be 0.3 to 0.6 m high and up to 2m in diameter and may result from accumulations from several years (Flyger and Gates, 1982). Middens consist not only of cones but also scales, cone cores, and sometimes needles (Hoffmeister, 1986). A possible ecological factor influencing the evolution of large central place midden building, or larderhoarding, is the availability of good caching sites (Hurley and Robertson, 1986). It is critical that cones remain humid, otherwise they open and the seeds become susceptible to theft by other animals. Therefore red squirrels look for damp shaded spots (Rothwell, 1979) and continued use leads to accumulation of organic debris that helps retain moisture. In time, excellent storage sites evolve, and they encourage larderhoarding behavior (Hurly and Robertson, 1986). The requirements for good caching sites make obvious the roles of tree cover and microclimate effects in red squirrel habitat selection. Vahle and Patton (1983) analyzed cover requirements for red squirrel in Arizona mixed conifer forests, including eight species: Douglas- fir, white-fir, corkbark-fir, Engleman spruce, blue spruce, Ponderosa pine and southwestern white pine. Stands of Aspen, a deciduous species, were also examined. Size, density, and grouping of conifers are the most important overstory components of red squirrel habitat in the forests studied, and the best habitat is formed by multi-storied stands of mixed conifers, containing trees from 12 to 14 inches d.b.h. in dense groves of less than 0.1 acres. At least one tree, generally a Douglas-fir is 18 inches d.b.h. and middens are built around one of these large trees, that may be snags, or even downed logs (Vahle and Patton, 1983). These cover conditions are preferred by the red squirrel for multiple reasons. Damp, shaded midden locations, not only keep cones from drying out and opening, but they also encourage mushroom growth, another important food source. The closed canopy layer of a dense stand of large trees also provides good nesting sites near the middens, and a system of interlocked tree branches facilitates movement between trees, useful for cone collection or escape from predators (USDA, 1988).

Forest cover conditions that create good microclimate are especially necessary for the Mount Graham red squirrel, because the Pinalenos are located at 32° N latitude, the southernmost situation for both a continuous spruce fir forest and a red squirrel population in North America. Therefore, significantly more solar radiation reaches the top of the canopy layer here than on almost anywhere else in the red squirrel's distribution range, and good habitat at the forest floor level can only be created if tree crowns intercept most of the incoming radiation. This forces the Mount Graham red squirrel to be more selective in choosing locations, not only for middens but also for general activity areas (USDA, 1988).

Based on these considerations, a Coronado National Forest team of experts mapped vegetation stands and red squirrel activity area locations for the study area. These maps are part of the digital data base that was developed for the habitat suitability model, and is described in the next chapter.

THE OBSERVATORY PROJECT

The University of Arizona's Steward Observatory (S.O.) is an internationally recognized astronomical research institution. In 1980, S.O. initiated a search for a site for a new astronomical observatory (Steward Observatory, 1986). The need for this project is described in S.O. (1985) and U.S. Forest Service (1986) as resulting from: 1) the development of new types of telescopes and other instrumentation sensitive to a wider range of the electromagnetic spectrum; 2) different site requirements of this new instrumentation, compared to those of previous technology; 3) the costs and incipient development of space-based astronomy; 4) increasing demand for observation time, that already excedes supply; 5) the interest of conducting ultraviolet/infrared and sub-milimeter wave observations from a single site; 6) light pollution problems faced by most existing facilities. S.O. focused its attention on U.S. sites, since nothing indicates these to be inferior to other northern hemisphere sites, and because of extra costs and complexity of working in foreign countries (Columbus Project Science Advisory Committee, 1987). Mauna Kea, Hawaii has excellent characteristics but is becoming saturated with astronomical facilities and is far from the continental U.S., implying higher construction and operation costs. Also "...it is scientifically inappropriate to concentrate all the front line astronomical facilities in the northern hemisphere at one site" (Columbus Project Science Advisory Committee,1987).

For these reasons, S.O. conducted a survey of all continental U.S. peaks above 9000 ft., excluding Alaska, in the attempt to identify a site suitable to satisfy the needs and goals listed above. 280 sites passed the initial screening condition (elevation > 9000 ft.). A second screening, focusing on number of sunshine hours per year and cloud cover reduced this number to 22 mountains. To these were added 5 other logistically attractive sites, that either already support an observatory or have easy access.

Quality indices were then derived to provide quantitative evaluations of merit for each of the remaining 27 sites. These indices evaluated sky clarity, sky darkness, water vapor in the atmosphere and wind speed. Three different rankings, based on these indices were developed, assessing the sites on their quality for general purposes, for infrared/submilimeter observations and for "dark sky" astronomy. Combinations of these three rankings were also considered. The analysis of these data identified Mt. Graham as an exceptional site, deserving further research (Columbus Project Science Advisory Committee, 1987). Additional on-site measurements confirmed Mt. Graham's outstanding quality as an astronomical site. The mountain has very clear skies during most of the year, steady, low to moderate winds, low percentage of water in the atmosphere, very dark skies and a convenient location, close to the University of Arizona and Tucson International Airport.

The realization of Mt. Graham's quality as an astronomical site led Steward Observatory to submit an astrophysical site and facility development proposal to the Coronado National Forest in June of 1984 (U.S. Forest Service, 1986). In this proposal S.O. outlined an area of approximately 3500 acres of land on the top of Mt. Graham, including High Peak, the highest point in the mountain. The area was designated the Mount Graham Astrophysical Area (MGAA) and defined on the base of both astronomical and logistic considerations (Steward Observatory, 1986). The MGAA was sized to permit adequate buffering to the astronomical facilities and control over activities that could interfere with their operation. Eleven potential astronomical sites and three possible logistic sites were identified within the MGAA (Steward Observatory, 1986).

Steward Observatory's proposed project initially consisted of thirteen telescopes, twelve of which could be placed on three to five of the eleven potential astronomical sites. Additionally, one of the three logistic sites would be chosen as the location for support facilities. Seven of the telescopes are considered large (>7.5 meters in diameter), and five small (<4.0 meters in diameter). The thirteenth would be a movable interferometer, operated on a roadway with nine turnouts.

This proposal was considered unacceptable by both the Forest Service and the Fish and Wildlife Service because of its potential negative effects on the long-term survival of the endangered Mt. Graham red squirrel. After much controversy and heated debate, Steward Observatory finally got Congress to approve a toned down two-phase alternative. Its implementation wiil require development along a corridor extending from Swift Trail, just northwest of Fort Grant vista point, up to Emerald Peak. This includes a new access road that leaves Swift Trail at the above mentioned point and provides access to the relatively flat area around Emerald Peak. Phase 1 of the project includes this stretch of road and a small extension of the western branch of the old road leading to Emerald Peak (Appendix 1). Here will be located an optical/infrared 11.3m. telescope, a 10m.submilimeter telescope and an optical/infrared 8m. telescope. Support facilities will include a parking area, residential, storage, utilities and communications buildings, and an helicopter pad.

In the second project phase four more telescopes and one support building will be constructed. Three telescopes are fixed structures, two of them 8m. optical/infrared telescopes and one 5m. submilimeter telescope. The support building will be located near this last telescope. The fourth astronomical structure is a submilimeter interferometer array, a series of up to 6 movable radio dishes that will stand on nine concrete pedestals, to be built on 1300 sq. ft. roadside turnouts adjoining the T-shaped stretch of road between Emerald Peak and Hawk Peak.

CHAPTER 4

THE DIGITAL DATA BASE

Spatial modeling of habitat suitability for the Mount Graham red squirrel required the development of a computerized database that would provide the necessary model inputs. The main advantages of using a computerized database are increased analytical power, through interface with Geographic Information Systems (GIS) and statistical analysis programs, and improved graphic display.

Considerations related to software availability and appropriateness for the type of analysis desired dictated the choice of a raster data structure. These are arrays of grid cells, where each cell is referenced by a row and column number and contains a number representing a type or value of a spatial attribute being mapped (Burrough, 1986).

Creating the red squirrel habitat data base did not require gathering of field data, nor development of new paper maps. It was constructed by digitizing maps made available by U. S. Forest Service/Coronado National Forest, and USGS topographic maps. All paper maps used were referenced to the Universal Transverse Mercator (UTM) rectangular coordinate system, and represented at a scale of 1:24000. The study area has an irregular shape (figure 1) and was delineated by a group of experts working for the Coronado National Forest. It contains the vast majority of the areas believed to provide suitable red squirrel habitat in the Pinalenos. The Blue Jay Peak area was left out of the present study due to lack of data on habitat use, although it may offer suitable habitat.

The area analyzed is contained within two adjacent USGS 7.5 minute series topographic quadrangles, the Webb Peak Quadrangle and the Mount Graham quadrangle. The minimal rectangle that bounds the study area is defined by the following pairs of coordinates, interpolated from 1000-meter UTM grid ticks on USGS quadrangles:

SW corner - ^{38}11000 latitude N, ^{5}95819 longitude (Webb Peak quadrangle)

NW corner - ^{38}22735 latitude N, ^{5}95819 longitude E (Webb Peak quadrqngle)

NE corner - ^{38}22735 latitude N, ^{6}09578 longitude E (Mt. Graham quadrangle)

SE corner - ^{38}11000 latitude N, ^{6}099578 longitude E (Mt. Graham quadrangle)

A cell size of 0.5 ha (1.22 acres), corresponding to a length of 70.7 meters (232 feet) on a side was selected, resulting in an array of 164 rows by 193 columns, for a total of 31652 cells. Of these, 12920 are contained in the study area and 18732 outside of it. The area of the rasterized study region is 6460 ha (15963 acres).

Several reasons dictated the choice of a cell size of 0.5 ha. First and foremost, it corresponds approximately to the smaller sizes of the range of red squirrel activity areas, which is the basic unit of analysis of this study. Second, mapping accuracy in the original paper map of activity areas provided by USFS, made it unadvisable to use a smaller cell size (Randall Smith, pers. comm.). Third, there were software limitations, imposed by Map Analysis Package (MAP) (Tomlin, 1986), the GIS to which digitized data was first input. MAP can not handle arrays larger than 32767 cells, which is very close to the number actually used for this data base.

Three different paper maps were used to create the digital database. Topographic and road network data were obtained from the above mentioned USGS topographic quadrangles, vegetation data from USFS forest stands map, and squirrel activity areas from a USFS habitat use survey map. Development of the last two maps is described in USDA (1988). All maps were digitized using the CADGRID software package (Itami, 1988).

The topography data file contains all 200 foot contours within the study area's minimal bounding rectangle (MBR).

Intermediate contours were also included for the regions within the study area itself. The resolution of intermediate contour data varies from 120 foot intervals in the steeper regions of the study area's periphery, to 40 foot intervals in some of the flatter zones in the central portion of the study area. These data, originally in vector format were rasterized with CADGRID, using the algorithm proposed by Douglas (1983). The original vector files were kept and are available for inspection. MAP was used to derive slope steepness and slope aspect maps from the grided elevation data. MAP does not have real number processing capabilities and therefore elevation, slope, and aspect data only take integer values.

The map depicting squirrel activity areas is binary, meaning that it contains only two categories of cells, those where squirrel activity was detected and those from where it is absent. For the purposes of the present study the distinction between activity areas containing active versus those containing inactive middens was ignored. The original map is based on data from a single year (winter 86/spring 87), which is insufficient to establish whether inactivity around a given midden is temporary or represents definitive abandonment. It has been observed that middens may be abandoned during one year and reoccupied in subsequent years

(Randall Smith, pers. comm.). Therefore, all activity areas, regardless of the occupancy status of their central middens, were digitized. However, of the 216 activity areas shown in the original map, only 212 were preserved in the rasterized map, due to the way CADGRID grids point data. If the program finds that more than one point in the vector file would fall in the same grid cell, it only takes the last point entered during the digitizing process. The loss of 4 active cells is fairly inconsequential for the analysis, not only because they represent less than 2% of the original data, but also because the squirrel activity map is meant to show only presence or absence of activity, not density of use.

The vegetation map provided by USFS depicts homogeneous vegetation stands as polygons and was derived based on 1977 aerial photographs, timber compartment histories, maps made on the ground during the early 1960's, and timber files from the Safford Ranger District of the Coronado National Forest (USDA, 1988). The polygons in the original maps are homogeneous regarding three different attributes: vegetation type, diameter at breast height (dbh) and canopy coverage. Rasterization of the polygon vector file is based on sampling of cell centroids, which may account for small discrepancies between vector and raster maps in appearance and areas in each category, or even in the loss of very small polygons. However, an informal comparison of areas of each vegetation type between the original USFS paper maps and the rasterized map reveals that discrepancies are smaller than 0.2% of the size of the entire study area, and smaller than 1% for the most representative vegetation types. Using MAP, the gridded stands map was disagregated into the three constituent map layers, each one representing a single vegetation attribute, according to the original map key. The canopy coverage overlay required some additional work, because the classification scheme used by the USFS considered three coverage categories for poles and mature timber stands, but only two for old growth stands. This was inconvenient for analytical purposes and so all old growth stands had to be reclassified into three categories using aerial photography made available by the USFS and described in table 1.

Road network data was obtained from the USGS topographic quads and distinguishes two types of roads, paved and unpaved. This map was later combined with the canopy coverage map to derive a map of distances to areas without tree cover, that is used as a proxy measure for microclimatic disturbances of squirrel habitat. Openings in the forest expose the ground to the detrimental effects of increased solar radiation and wind, that may degrade habitat quality. Table 2 summarizes the most relevant information regarding the entire Mount Graham red squirrel habitat database and the maps are shown in Appendix 1.

TABLE 1

AERIAL PHOTOGRAPHY SPECIFICATIONS

PROJECT I.D.: CNF 613050
DATE: 1977, 1978
NEGATIVE SCALE: 1:24000
FILM TYPE: color negative
CALIBRATED FOCAL LENGTH: 153.15 mm
DIRECTION OF FLIGHT: North - South
SOLICITATION #: ASCS/FS 15-77 SLC
CONTRACTOR: Pacific Aerial Surveys
Roll #: 477, 1077

TABLE 2

DIGITAL DATABASE

	Topography	Elevation	Slope	Aspect
File Name	Topo	Elevatio	Slope	Aspect
Data Type	interval/ continuous	interval/ continuous	interval/ continuous	interval/ continuous
Units	ft.	ft.	%	degrees azimuth
Cate-gories	NA	NA	NA	NA
# Code	NA	NA	NA	NA
Min./ Max	4800-10720	6520-10720	0-260	0-359
Paper Maps	USGS quads	USGS quads	Elevation	Elevation
Map Type	source	source	derived*	derived*

* Using MAP operations DIFFERENTIATE for Slope and ORIENT for Aspect.

TABLE 2 (continued)
DIGITAL DATA BASE

	Vegetation Types	Canopy Closure	Dbh	Food Productivity	
File Name	Vegtype	Canopy	Dbh	Foodprod	
Data Type	nominal	interval/ categorical	interval/ categorical	nominal	
Units	NA	%	in.		
Cate-gories	Spruce-fir Mixed conifer Ponderosa pine Aspen Barren ground Meadow/cienega	No trees 10-40 41-70 71-100	No trees <5 5-9 >9	High Medium Low None	
# Code**	1 2 3 4 5 6	1 2 3 4	1 2 3 4	1 2 3 4	
Min/	NA	NA	NA	NA	Max
Paper Maps	USFS stands	USFS stands and aerial photos	USFS stands	Vegetation Types	
Map Type	derived*	derived*	derived*	derived*	

* Maps derived using MAP operator RECODE.

** Codes correspond to categories listed.

TABLE 2 (continued)
DIGITAL DATA BASE

	Roads	Distance to Openings	Squirrel Activity	Observatory
File Name	Roads	Distopen	Sqactiv	Astrobs
Data Type	nominal	interval/ continuous	binary	nominal
Units	NA	# cells	NA	NA
Cate- gories	paved/ unpaved	NA	activity/ no activity	phase 1 phase 2
# Code	1 2	NA	1 0	1 2
Min/ Max	NA	0-32	NA	NA
Paper Maps	USGS quads	Canopy+ +Roads	USFS squirrel survey	USGS quads
Map Type	source	derived*	source	source

* Using operations RECODE, COVER, and SPREAD.

CHAPTER 5

METHODS

PROBLEM DEFINITION: ASSUMPTIONS AND BOUNDS.

Development of the Mount Graham red squirrel habitat suitability model and impact assessment follows conventional model building procedures as described for example in Giordano and Weir (1985) or Grant (1986). The first step consists of identifying the problem and setting bounds on the system of interest. The present problem was already defined as determining habitat suitability for the Mount Graham red squirrel and assessing potential habitat losses due to development of an astronomical observatory. The first and most obvious bound to impose on the system is geographic, since the analysis is focused on the previously defined study area. Other constraints are defined on the problem by postulating a set of assumptions, required in order to simplify representation of the real world system down to a level that can be captured in a usable mathematical model.

Some of the assumptions needed for model formulation deal with categorization of variables and identification of relationships among them. This leads to a formal conceptual representation of the model that must subsequentially be specified in quantitative terms, through selection of a general mathematical structure and functional forms for the equations relating model components. Next, empirical data are used to estimate model parameters and the fully developed model is used to make predictions concerning the system of interest. The predictions are then compared with observed data for the model testing phase. Model predictions are presented in the form of habitat suitability maps. Areas affected by the observatory project are located on these maps, providing an assessment of potential impact measurement in terms of habitat losses.

The format of the model development procedure outlined here is closely related to the HEP/HSI methodologies discussed previously. In fact, the Mount Graham red squirrel habitat suitability model can be considered as an HEP/HSI multivariate statistical model, with some variants introduced primarily because of its explicit spatial nature. The impact assessment procedure is also similar to those described in USFWS (1980, 1981).

Since problem definition and geographic location of the study area were already addressed, the remaining assumptions are now discussed. They represent system simplification legitimazed by the ecological theory concepts presented in chapter 2 and relate to selection of relevant problem variables, relationships between these variables and their use as proxy measures.

From the discussion of environmental conditions at the study area and red squirrel ecology, and also from database description, it becomes obvious that the experts who have been studying the problem have clear, and apparently very reasonable expectations regarding variables supposed to be important determinants of habitat quality for the red squirrel, as well as concerning appropriate or at least acceptable ways to measure the animal's preference for different habitat types. A central assumption of this study is that the red squirrel preference or dislike for given habitat conditions may be inferred from its pattern of presence or absence at specific known sites (USDA, 1988). Although it may be acknowledged that a higher measurement level for the dependent variable, like density of use or number of cones stored in a midden, would be preferable , the dichotomous data available is considered sufficient for the purpose of this study. Time and budget constraints are, of course, not alien to this decision. The nature of the data will be one of the most influential factors shaping key features of the model. A second, closely related assumption deals with identifying the subset of all measurable environmental variables that is supposed to affect habitat choice. Here, again, practical considerations interfere with theoretical ones and narrow down the list of niche dimensions that can possibly be included in the model. The exclusion of other animal species from most HEP/HSI models, and also from the present case study was already justified on practical grounds. The database described in the previous chapter lists the data available from the Forest Service and, explicitly, the environmental variables for which the map layers were constructed. A first group describes the physical terrain attributes of elevation, slope and aspect, while a second one summarizes vegetation characteristics, namely type of vegetative community, average density of canopy coverage and average diameter at breast height (d. b. h.) of arboreal vegetation. One last variable was included to measure distance of any site from clearings in the forest and is treated as a proxy measure for habitat disturbance. Other variables expected to be relevant but ignored due to lack of data, are density of downed logs and density of snags per unit area. These trees are known to provide caching places and escape from predators.

A final simplifying assumption concerns the impact assessment part of the study. Here it is assumed that impacts of the astronomical observatory project on the red squirrel habitat can be assessed by measuring areas lost to development. Given the suitability model's spatial character, this seems to be a reasonable assumption.

METHODOLOGY

The disadvantages of validating habitat suitability models exclusively through the opinions of experts and other data-free procedures have been noted by authors such as Lancia et al. (1982) and Schamberger and O'Neil (1986). Validation according to this format is especially risky when the models were also developed using expert judgement because then the entire process becomes highly circular.

The problems associated with this deductive, expert based approach to model development can be avoided by using inductive, empirical methodologies of the statistical type. This way of doing things has, of course, its own problems and limitations, but they were considered less damaging than those of the alternative approach.

Univariate Analysis and Sampling Design

One question is immediately obvious when progressing toward a quantitative specification of a predictive habitat suitability model. Are the variables considered by experts to be important actually relevant? This question points out that it is not possible to develop a purely objective and inductive model. Stated differently, do Mount Graham red squirrels actually select or discriminate among sites based on those environmental factors? If this is actually the case, it should be expected that mean values of environmental variables differ among locations that squirrels selected as habitat, and locations they avoided. It is also expected that variance of the data would be smaller for selected locations than for the background environment. Kvamme (1985) develops this reasoning in a archeological context, analyzing site locations of prehistoric hunter-gatherers in the western U.S.

Identification of an active, non-randomly patterned habitat selection process requires the establishment of a control group, randomly selected from the population of all available sites, against which the data for selected habitat locations can be compared. Then, both descriptive statistics and inferential tests can be derived for each variable in order to determine whether it actually could be used as a discriminator between desirable and undesirable sites.

The sample data for both univariate and multivariate statistical analyses was taken from the digital database maps. Henceforth, database grid cells where squirrel activity is present will be refered to as "sites" or "active" cells, while cells where squirrels are absent will be called "non-sites" or "inactive" cells. The sample data can be conceptualized as a two-way table or matrix, with observations (grid cells) as rows, and cell descriptors as columns. These descriptors include environmental variables of the database overlays, the cell's x and y coordinates, and an indication of the presence (1) or absence (0) of squirrel activity.

Spatial statistical work often faces the problem of non-independence among observations that poses some serious constraints on how it has to be carried out. This problem, called spatial autocorrelation, is defined as the dependence of the values of a variable on values of that same variable at spatially adjoining locations (Sokal, 1979; Cliff and Ord, 1981). Since classical statistical inferential methods assume independence of the variates, not only to ensure desirable sample properties of selected estimation procedures, but also to guarantee conformity with tabulated sampling distributions, both estimation and hypothesis testing is affected by spatial autocorrelation. Its presence reduces in some sense the number of "truly" independent observations in a sample and leads to uncertainty regarding the number of degrees of freedom actually available in that sample (Haining, 1980). This usually leads to overestimation of significance levels, inaccuracies in parameter estimation and inflation of correlation statistics (Haining, 1980; Cliff and Ord, 1981; Upton and Fingleton, 1985).

Spatial sampling schemes can be designed so that the spatial autocorrelation problem is mitigated, if not eliminated. Haining (1980) suggests the use of large samples, to ensure presence of a high number of degrees of freedom or, conversely a systematic sample approach that forces a maximal spacing between observations in an attempt to reduce dependence. These techniques must be used cautiously or they may become counterproductive. Use of a very large sample may require the collection of very close observations, increasing the autocorrelation problem. On the other hand an excessively coarse systematic sampling scheme may leave us with too few observations for inferential purposes.

Two major considerations affected the present study's sampling design. Since nonsite locations represent nearly the entire background environment larger variation is expected in environmental attributes for this group. A ratio of non-sites to sites larger than one therefore is desirable (Kvamme, 1985). There are 212 active cells in the Mount Graham database and, therefore, the size of the inactive cells sample should be larger than that. On the other hand, the structure of autocorrelation in the independent variables had to be considered, in order to assess how it could be minimized through systematic sampling. A quick analysis using Moran's I coefficient (Cliff and Ord, 1981; Upton and Fingleton, 1985) as implemented in the AUTOCORR subroutine of IDRISI (Eastman, 1987) provided useful information. For spatial lag of 1 between grid cells, correlation values were close to unity but when a 7th order lag was reached, values of Moran's I had dropped to between 0.34 for the elevation overlay, down to 0.16 for slope data. A systematic sampling scheme was then used where each seventh cell in the database was selected, in both the row and column directions. Cells falling outside the study area or coinciding with areas of squirrel activity were dropped, leaving a total of 259 observations. This set of environmental background sampling locations was then imposed on each map overlay, thus generating the non-sites data subset of the data array. Professor Robert Itami wrote the computer program used to perform the sampling operation.

The goal of the univariate statistical analysis being to identify which environmental variables effectively discriminate between sites and non-sites, the data array was sorted in two groups, corresponding to these categories. Descriptive statistics of mean, range, variance and coefficient of variance were derived for the interval scaled variables, while simple frequency measures are provided for ordinal scaled data. Statistical significance of differences between mean values for sites and non-sites are tested with chi-square statistics for ordinal data and with t-tests for interval data. Tables and graphs summarizing the results of the univariate analysis are presented in the next chapter.

Multivariate Analysis

Selection of a Technique

A univariate analysis of the data matrix is insufficient for modeling habitat suitability because it cannot handle the question of overall environmental differences between sites and non-sites when all variables are considered jointly (Kvamme, 1985). Multivariate models can take all variables simultaneously into account, plus their interrelationships providing in the n-dimensional sample space a powerful analogy with the hypergeometric concept of the ecological niche (Shugart, 1981; Carey, 1981) which makes them especially well suited for ecological studies.

The problem of measuring habitat suitability for the red squirrel as a function of an n-dimensional set of environmental variables can be conceptualized in two different ways, each leading to distinct multivariate modeling approaches. One possibility is to interpret the problem as dealing with the classification of observations of habitat sites described by multiple environmental variables into one of two alternative populations, one including suitable and the other unsuitable locations. Discriminant analysis would be the multivariate statistical technique used to model this type of problem. The alternative conceptualization is that of relating a dichotomous dependent variable to several independent variables that may be qualitative or quantitative. This is a logistic regression problem (Press and Wilson, 1978). Although the two problems are related and both techniques may be used interchangeably, in some situations differences in solution become quite marked. This occurs, for example, when at least one independent variable is qualitative (Press and Wilson, 1978), as is the case with this study where in fact all three vegetation related variables are qualitative. Press and Wilson clearly state in their article that when the independent variables do not follow a multivariate normal distribution with equal covariance matrices, discriminant function techniques provide inconsistent estimators and methods using maximum likelihood estimation (MLE) techniques, like logistic regression are preferrable.

This is the case in many applications and most certainly in a majority of ecological analyses. Since these theoretical views have recently been adopted and corroborated by various authors doing ecological work (Jongman et al., 1987), and more specifically in species-habitat relationships modelling (Smith and Conors, 1986; Capen et al., 1986; Brennan et al., 1986), logistic regression was selected as the multivariate analysis technique for developing the red squirrel habitat suitability model. The mathematical formulation of the logistic regression model is given by Wrigley (1985):

$$P_{1/i} = \frac{e\ \alpha + \beta_1\ x_{1i} + \beta_2\ x_{2i} + \ldots + \beta_n\ x_{ni}}{1 + e\ \alpha + \beta_1\ x_{1i} + \beta_2\ x_{2i} + \ldots + \beta_n\ x_{ni}}$$

where $P_{1/i}$ is the probability that observation i belongs to group 1, x_{ji} are the j independent variables for observation i, and $_i$ are the weights on variables. In the habitat suitability model the $P_{1/i}$ are probabilities that a given grid cell will be considered as suitable habitat, conditional on the set x_i of explanatory variables.

Selecting the Best Environmental Model

Once logistic multiple regression was chosen as a modeling technique to predict the probability of the habitat at any given cell being suitable for red squirrel use, it is necessary to define a strategy for selecting the best regression model that can be constructed with the available sample data. Kleinbaum et al. (1988) propose the following five step procedure for selecting the best model:

- specifying the maximum model
- specifying criteria for selecting a model
- specifying the strategy for selecting variables
- conducting the analysis
- evaluating model reliability with split samples

This strategy was followed in the development of the red squirrel habitat suitability model and is now described in detail.

The maximum model is the one having the largest number of predictor variables considered at any point during the selection process (Kleinbaum et al., 1988). This model includes the following variables: elevation, slope, aspect, food productivity, canopy cover, d.b.h., and distance to openings.

Aspect, a variable representing circular data, had to be broken down into two linear components so that it could be used in the regression analysis. These two variables represent the north-south and the east-west components of each grid cells' aspect. They were coded so that the due north and the due east direction on each respective variable received a value of 180, while due south and due west orientations were assigned a value of zero.

In general the size of the available sample imposes some restrictions on the number of variables that can be included in the maximum model. A large number of independent observations are necessary in order to obtain reliable estimates of a large number of regression coefficients (Kleinbaum et al., 1988). A sample of 471 observations (212 sites and 259 non-sites) and a maximum model with 8 variables gives a ratio of about 59 observations per variable, which should be enough to produce reasonably stable models.

The second step of the model selection process is to specify selection criteria, indices that can be calculated for each separate model and used to compare them (Kleinbaum et al., 1988). Two criteria were calculated for the models, one that measures goodness of fit of a model with the data from which it was derived (^{2}) and another for measuring how well a model generalizes to samples independent from the one used in its development (classification error rates).

The most common goodness of fit measure of a logistic model is the likelihood ratio statistic, ( ), defined as (Clark and Hosking, 1986):

$$= \frac{L_0}{L_{max}}$$

Where L_0 is the likelihood function evaluated when all parameters but the constant are set equal to zero, and L_{max} is the value of the likelihood function when all explanatory variables for a given model are included. The first goodness of fit statistic derived for the red squirrel model is related to , but modified so that it becomes more similar to R^2 (Clark and Hosking, 1986):

$$^2 = 1 - \frac{L^*(B)}{L^*(0)}$$

where $L^*(B)$ is the maximized value of the log-likelihood and $L^*(0)$ its value when all explanatory variables are ignored. Values of ^{2} between 0.2 and 0.4 are considered extremely good fits (Hensher and Johnson, 1981).

To evaluate how well a model fits new samples of data, from the same or similar populations from which it was constructed, classification error rates were used. They test the percentage of correct predictions on an independent sample. In order to do this the interval-scaled outputs of the logistic regression model, measuring probability of success (i.e. probability of a sample cell being suitable habitat), are converted to dichotomous 0-1 data, through specification of cutoff points or threshold levels. Any cells with values below this point are declared unsuitable, while all above it become suitable. The test measures what percentage of cells predicted as suitable actually contain squirrel activity and, conversely, the percentage of cells predicted to be unsuitable from where squirrels are indeed absent. Moving the cutoff points along the 0-1 probability interval allows estimates of optimal cutoff points to be made by identifying the values for which the most successes are correctly classified while minimizing the number of failures. These results are presented in the following chapter as well as confidence intervals for the curve representing the best model.

The next step towards selection of the best model involves specification of the strategy to be used for variable selection, in order to reduce the maximum model to a more parsimonious set of statistically significant variables. In multiple regression analysis this is usually accomplished through stepwise procedures that permit reexamination, at every step, of the variables incorporated in the model in previous steps and of the various performance statistics for each reduced model. The strategy used here is an attempt at establishing convergent validity of the models and consisted of using both backward elimination and forward selection procedures for each one of three independently derived random sub-samples of the original data matrix. Detailed descriptions of these methods can be found in Draper and Smith (1981) and Kleinbaum et al. (1988). The strategy adopted for identifying reduced models in each case, was to consider the variation in chi-square goodness of fit statistics and keep all the variables whose inclusion or deletion determined a change of this measure significant at $p>0.05$.

As recommended by Kleinbaum et al. (1988) "P-to-enter" values for forward selection were set equal to 1.00 and "P-to-leave" values for backward selection at 0.00. This guarantees that all variables are included in the first case, and removed in second, exploring the full range of possible model specifications. Plots of ^{2} against regression step, identifying the point at which variable elimination or selection loses significance are presented in the next chapter.

Conducting the analysis is the fourth step of the process. This was done using PC-SAS routines for the univariate analysis and the mainframe version of BMDP, running on the Cyber 175 at the University of Arizona computer center, for the multivariate analysis, using the routines BMDP-LR.

The fifth step in the best model selection process consists of doing a comparative model reliability evaluation, using split samples. This was done by extracting three random sub-samples from the original sample data matrix, each containing 25% of the data. The use of 75% of the data as training samples is supported by a numerical example provided by Kleinbaum et al. (1988) and resulting from their rule of thumb that relative size of the training sample should be increased as total sample size decreases and decreased with increasing total size. In a study of over 3000 subjects, these authors used a stratified random training sample of 10% of the total size, while 75% of the data was used for training purposes in another study where only 200 subjects were available.

The six habitat suitability models using environmental explanatory variables used in this study result from performing two types of model reduction techniques (forward selection and backward elimination), on each one of three random subsamples of the original sample data matrix.

Trend Surface Analysis and Bayesian Integration

Another methodological issue of this study is the development of a separate habitat suitability model based on distributional or positional trends exhibited by the known squirrel sites and its combination with the best of the environmental model using bayesian statistics methods. This second model is also based on logistic regression and was constructed using the random subsample that yielded the best environmental model, but differs from it in that it uses power series polynomials of row and column coordinates of the grid cells as independent variables. These types of models are generically designated by trend surface models (Davis, 1987) and the version that handles dichotomous dependent variables, introduced by Wrigley (1976, 1985) under the name of probability surface models or logistic trend surfaces, is of the form:

$$P_{1/I} = \frac{e^{x_I'\beta}}{1+e^{x_I'\beta}}$$

where

$$x_I'\beta = \beta_1 + \beta_2 x_I + \beta_3 y_I + \beta_4 x^2_I + \beta_5 y^2_I + \beta_6 x_i y_i + \ldots$$

and x_I and y_I are the geographical coordinates of location i. This is a purely locational model, where the probability of a cell being considered suitable habitat depends solely on the spatial pattern of presence/absence of squirrel activity on neighboring cells. Trend surfaces may suffer distortion effects near the edges of the data, and also if control data are not evenly distributed throughout the study area (Unwin and Wrigley, 1987). Since locational data is available for the entire minimal bounding rectangle of the database, edge effects concentrate on the boundaries of the MBR, not affecting the study area contained within it. The second problem is also avoided due to the use of a regular sample grid which was selected initially to minimize spatial autocorrelation. A fourth order polynomial was selected for modeling red squirrel habitat use, based on visual inspection of the data's clustering patterns.

Authors like Harvey (1973), Whitley and Clark (1985) and Peuquet (1988) emphasize the dual nature of geographic data, that can be individuated and defined in both a substance language, as objects with size, color, weight etc., and in a space-time language, based on locational attributes, like position relative to, or distance from other objects. In this study, environmental models represent the first language, and characterize raster cells with "object-type " descriptors like vegetation type or slope, while the trend surface model is derived from strictly locational concepts, characteristic of the space language. In principle, integration of these two types of models should provide better, more valuable information than each one by itself. The two models are combined using Bayesian statistical inference techniques. Bayes' theorem results from the definition of conditional probability and sets the framework for revising probability estimates in the light of new information (von Winterfeldt and Edwards, 1986). This is a technique commonly used in remote sensing where, for example topographic information provides prior probabilities of a pixel containing a given vegetation type and then spectral information is used to revise these probabilities, resulting in improved vegetation cover classification accuracy (Strahler, Logan and Bryant, 1978; Strahler, 1980; Maynard and Strahler, 1981). For the Mt. Graham habitat suitability analysis the trend surface was treated as generator of prior probabilities and the environmental model as source of additional information used to revise the first one. The mathematical formulation of this procedure is (Maynard 1981):

$$P_{new} = 1/1 + e^{[\log(1-P_{env}/P_{env}) - \log(P_{trend}/1-P_{trend})]}$$

where P_{new} is the new revised probability estimate, and P_{env} and P_{trend} are the probability estimates of environmental and trend surface models respectively. Classification error rates and other performance statistics were derived to compare the trend surface, the environmental and final models are present in the next chapter.

<u>Impact Assessment</u>

The assumption that area lost to development of the astronomical observatory could be used as proxy measure for the project's impact on the red squirrel population was already set as a premise of the analysis. Squirrel habitat equivalents (USDA, 1988) is the concept that translates measurements of affected area into population impacts. Squirrel habitat equivalents equal the number of red squirrels that could be supported by a given habitat acreage, and are calculated by first, discretizing the habitat suitability map into a relatively small (5-10) number of classes, and then overlaying the observatory project sites map on it. This determines the number of cells, or acreage that would be lost in each suitability class, due to the development of each potential telescope or logistic site. The density of squirrel activity areas in each suitability class can also be determined overlaying the squirrel activity map on the discrete habitat suitability map and dividing the number of activity areas in each suitability class by the number of cells (or acreage) in that class. Multiplying density of activity areas by acreage lost in each class gives the number of squirrel habitat equivalents destroyed as a consequence of developing the project.

CHAPTER 6

RESULTS AND DISCUSSION

Results of the Mount Graham red squirrel habitat modeling and impact assessment can be divided into three main groups, corresponding respectively to univariate statistical analysis, multivariate analysis, and impact assessment components of the project. Presentation of the results rely substantially on graphical displays such as maps, graphs and charts that, it is intended, will help summarize and clarify the study's findings.

UNIVARIATE ANALYSIS

At this first stage of the study all variables considered ecologically relevant and for which data was available were included in the analysis. The goal was to identify if, and to what extent they may be effective discriminants between suitable and unsuitable habitat sites. The underlying rationale is that if red squirrels are actively selecting for given environmental features, out of the total range of environmental conditions available, then the set of selected sites should exhibit smaller values of dispersion measures than the set containing the unselected sites, and they should also differ on values of central tendency measures (Kvamme, 1985). For example, if red squirrels select for sites located at higher elevations, then it would be expected the mean elevation value of selected sites be significantly higher than the overall mean elevation value of the entire study area, and preferred locations would be more tightly clustered around the mean value than the set of background environmental data.

Table 3 shows means, medians, variances, and coefficients of variation for site and non-site samples of the interval-scaled variables in the data matrix. Median values are provided as a second measure of central tendency because they are less biased statistics for skewed distributions. Also, since size of the variance depends on size of the mean, coefficients of variation (standard deviation/mean), which correct for this effect (Kvamme, 1985) are also presented. Cumulative frequency graphs and significance levels of Kolmogorov-Smirnov and t tests are shown in figures 2 and 3. Kolmogorov-Smirnov tests are appropriate to assess differences between sites and non-sites on the Mount Graham study because they are sensitive to distributional differences with respect to location, dispersion or skewness (Kvamme, 1985; Miller and Freund, 1985).

TABLE 3

SAMPLE MEANS, MEDIANS, VARIANCES AND COEFICIENTS OF VARIATION OF THE MT. GRAHAM DATA

ACTIVE SITES (N=212)

VARIABLES	MEAN	MEDIAN	VARIANCE	CV*
ELEVATION	9954.33	10170	269834	0.05
SLOPE	25.64	23.5	214.41	0.57
ASPECT (E-W)	97.66	97	2605.20	0.52
ASPECT (N-S)	94.29	90	2419.55	0.52
DISTANCE	2.17	2	1.91	0,79

INACTIVE SITES (N=259)

VARIABLES	MEAN	MEDIAN	VARIANCE	CV*
ELEVATION	9020.59	9080	583536	0.08
SLOPE	43.98	39	884.80	0.68
ASPECT (E-W)	85.03	80	2411.74	0.58
ASPECT (N-S)	88.03	89	2431.23	0.56
DISTANCE	4.03	2	33.15	1.43

* CV = VARIANCE $^{1/2}$ x 100/MEAN

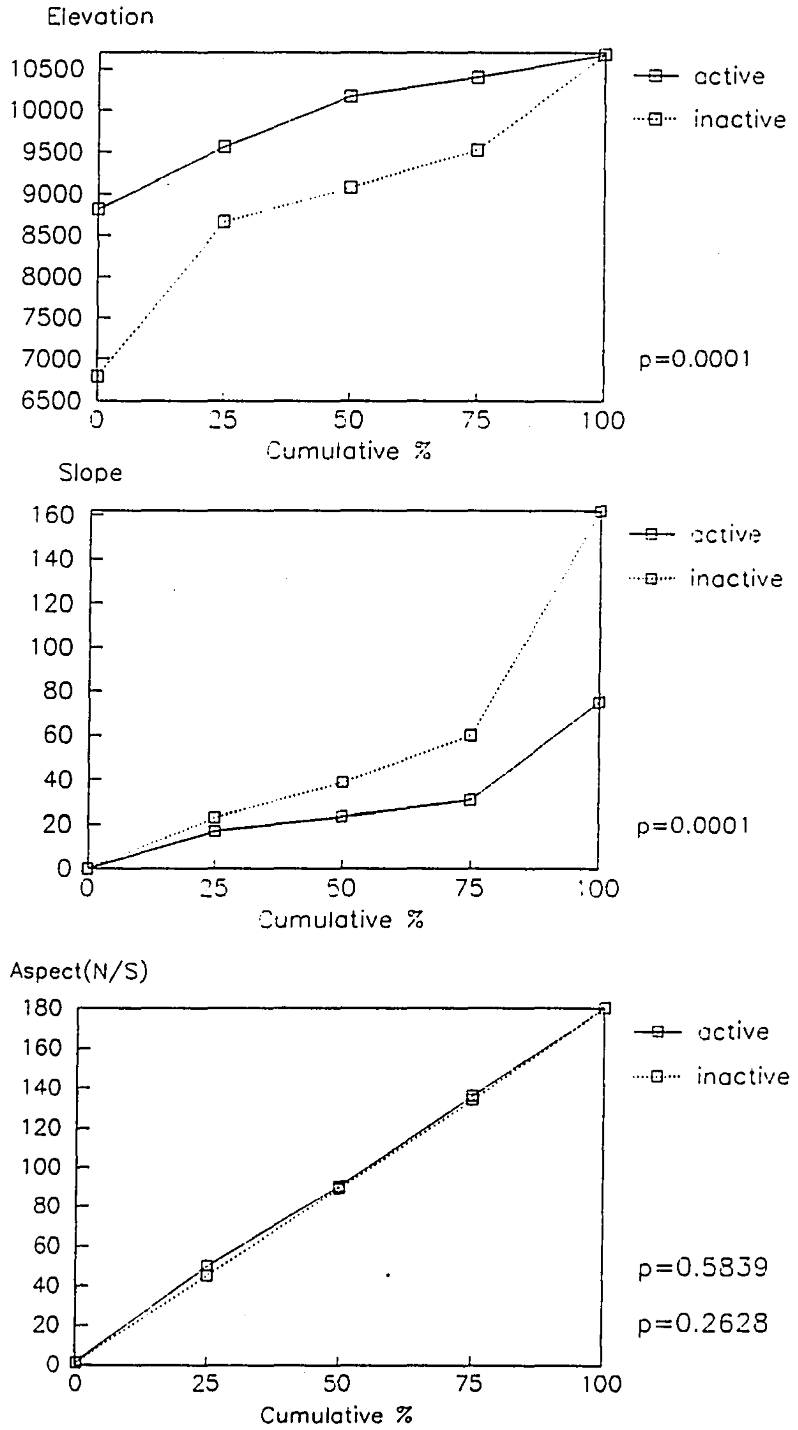


Figure 2. Histograms of elevation, slope and aspect

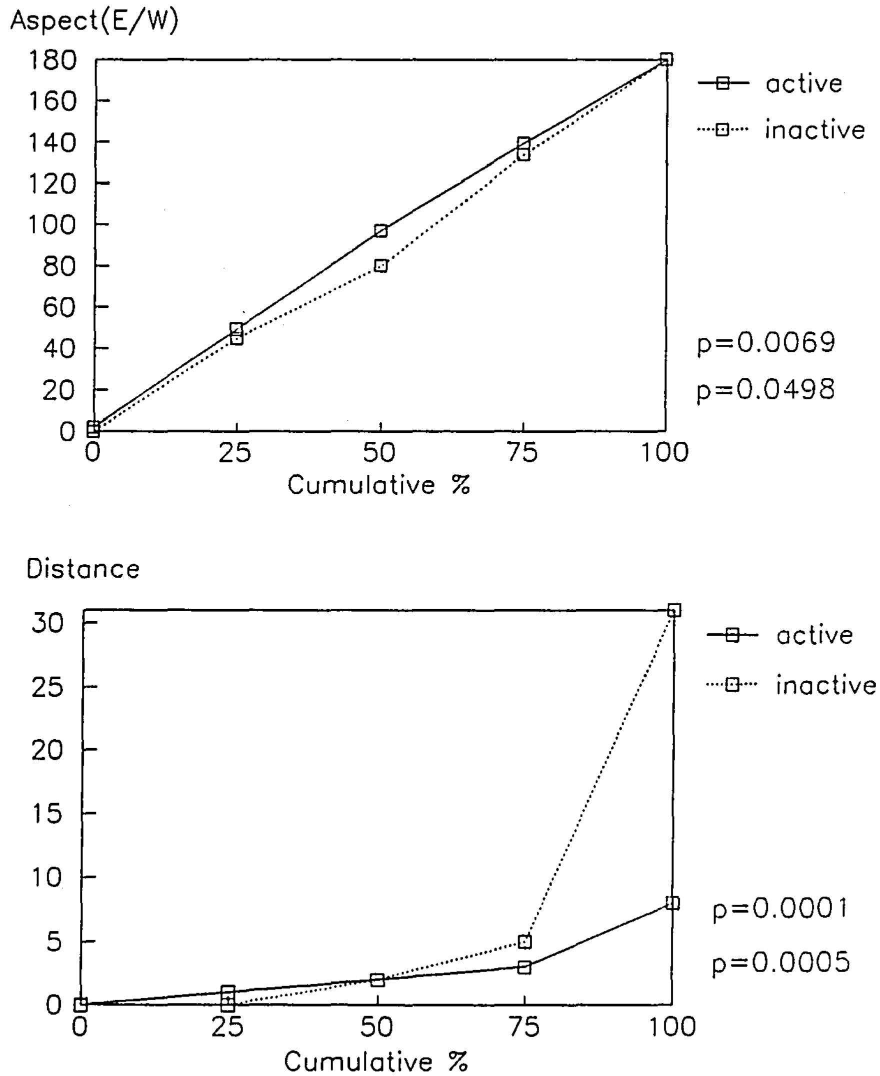


Figure 3. Histograms of aspect (E/W) and distance to openings.

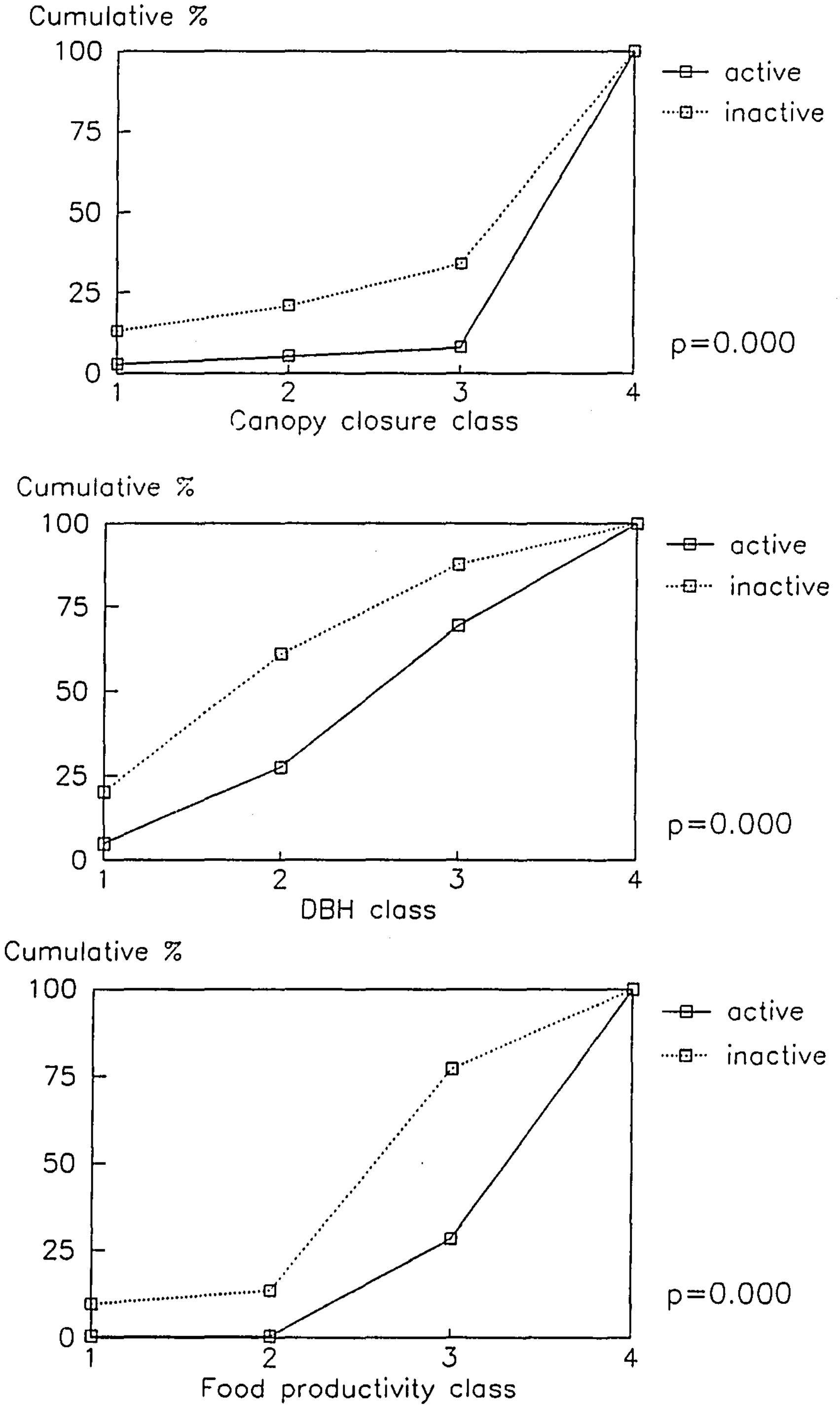


Figure 4.Histograms of canopy closure, d.b.h. and food productivity

Data for the categorical variables, is graphed in figure 4, together with significance levels for chi-square tests. A discussion of findings of the univariate analysis follows.

Elevation. There is a significant difference between sites and non-sites, showing that red squirrels actively select for locations of higher altitude than the study area's mean value. It confirms previous expectations regarding the role of this variable. Higher elevations provide cooler, more humid sites that make good squirrel habitat.

Slope. Theoretical expectations concerning slope suggest that flatter sites are preferable, especially given Mount Graham's topography where a rolling, gently sloping mountain top is surrounded by extremely steep slopes. These may be undesirable because of excessive insolation or inability to retain enough soil for supporting the type of vegetative community the red squirrel favors. The differences between sites and non-sites regarding slope are significant in the direction expected, that is with lower mean steepness and smaller variance values for sites than non-sites.

Aspect (N/S). There is not a significant difference between sites and non-sites, concerning the North-South component of aspect. A priori expectations would suggest preferential location of active sites on North facing exposures, where insolation is minimized. However, effects due to resolution of the data base, the specific topography of Mount Graham, and possibly correlations with other variables may account for this result.

Aspect (E/W). Significant differences between sites and non-sites were detected for the East-West aspect component. Active sites are preferentially located in more eastern exposures than non-sites, in agreement with expectations based, as for the North-South component, on the notion that minimal insolation allows for higher quality habitat.

Distance to openings. The distance at which a grid cell is located from an opening in the forest canopy reveals significant differences between sites and non-sites. However, this effect occurs in the opposite direction to what would be expected, with active sites located closer to openings than the overall background environment. Dispersion measures reveal a significantly smaller spread of values for sites than for non-sites, suggesting active selection for sites located close to disturbed areas. It is known that openings in the forest canopy increase the amount of solar radiation that reaches the forest floor, and generate increased wind speeds that create dryer conditions. Both these consequences of proximity to openings are unfavorable for red squirrel habitat and therefore, the results seem paradoxical. Nevertheless, two explanations are possible, one due to database limitations and the other resulting from correlations between variables. In the first case, it is possible that the negative effect of proximity to openings decays so fast that a cell size of 70.7 m on the side fails to capture it. If this is true, then distance to opening should not be significant, but inter-variable correlations may account for the counter intuitive finding. The type of openings most squirrel activity areas are close to are roads linking high elevation areas in the flatter part of Mt. Graham. Roads were preferentially built on gently sloping areas, with the purpose of providing access to the mountain top and, therefore, proximity to openings is positively correlated with high elevation and gentle slopes, two very strong contributors to good quality habitat. It is a typical case of correlation due to joint dependence on extraneous variables and not implying a casual relationship between the two being analyzed.

Food productivity. The first of the three vegetational variables finds significant non-randomness in location of red squirrel activity areas. High and medium productivity areas, corresponding respectively to the spruce-fir, and mixed conifer categories of the original vegetation types variable contain all but one of the activity areas, while non-sites are distributed through the four classes in a way approximately proportional to their areal extent. This corresponds very closely to previous expectations, and is understandable since the low productivity category, corresponding to Ponderosa pine covers a very small portion of the study area, and the fourth category represents areas with no food productivity, due to absence of conifer forests. It is possible the presence of one activity area in this class is due to registration error.

Canopy closure. Mount Graham red squirrels prefer areas of dense forest, with high percentages of canopy closure, so that the excessive solar radiation reaching the top of the canopy layer may be effectively filtered out and not affect the forest ground level. This is confirmed by the results, revealing a concentration of activity areas in the two higher classes, while non-sites are again distributed by the four classes proportionally to their representativeness.

Diameter at breast height (d.b.h.) The difference between sites and non-sites regarding d.b.h. is also significant. Red squirrels are shown to prefer areas of old growth forest, with large trees capable of producing big cone crops and provide good nesting conditions. The frequency differences are not as obvious for this variable because one single class (d.b.h.$\geq$ 9") covers the vast majority of the study area, minimizing the possibilities for very effective discrimination along this dimension.

MULTIVARIATE ANALYSIS

Univariate statistical analysis of the Mt. Graham data revealed that, out of eight environmental variables initially considered, only aspect (N/S) fails to detect significant differences between sites and non-sites. It also became apparent that some of the univariate results can only be explained by considering possible inter-variable dependencies, such as those among elevation, slope and proximity to openings. This emphasizes the need for a multivariate analysis, capable of accounting for multiple variables and their inter-relationships.

Environmental models

The maximum environmental model includes eight variables, of which five are continuous (elevation, slope, aspect(N/S), aspect(E/W) and distance to openings) and three categorical (food productivity, canopy closure, and d.b.h.). Six environmental models were generated by applying both forward inclusion and backward elimination regression procedures to three random sub-samples of the sample data matrix, and keeping those variables whose presence significantly improved the log-likelihood statistic at $p<=0.05$. The models are presented in Table 4, with variables listed in order of selection and after having corrected intercept values for the bias introduced by the use of different sample sizes for sites and non-sites. This correction is given by the formula (Maynard, 1981):

$$int_c = int + \ln (N_{NS}/N_S)$$

where int_c is the corrected intercept value, int is the biased intercept value generated by the BMDP Logist procedure, ln is the natural logarithms base, and N_{NS}/N_S is the ratio of non-site to site observations. The ratio of 194 non-sites to 159 sites used in the present study determined a correction factor of 0.19.

Table 4 shows that sub-samples 2 and 3 produced identical models under both selection procedures, while sub-sample 1 generated models differing on the third variable selected, canopy under backward elimination, and d.b.h. under forward inclusion. It is also interesting to note how model 1b is very similar to models 3b and 3f, suggesting that the formulation including elevation, slope, canopy and aspect(E/W) should be considered as the strongest candidate for best environmental model. There are no sign reversions for any of the variables in all six models and the coefficient magnitudes are also very stable. Also, signs of the coefficients match previous expectations and univariate results, indicating preference for higher elevation, higher levels of the vegetation variables, flatter slopes and more eastern exposures. Model performance statistics are given in figures 5 through 8 and again there are very apparent similarities between models. Figure 5 depicts improvement in ^{2} against forward regression step (the backward procedure gives virtually identical results, but of course with ^{2} decreasing as variables are gradually eliminated). Relevant features of this graph are the importance of the first variable,

TABLE 4

ENVIRONMENTAL MODELS

MODEL	VARIABLES	COEFFICIENTS*	INTERCEPT
	Elevation	$.24841\text{x}10^{-2}$	-24.111
	Slope	$-.22821\text{x}10^{-1}$	
1b	Canopy 1	.68454	
	Canopy 2	.44270	
	Canopy 3	$.48143\text{x}10^{-1}$	
	Aspect(E/W)	$.94916\text{x}10^{-2}$	
	Elevation	$.23172\text{x}10^{-2}$	-22.620
	Slope	$-.21780\text{x}10^{-1}$	
1f	D.B.H. 1	.15373	
	D.B.H. 2	.99746	
	D.B.H. 3	.45417	
	Aspect (E/W)	$.98096\text{x}10^{-2}$	
	Elevation	$.18056\text{x}10^{-2}$	-20.078
	Slope	$-.31227\text{x}10^{-1}$	
2b	Food 1	-6.2694	
	Food 2	2.5795	
	Food 3	3.1711	
	Aspect (E/W)	$.12294\text{x}10^{-1}$	
	Elevation	$.18042\text{x}10^{-2}$	-20.092
	Slope	$-.31232\text{x}10^{-1}$	
2f	Food 1	-6.3560	
	Food 2	2.6079	
	Food 3	3.2005	
	Aspect (E/W)	$.12291\text{x}10^{-1}$	
	Elevation	$.24921\text{x}10^{-2}$	-24.228
	Slope	$-.24982\text{x}10^{-1}$	
3b	Canopy 1	.64146	
and	Canopy 2	.13568	
3f	Canopy 3	.16696	
	Aspect(E/W)	$.11448\text{x}10^{-1}$	

Notes: * In model names, the number stands for the subsample, b and f for backward and forward regression, respectively

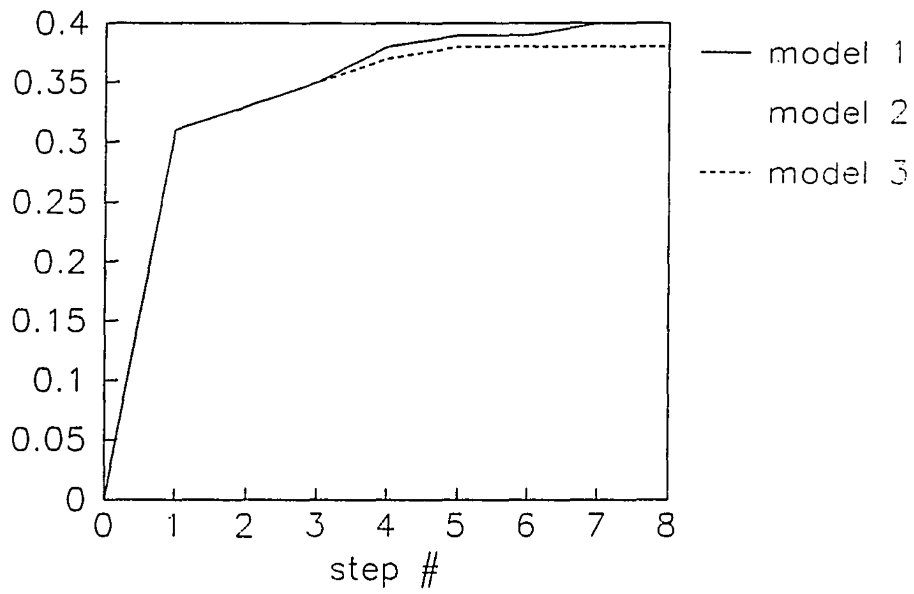


Figure 5. against regression step, for all environmental models.

elevation in all cases, that brings ^{2} to values near 0.3, the still significant contributions of the three following variables, and the flattening of the curves from the fourth step onwards. Subsequent additions of new variables fail to significantly improve the log-likelihood statistic. It can also be seen that models 1 and 2 with four significant variables result in slightly higher values of ^{2} than model 3.

The following set of figures shows classification error rates (figure 6), percent of sites correctly classified over percent of study area covered by the model (figure 7), and percent of increase in predictive ability over chance (figure 8), for each model. Once more, forward and backward versions of models 2 and 3 are identical. Figure 8 shows that the maximum improvement over chance of the models' predictive power is given by model 1b, at a cutoff point of 0.4, where the model correctly identifies squirrel activity areas 63% better than would be accomplished by chance. Model 1f at the same cutoff point, model 2 at 0.5 and model 3 at 0.6 give only slightly worse results. These are all very high figures, showing that any of the models would do a very good job at predicting habitat suitability for the Mt. Graham red squirrel, based on the empirical data available. However small the differences between models may be, a final choice must be made and considering that 3 of 6 models converged on formulations including elevation, slope, canopy, and aspect(E/W) as the significant variables, and that one of these (1b) has the best ^{2} and error rate performance statistics, 1b was chose as the best environmental model.

A habitat suitability map for the red squirrel was created by applying the multiple regression equation of model 1b to the map overlays representing variables in the model. This results in a continuous map of probability values that was discretized into 5 categories for display purposes and overlaid with the activity areas map (figure 9) to facilitate comparisons between observed spatial patterns of squirrel activity and model predicted suitability.

The fit between observations and predictions is very good, especially at the four major concentrations of middens: 1) on the highest part of the study area, around High, Hawk, and Emerald Peaks and along the ridge extending South from High Peak, 2) around Heliograph Peak, in the southeastern edge of the study area, 3)northeast ofWebb Peak and around the headwaters of Ash Creek, and 4)at the headwaters of the northern branch of Marijilda Creek, north of Heliograph Peak and west of the main

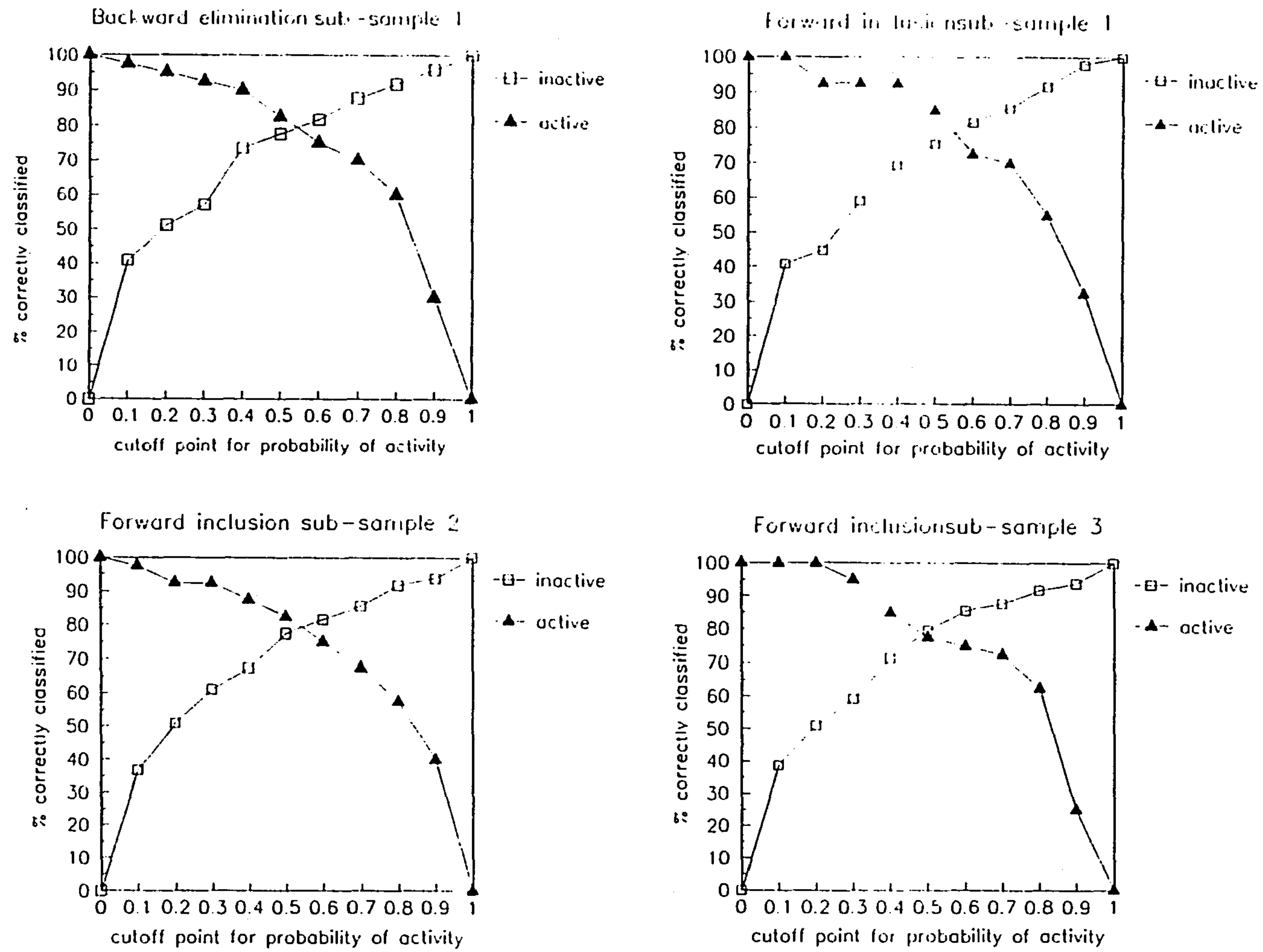


Figure 6. Classification error rates for all environmental models.

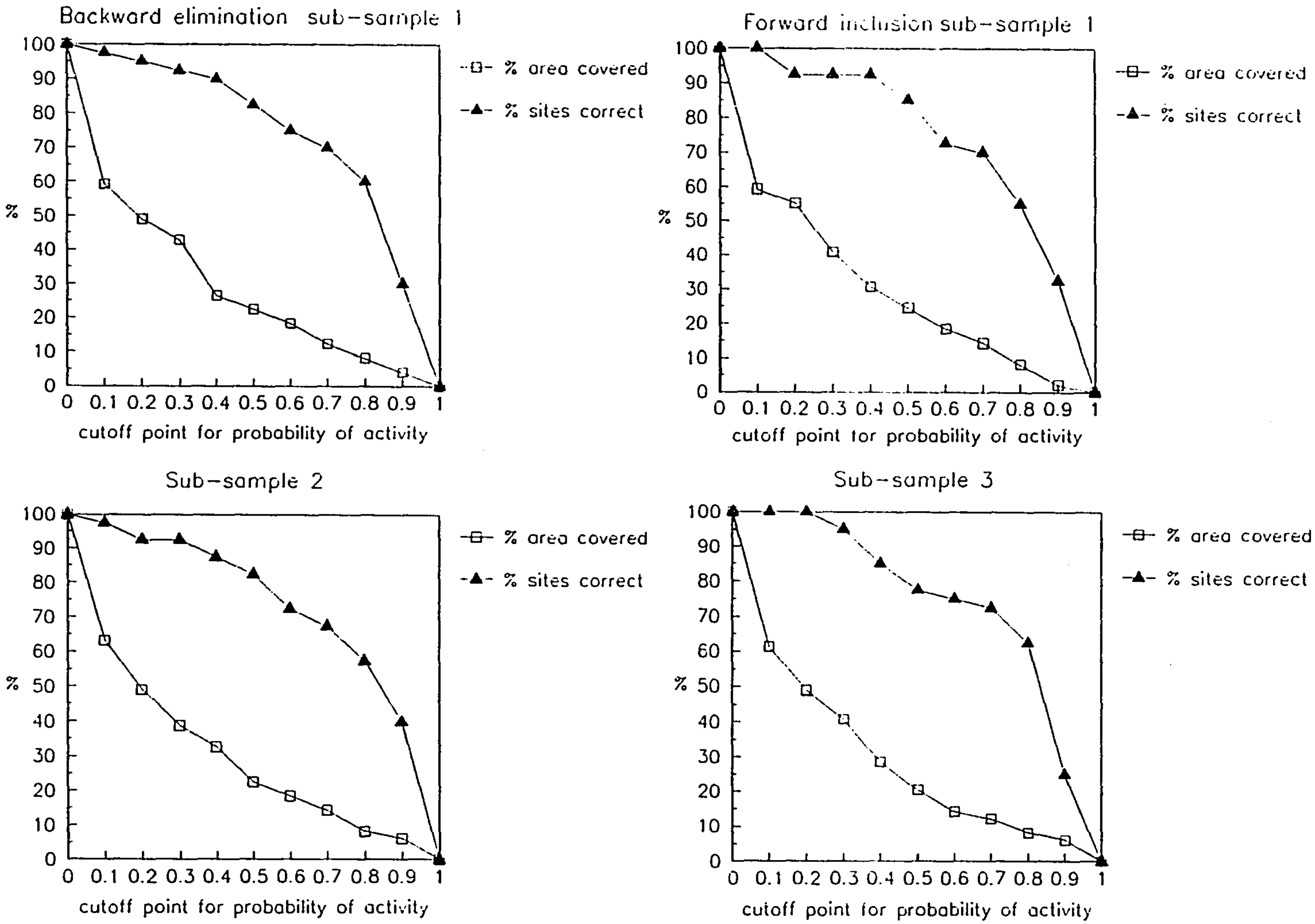


Figure 7. Percentage of sites correctly classified, over percentage of area covered, for all environmental models.

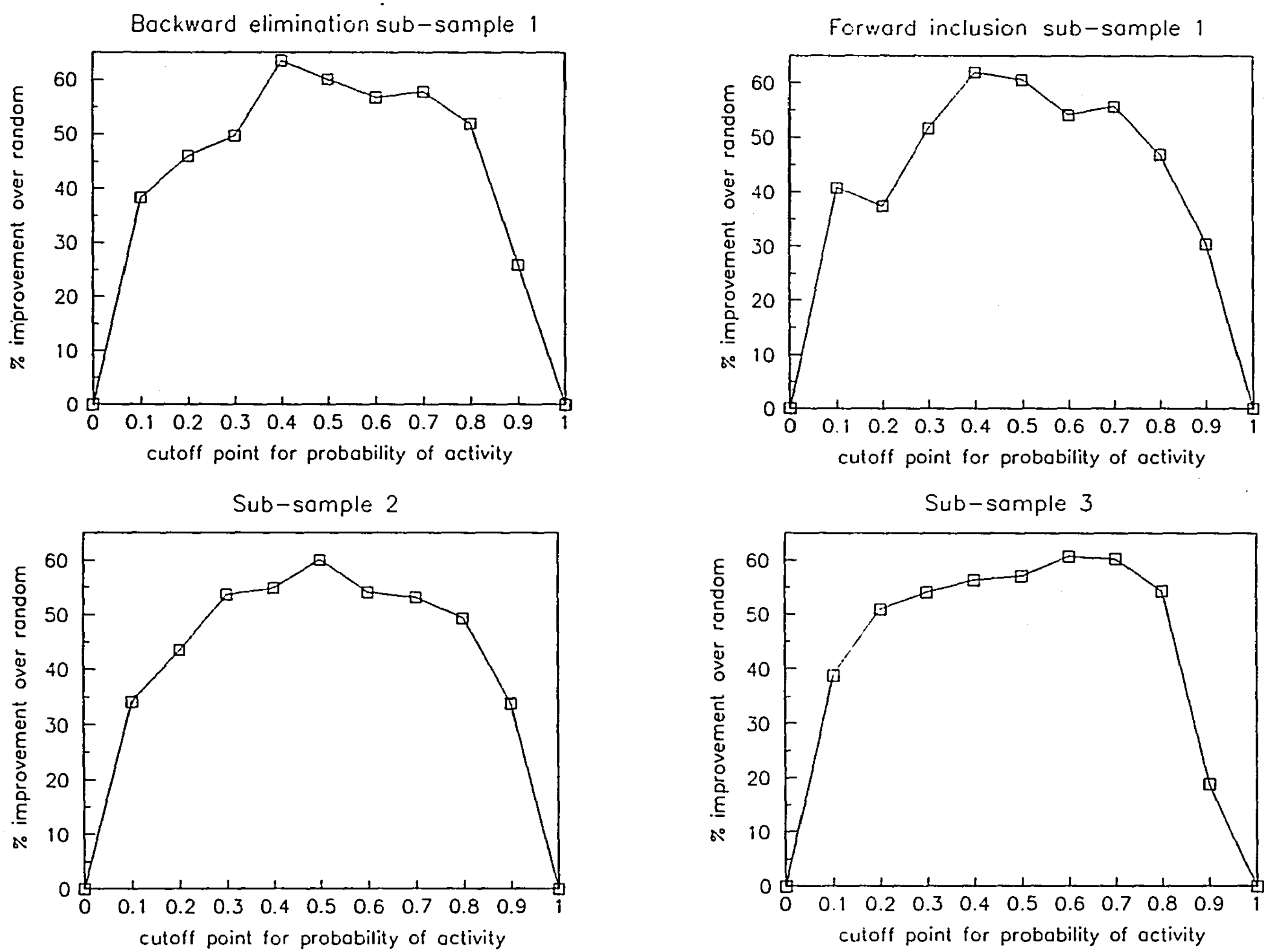


Figure 8. Improvement over chance in predictive power,for all environmental models.

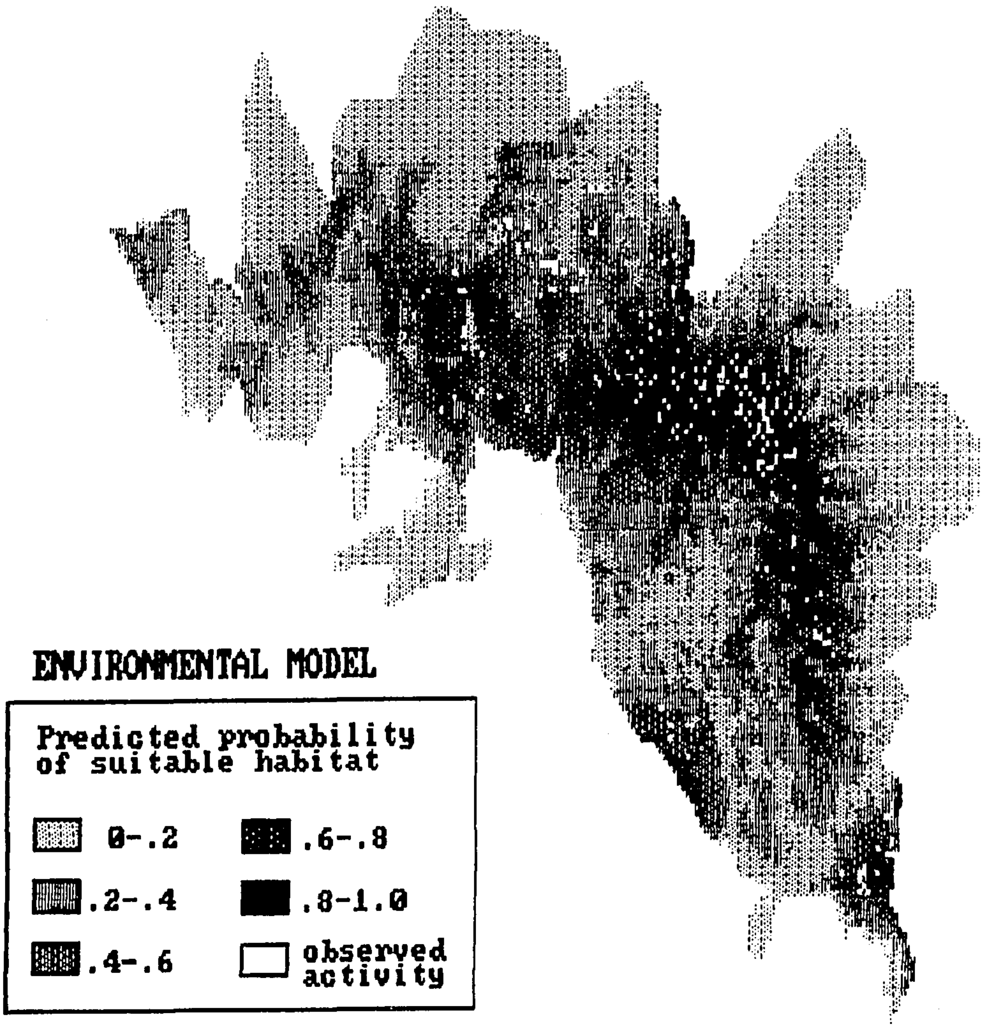


Figure 9. Environmental habitat suitability model.

north-south ridge. Besides these major clusters, the model also identifies good quality habitat in the Grant Hill/Hospital Flat area and in the Grand View Peak area, where there is an isolated activity area. One of the most obvious differences between model predictions and observed activity can be seen at the northwestern edge of the study area, near Riggs Lake, where two isolated activity areas are present in what the model predicts to be poor quality habitat. However, one of these areas corresponds to an inactive midden and the location is actually believed to provide very poor habitat (Randall Smith, pers.comm.).

In close agreement with testing results obtained from the validation sub-sample, when a binary suitable/unsuitable model is implemented at a cutoff point of 0.4 (figure 10), 88% of squirrel activity areas are correctly identified by a model covering only 33% of the study area. This leads to a predictive improvement over chance of 56%, which indicates that the environmental model alone, is a very good predictor of habitat suitability for the Mt. Graham red squirrel but for reasons described in the previous chapter, a fourth order trend surface model was also developed and is presented and discussed below

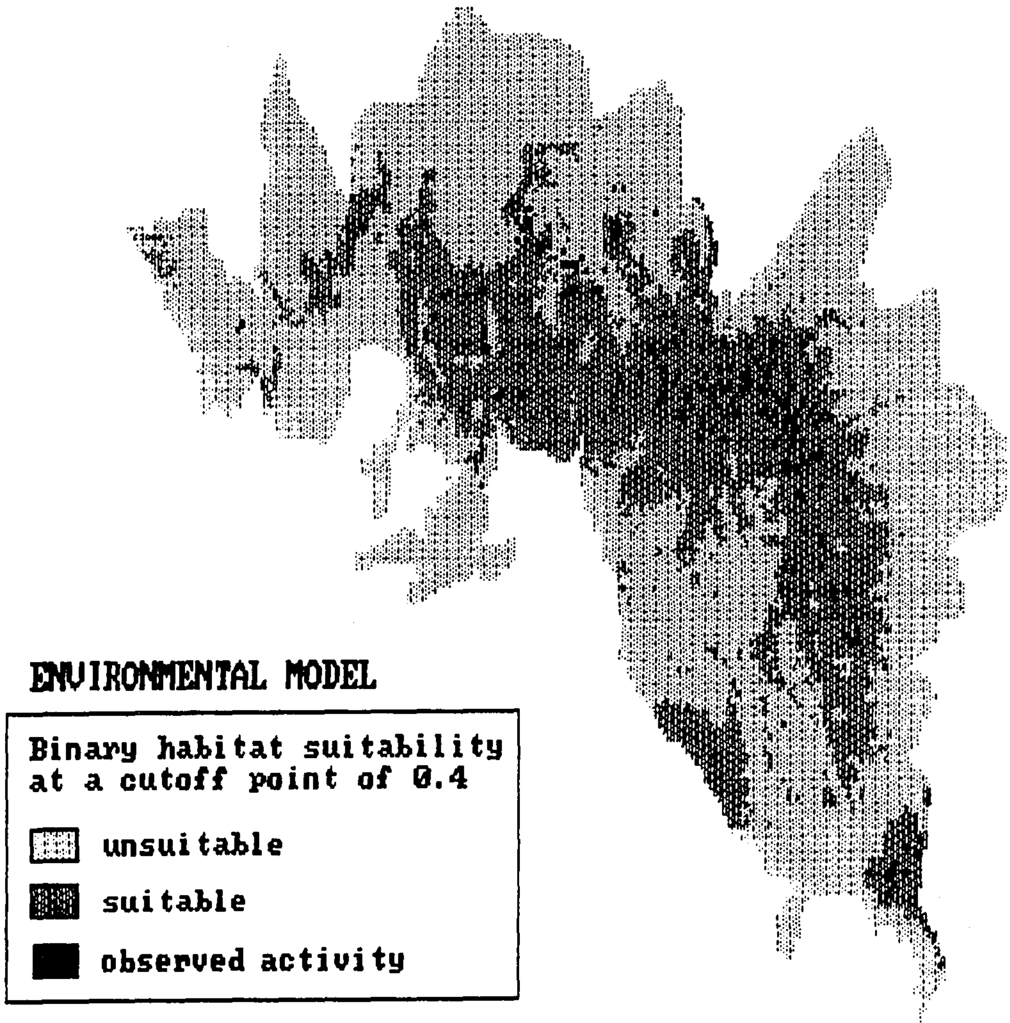


Figure 10. Binary environmental model.

Trend surface model

The logistic trend surface model for habitat suitability analysis is a multiple regression model that uses a fourth order polynomial of the **x** (column) and **y** (row) coordinates of the grid cells as explanatory variables. The polynomial's order determines the number of bends allowed for the resulting probability surface (number of bends = order of polynomial-1) and therefore, controls how closely the model can fit the data. Selection of a fourth order polynomial was based on visual inspection of the spatial pattern of squirrel activity. The trend surface was developed using the same data sub-sample that yielded the best environmental model and resulted in the model presented in table 5.

The regression equation was then generalized to the entire study area and manipulated in the same way as the environmental model (figure 11). Model performance statistics are presented in figure 12 revealing another very powerful model capable of correctly identifying 89% and 83% of the sites while only covering 32% and 26% of the study area, at probability cutoff levels of 0.4 and 0.5, respectively (figure 13). In both cases the improvement over random is equal to 57%, almost exactly

TABLE 5
TREND SURFACE MODEL

VARIABLE	COEFFICIENT
x	.18247
y	1.0007
x^2	$-.64560 \times 10^{-2}$
y^2	$-.24499 \times 10^{-2}$
xy	$.82380 \times 10^{-2}$
x^2y	$-.10387 \times 10^{-3}$
y^2x	$-.13119 \times 10^{-4}$
x^2y^2	$-.23876 \times 10^{-5}$
x^3	$.80956 \times 10^{-4}$
y^3	$.21005 \times 10^{-3}$
x^3y	$.15757 \times 10^{-5}$
y^3x	$.21047 \times 10^{-5}$
x^4	$-.50270 \times 10^{-6}$
y^4	$-.12523 \times 10^{-5}$
Intercept	-21.806

the same as that provided by the environmental model. The mountain top area, where the major cluster of activity occurs was obviously identified as the best habitat. A second nucleus of high suitability is defined by the concentration of activity at Heliograph Peak. These two areas coalesce at the 0.5 probability level, under the influence of a small core of active cells located near the headwaters of Marijilda Canyon. In the study area's western section, scattered activity around Webb Peak is relegated to probability categories below 0.5, while to the northeast, a somewhat more compact cluster located at the headwaters of Ash Creek pulls the highest suitability region of the mountain top in its direction. At Grant

Hill, on the southwestern edge of the study area, a few scattered activity areas exert a weak attraction over the surface, but most are left in the lowest suitability class.

In spite of its high predictive power, comparable to that of the environmental model, the trend surface is a simple interpolator that smooths an existing point pattern. Its interpretability and usefulness from a management standpoint are low, because it cannot identify variables that can be controlled in order to modify existing conditions in a desirable direction. This may be asking too much from a predictive model, but is certainly provided to some extent by the environmental model. The trend surface will be useful for predictive purposes, as a complement to the environmental model if the latter ignored variables that may affect site suitability. If variables left out of the environmental model influence the spatial distribution of activity, their effects will be indirectly captured by the trend surface and in principle, a model combining both types of information would be even more effective. Such a model is introduced next.

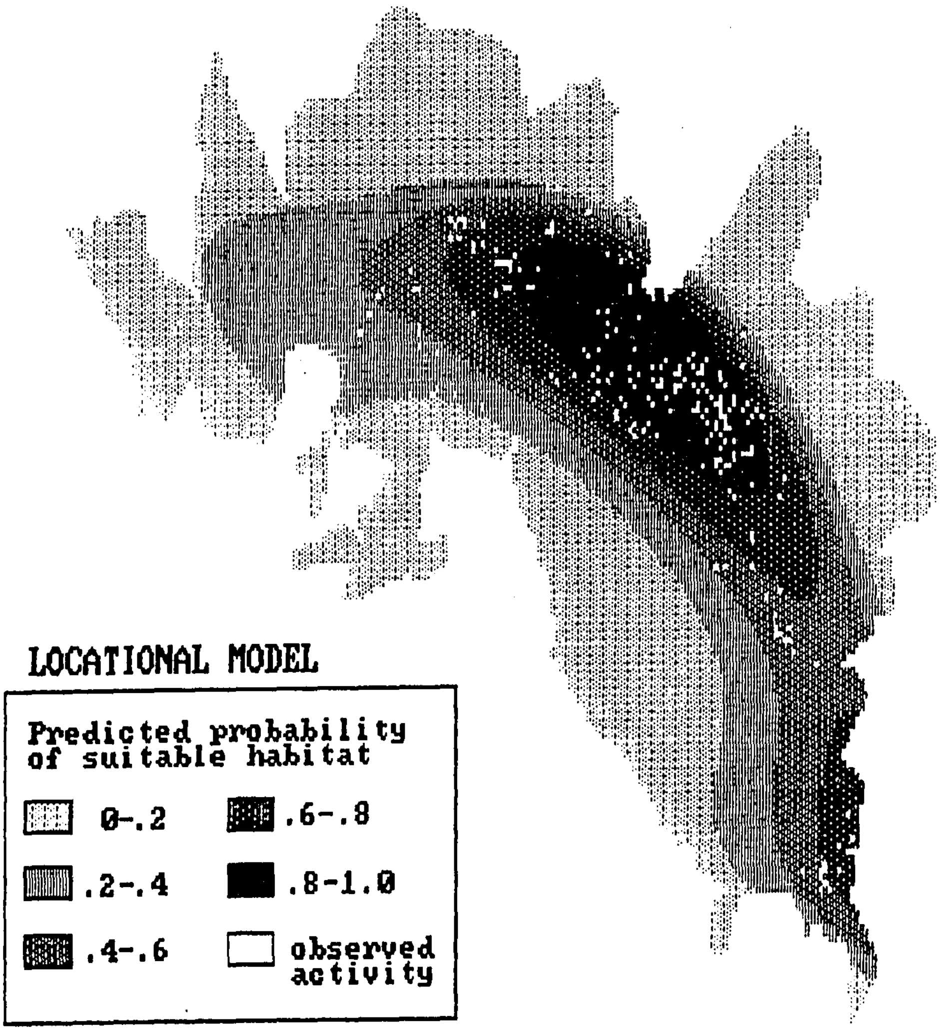


Figure 11. Trend surface habitat suitability model.

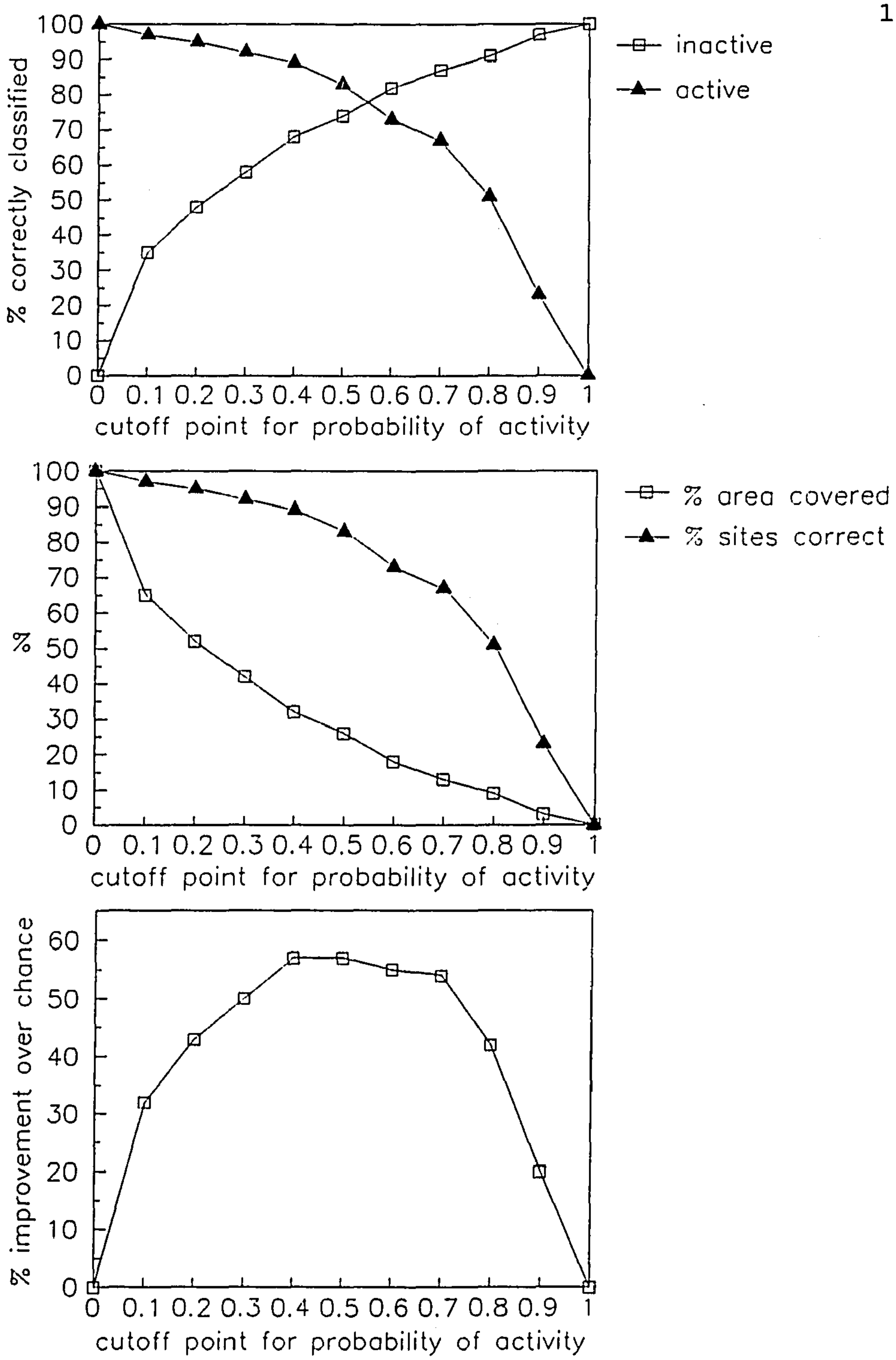


Figure 12. Performance statistics for trend surface model.

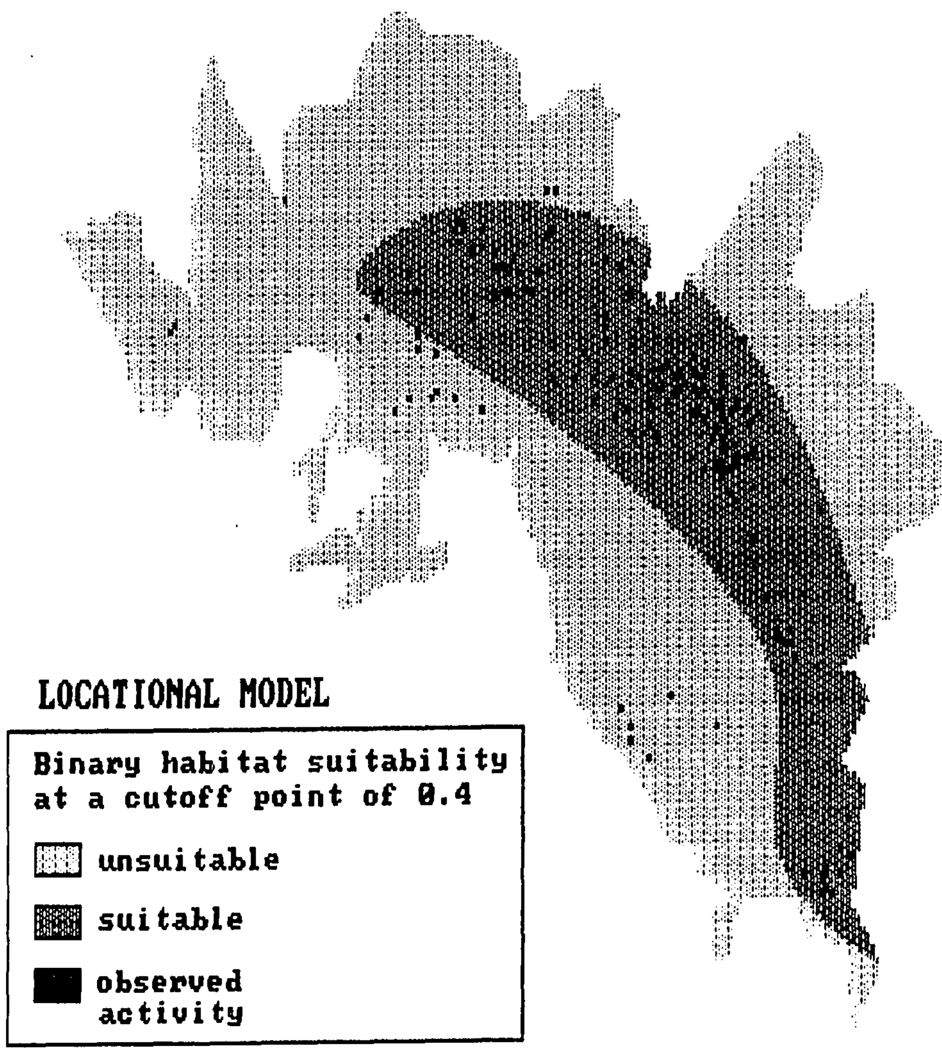


Figure 13. Binary trend surface model.

Combined model

According to expectations, the combined model, derived through integration of environmental and trend surface models using the Bayesian approach described previously, performed slightly better than its individual components. The usual model performance statistics are given in figure 14. A probability level of 0.5 is the optimal cutoff point for a binary model (figure 15) that identifies 87% of the sites while covering 24% of the study area, for a predictive improvement over chance of 63%.

The major effect of integrating the two models was an expansion of the 0.8-1.0 habitat suitability class to the south along the main ridge, down to the Marijilda area, and to the west/northwest capturing the southeasternmost activity of Ash Creek. Intermediate suitability areas almost link the mountain top zone with Heliograph Peak, under influence of the trend surface. Grant Hill activity is not well predicted, most sites being assigned to the lowest of five probability classes. The same thing happens with Two Ash Creek areas and those near Riggs Lake. Contributions of both models are well evident in figure 16, where it can be seen how the trend surface smoothed the environmental model, especially in the central, higher probability areas, while transitions between lower suitability classes remain jagged and complex, primarily under control of the environmental model. From a management standpoint, it is probably worthwhile to consider whether the small gain in predictive power produced by the Bayesian model is worth the trade-off for the simpler, more interpretable environmental model.

A dynamic population process is the main issue at stake and on this count the environmental model is preferrable, since it may identify unused areas suitable for expansion of the population. It does this based on environmental characteristics of the habitat and not only on their proximity to elements of a contingent spatial pattern. For this reason, the environmental model was selected for assessing the impacts of the proposed astrophysical development project.

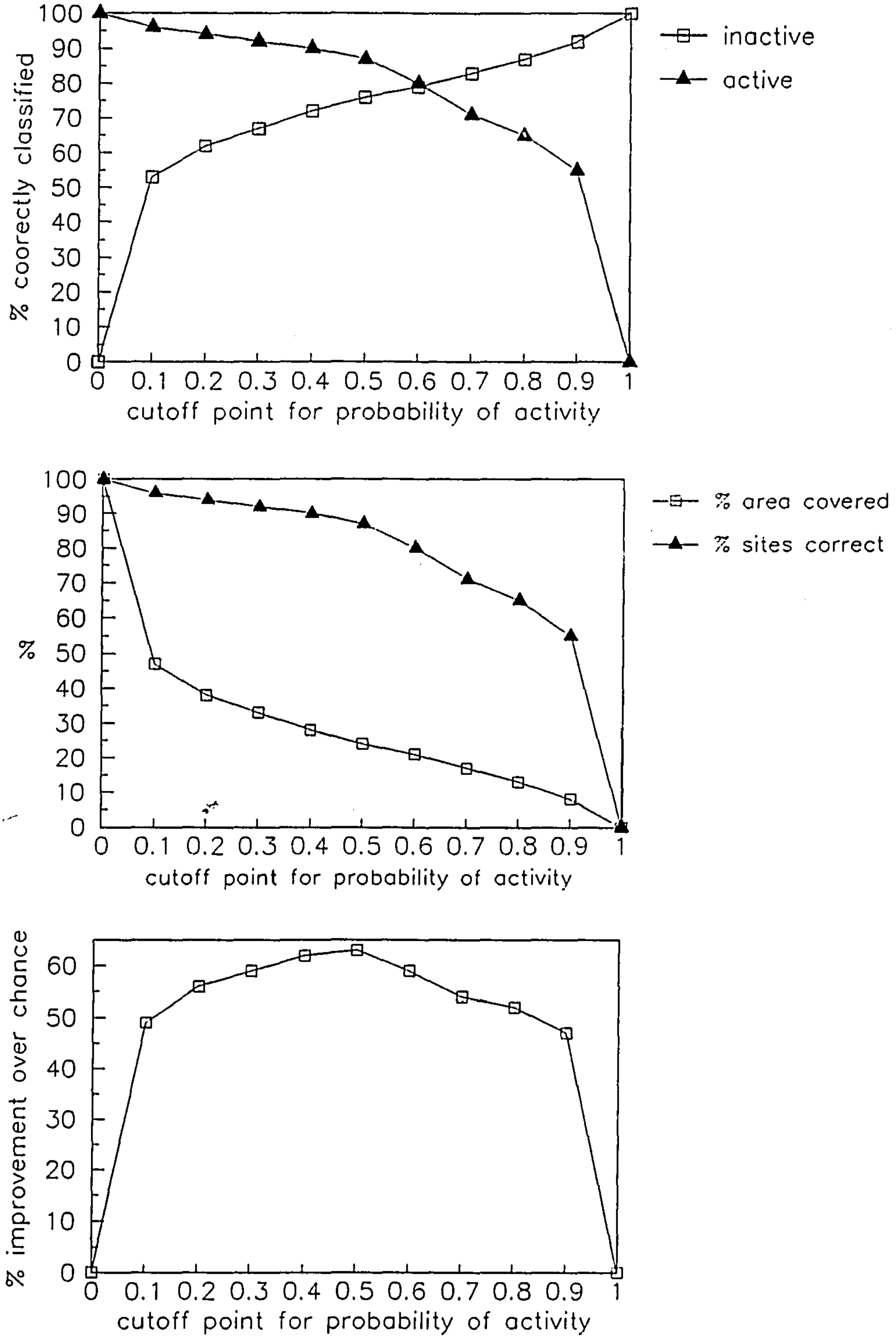


Figure 14. Performance statistics for the combined model.

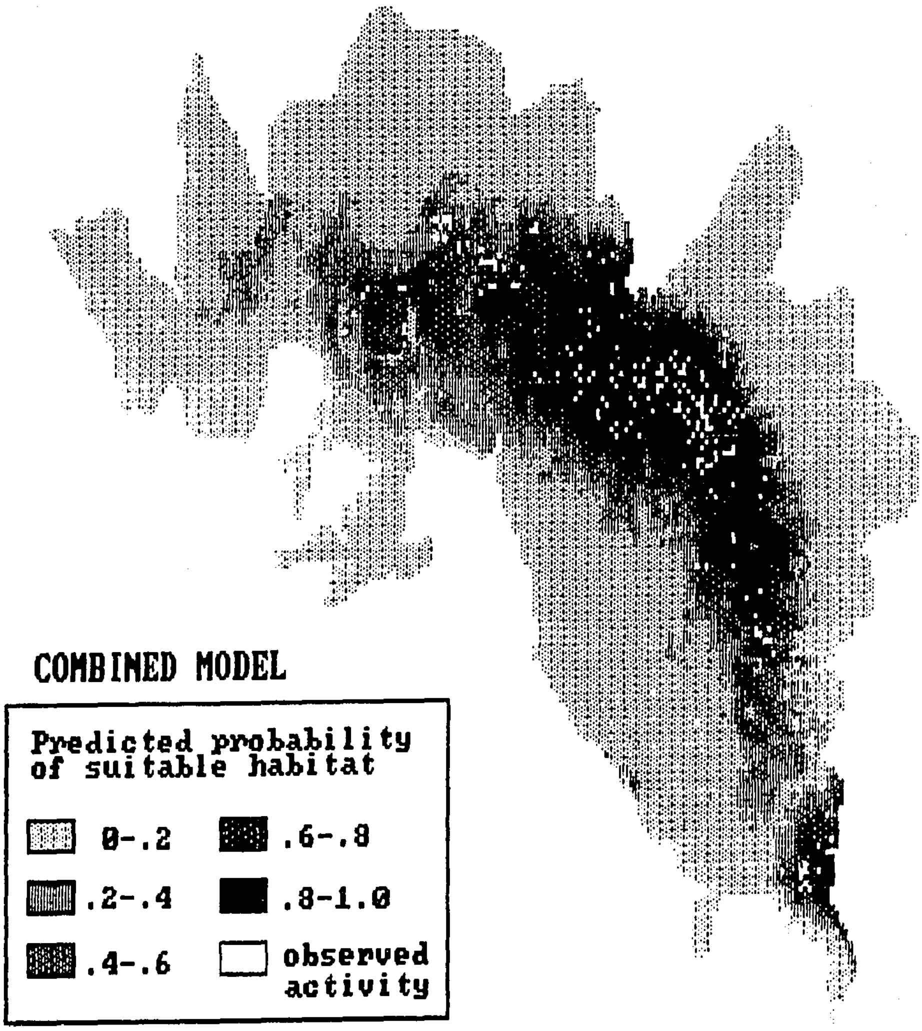


Figure 15. Combined habitat suitability model.

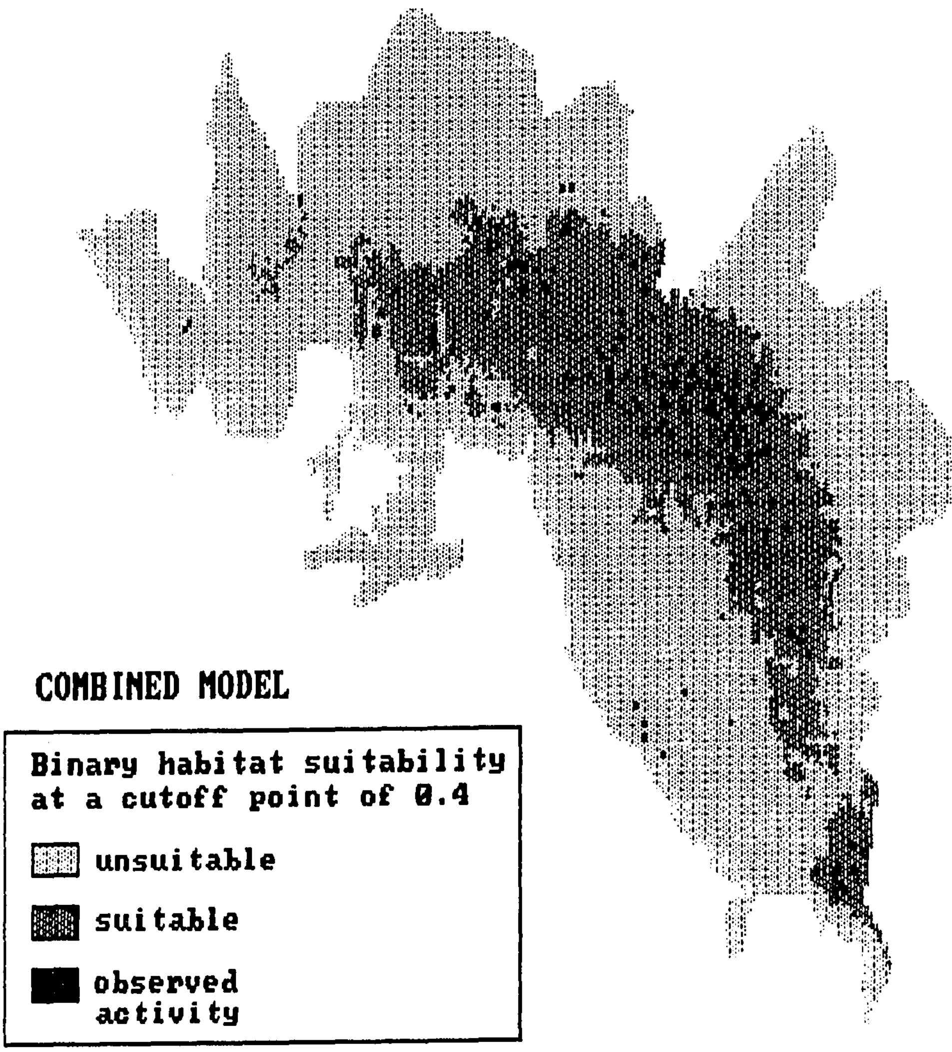


Figure 16. Binary combined model.

IMPACT ASSESSMENT

Squirrel habitat equivalents lost to development were calculated using the data in table 6. Phase 1 will cause the most impact, leading to the loss of 3.5 units while phase 2 is estimated to impact 3.2 habitat equivalents. A fully developed observatory would have an impact of 6.7 squirrel habitat equivalents, or approximately 3% of the 212 activity areas identified in the 1986-87 census and taken as a base population level for this study. These impact magnitude estimates assume that all habitat will be lost in a 70.7 m. wide corridor, which is the best approximation to the true impact, permitted by the grid-cell resolution. This value may overestimate the direct spatial impact of developing the observatory but it should be a better estimate of overall impact, that includes clearcutting, paving, construction, and other negative effects of human presence, such as noise, smells, movement, etc.

It is worth recalling that habitat area lost is a proxy measure of the project impact on population size. The Mt. Graham red squirrel is in danger of extinction and preservation of its habitat is a necessary, if not sufficient, condition for long-term survival. However, even

TABLE 6

SPATIAL IMPACT ASSESSMENT

Suitability Class	Activity Density	Number of cells Lost		Number of Habitat Equivalents Lost	
		Phase 1	Phase 2	Phase 1	Phase 2
0-0.1	0	0	0	0	0
0.1-0.2	0.004	0	0	0	0
0.2-0.3	0.005	0	0	0	0
0.3-0.4	0.009	0	0	0	0
0.4-0.5	0.017	2	1	0.034	0.017
0.5-0.6	0.025	8	1	0.200	0.025
0.6-0.7	0.019	19	1	0.361	0.019
0.7-0.8	0.028	11	4	0.308	0.028
0.8-0.9	0.089	12	5	1.068	0.445
0.9-1.0	0.150	10	18	1.500	2.700
Total	-	62	31	3.471	3.234

though impact magnitude can be estimated, it is much harder to determine what will be the importance of a given impact, that is, how it will influence the attainment of the desired goal of maintaining a viable red squirrel population. Continued monitoring of population dynamics and habitat status will be needed, to make sure that the various uses sought for the mountain can be conciliated and are not ultimately incompatible.

CHAPTER 7

CONCLUSIONS

Two main issues need to be addressed at this stage of the study: a reassessment of the modeling process and its results, and consideration of possible extensions of the present work. Looking back at the habitat suitability modeling and impact assessment for the Mt. Graham red squirrel, several questions seem pertinent. To what extent were study goals accomplished? What are the strengths and weaknesses of the approach and models constructed using it? What are the limits of model validity? How can the models be improved?

The dual goal of GIS-based statistical habitat suitability modeling for the Mt. Graham red squirrel, and impact assessment of the observatory project were accomplished. Selection of cell size, the most important decision in developing the digital database, was successful because most of the original data were preserved and species-habitat relationships were clearly identified. This is a critical step of the modeling process, and selection of cell size should reflect intended model use, size of the animal's home range, and habitat heterogeneity. Choice of an inappropriate grid-cell resolution will lead, at best, to inconclusive results (Laymon and Reid, 1986).

The univariate statistical analysis was very informative and effectively demonstrated the role of different environmental variables as dimensions of habitat selection, using the background environment as a control group. Most variables are good discriminators between desirable and undesirable habitat in a way that confirms previous expectations. One variable (aspect N/S) cannot significantly discriminate, and another (distance to openings) produced unexpected, counter-intuitive results, that can however be explained considering likely inter-relationships among variables.

Development of predictive multivariate models was the central topic of the study and it can also be safely concluded that good results were obtained. Three main habitat suitability maps were generated, based respectively on an environmental model, a trend surface or locational model, and a Bayesian combined model. They represent habitat suitability as the probability of squirrel presence at any given grid-cell, contingent on a vector of environmental, locational, or combined explanatory variables and compare model predictions with observed patterns of squirrel activity. A visual impression of good fit between model predictions and empirical observations conveyed by these maps, is clearly confirmed by model performance statistics. All models proved to be very good predictors, both for the data from which they were derived, and for independent test samples. Selection of the best environmental model revealed strong convergence between forward and backward stepwise regression procedures, and also between different subsamples. Agreement was especially high on selection of terrain variables (elevation, slope and aspect), but also very good for the vegetation variables, with canopy closure chosen in 3 out of 6 stepwise models. Preponderance of terrain variables in the final model formulations should not be attributed to biological insignificance of vegetation factors. It is probably due to correlations between variables, very obvious for example by looking at the elevation and vegetation types maps, which reveal strong association between high elevation and spruce-fir forest, the highest food productivity class. The fact that only categorical data were available to describe vegetation variables may also have influenced the variable selection procedure. Availability of interval- scaled data for these variables could increase their statistical significance in habitat models. Still, with vegetation type/food productivity excluded due to high correlation with a strong continuous variable (elevation), the next most important vegetation variables would be canopy closure, responsible for minimizing the amount of solar radiation reaching the forest ground and this is actually the variable selected in half of the models. D. b. h. is too homogeneous throughout the entire study area to be an effective discriminator and probably plays a more important role at a finer spatial resolution (Vahle and Patton, 1983).

Performance of the logistic trend surface model was very impressive, given its conceptual simplicity. The main spatial clusters of activity were captured by the model, that also showed enough flexibility to encompass some less central activity regions. Despite its conceptual limitations, trend-surface models may be able to complement environmental models, especially if these do not include important variables or are too noisy for useful interpretation.

Combination of the final environmental model with the trend-surface resulted in the most powerful predictor, although the trade-off between added predictive power and decreased interpretability and possibly excessive smoothing, may not be worthwhile. However, Bayesian combination techniques should be considered a very useful way of integrating data originated by independent regression models, while avoiding problems of model instability due to low observations/variables ratios. Instead of building a single model with a large number of variables, it is possible to develop two or more smaller, more stable models, and then aggregate them with Bayes' rule. This could also be a good procedure to combined expert-based deductive and inductive, statistical models such as those presented here.

The statistical approach to spatial habitat modeling is not, however free from some problems and limitations. Spatial autocorrelation and its consequences were mentioned previously, namely the invalidation of inferential analysis. The models are very powerful predictors but should not be used for hypotheses testing or estimation purposes, because of uncertainties relating to number of degrees of freedom available in the samples used to construct them. Spatial ecological data also frequently violate other common assumptions of multivariate statistics such as multivariate normality and equality of covariance matrices, and involve the use of categorical data. This introduces additional difficulties and requires the use of complex, computationally intensive algorithms like maximum likelihood estimation (MLE) for multiple regression, instead of the conventional least squares approach. Although the present problem was not too large, it could not be handled by the appropriate SAS routine CATMOD and therefore the analysis had to be moved over to mainframe BMDP. Despite these problems, and given the results obtained, benefits of minimizing subjectivity in model development and testing clearly overweight the implementation problems experienced.

Lancia et al. (1986) lists three advantages of assessing habitat suitability spatially and developing habitat suitability maps, namely (1) facilitated evaluation of model performance by comparing spatial habitat validity with population distribution; (2) managers can evaluate options with respect to spatial arrangement of habit types; and (3) the dependence of habitat suitability indices on arbitrary decisions about habitat types and boundaries can be reduced. The first two of these advantages were already claimed for the present study, relating to model testing and impact assessment respectively. The third advantage is also evident in that areas of homogeneous habitat suitability were not defined a priori, but emerged as results of the spatial modeling process.

One interesting conclusion of the red squirrel habitat analysis is that a few, probably small, moderate to high habitat suitability zones may have been left out of the study area. This appears to occur at Heliograph Peak, Grant Hill and maybe also just to the northwest of Frye Canyon, where high quality habitat is present at the very edge of the study area and probably extends somewhat beyond its boundary. The study also seems to indicate availability of a significant amount of unused good quality habitat. The probably is a direct relationship between habitat quality and density if use, with larger territories and home ranges being defined in zones of sub-optimal habitat. Nevertheless, the model apparently suggests that there is room for expansion to safer, more viable population levels, with the potential for even larger increases if the forest is managed appropriately. On the other hand the maps also show tight clustering of activity with squirrels inhabiting contiguous cells in some ares that are surrounded by unused regions of probable high quality habitat. This may reveal the influence of factors undetectable at the present scale of analysis but that make squirrels discriminate within what the model considers equally suitable areas. D.b.h., as mentioned above, may be such a variable. This could only be confirmed by higher resolution mapping and measure of d.b.h. on interval scale.

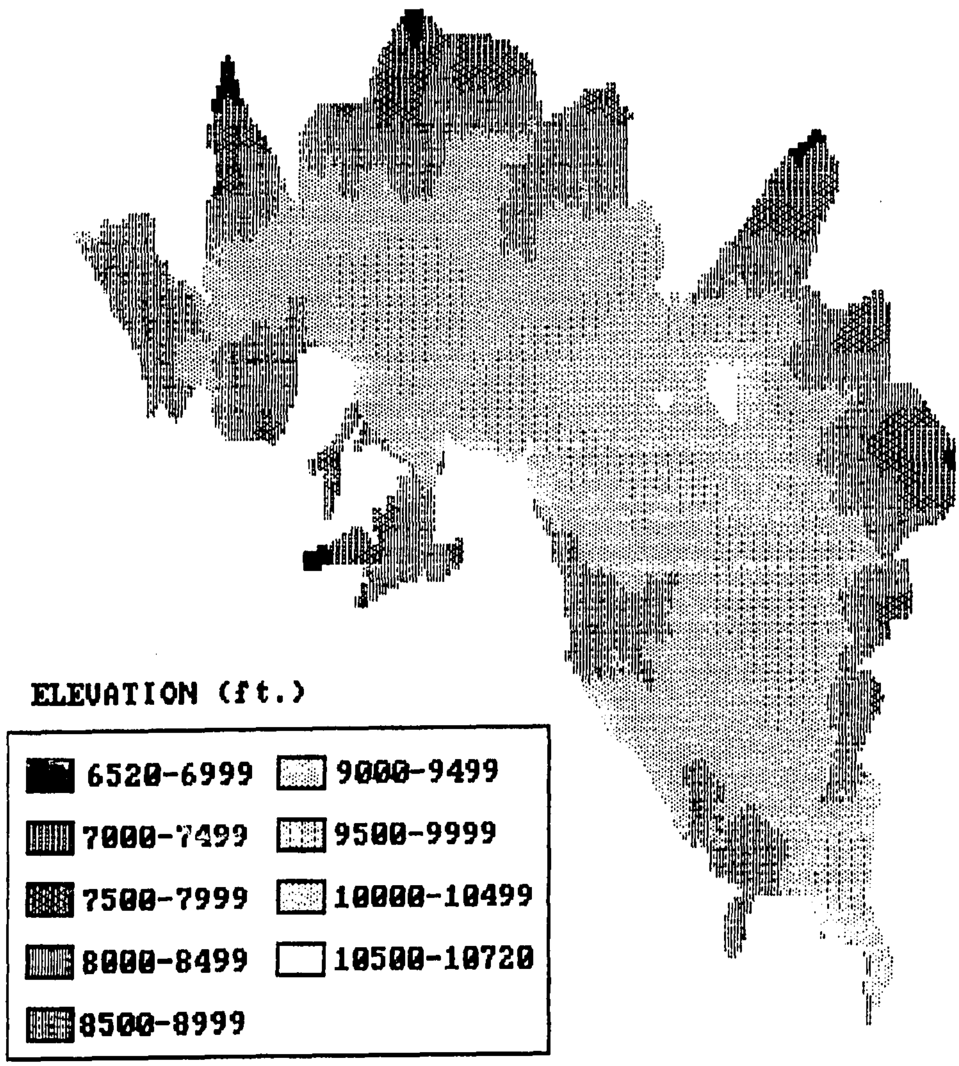
Assumptions and limitations inherent to the present models were made clear in the methodology section. It is appropriate however, to comment now on temporal and spatial aspects on the models that set limits on their validity and appropriate use. These considerations may also provide guidelines for future model improvement.

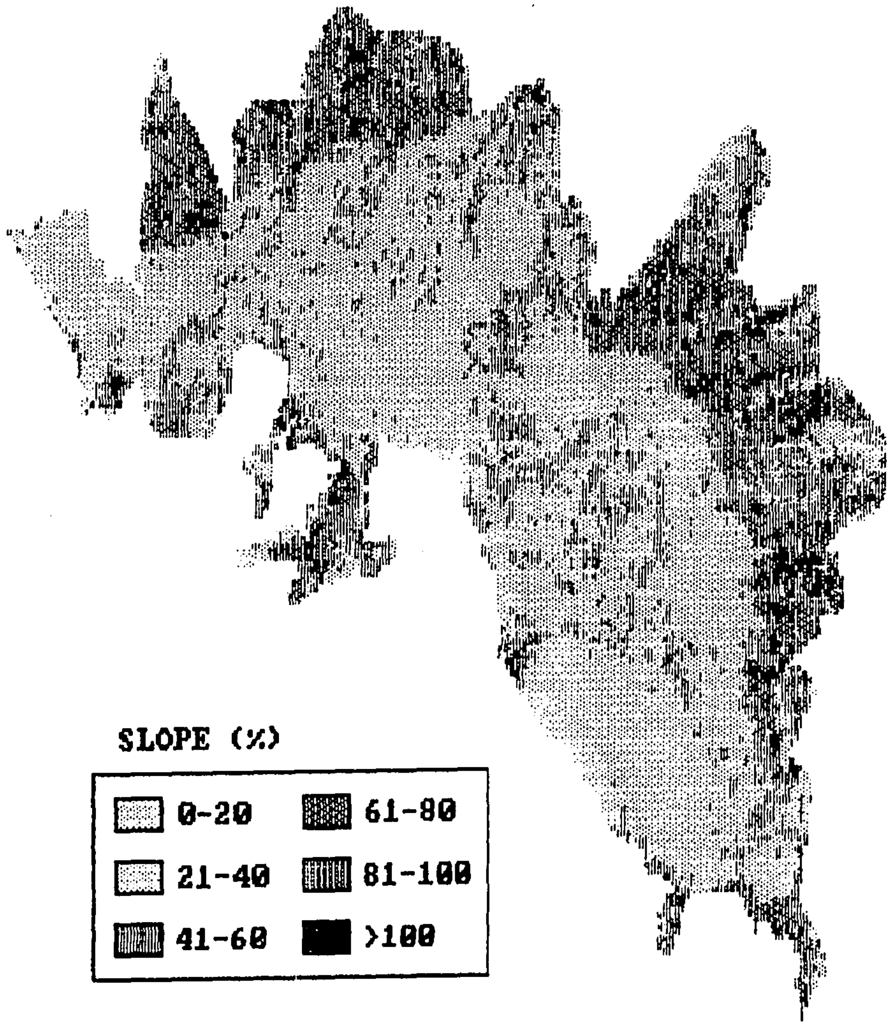
The habitat use data from which the model was developed cover a single year, which is insufficient for long-term management of animal populations, especially endangered ones. It is important to continue monitoring the red squirrel population and re-test the models on a longer time-series. Squirrel populations, like those of several other rodent species, are known to fluctuate strongly over time, with "boom" and "bust" temporal patterns. Therefore it may even be appropriate to develop two habitat suitability models, one for high and other for low population levels. Definition of positive responses of the dependent variable, i.e. squirrel activity areas, may also have temporal consequences. All activity areas were required to contain a central midden, which ignores possible patterns of habitat use of young squirrels and of adults over the winter time, when areas without middens are known to be used (USDA, 1988). Therefore, the models should be expected to work better for the spring and fall seasons. Spatial generality of the Mt. Graham red squirrel habitat models is not really an issue because the subspecies is endemic to the Pinalenos Mountains. It could be useful, however to obtain data for the neighboring Blue Jay Peak area and use them to test model performance. Validation through testing across time and space would be the strongest form of assessing model quality.

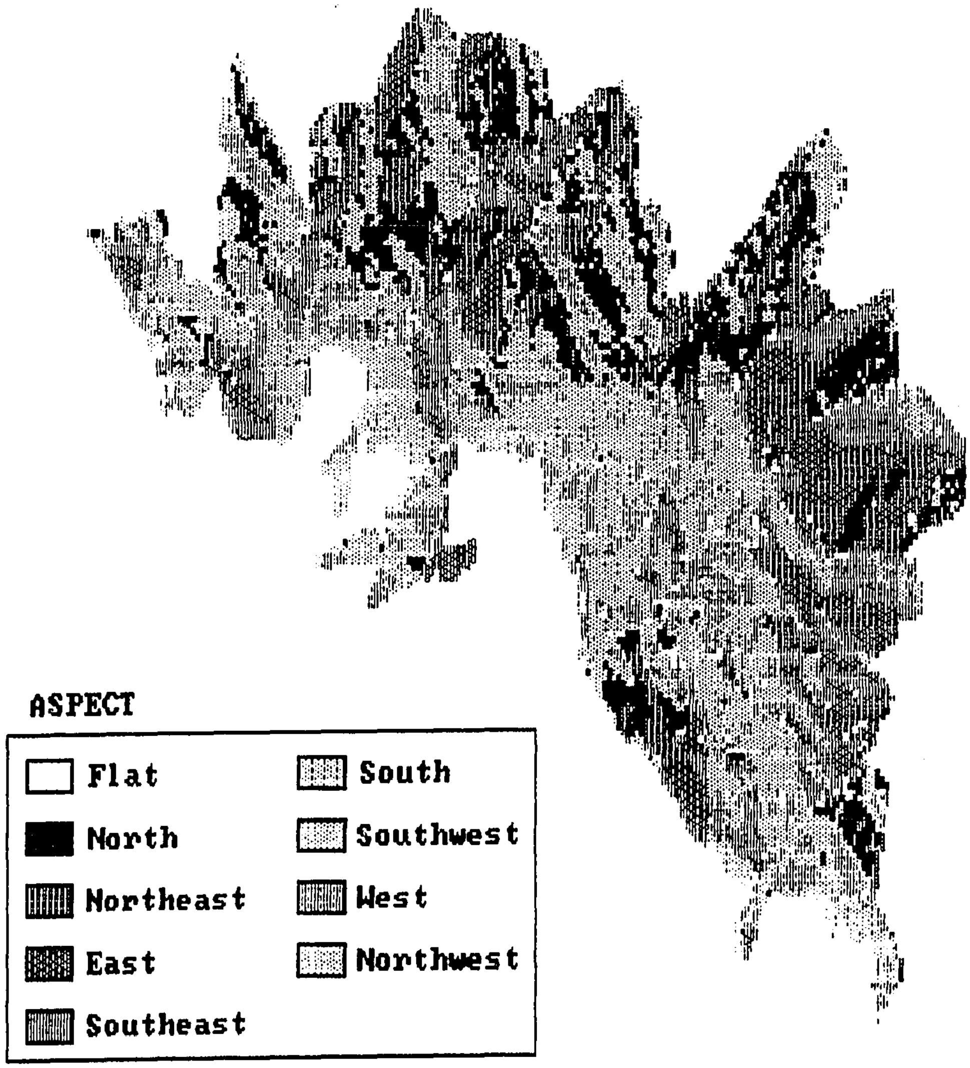
Ideally, a habitat model should be not only spatially explicit but also dynamic. This can be accomplished by linking static suitability analysis to a forest succession model that would simulate habitat suitability changes as a function of landscape dynamics. Substantial work has been recently developed on this area (11 papers in section V of Verner et al., 1986) and it seems especially appropriate in the case of an endangered species, whose long-term preservation is at stake.

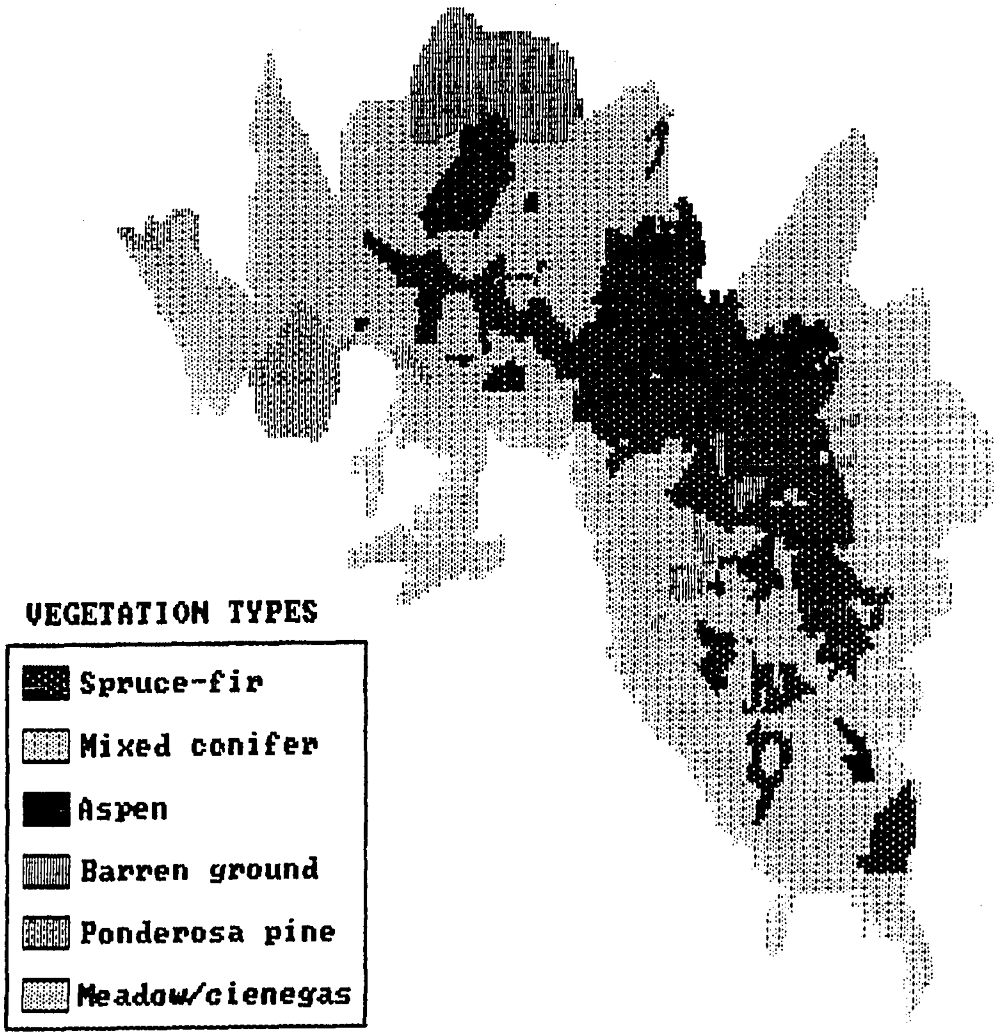
APPENDIX 1

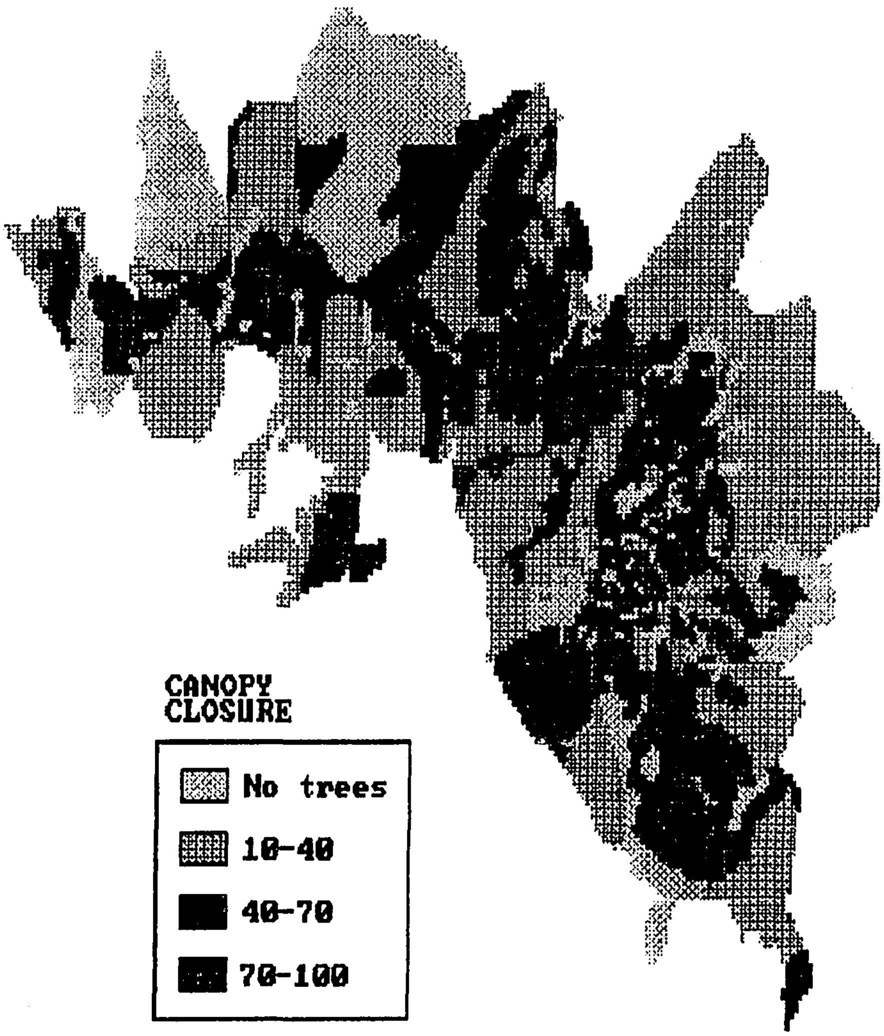
DIGITAL DATA BASE MAPS

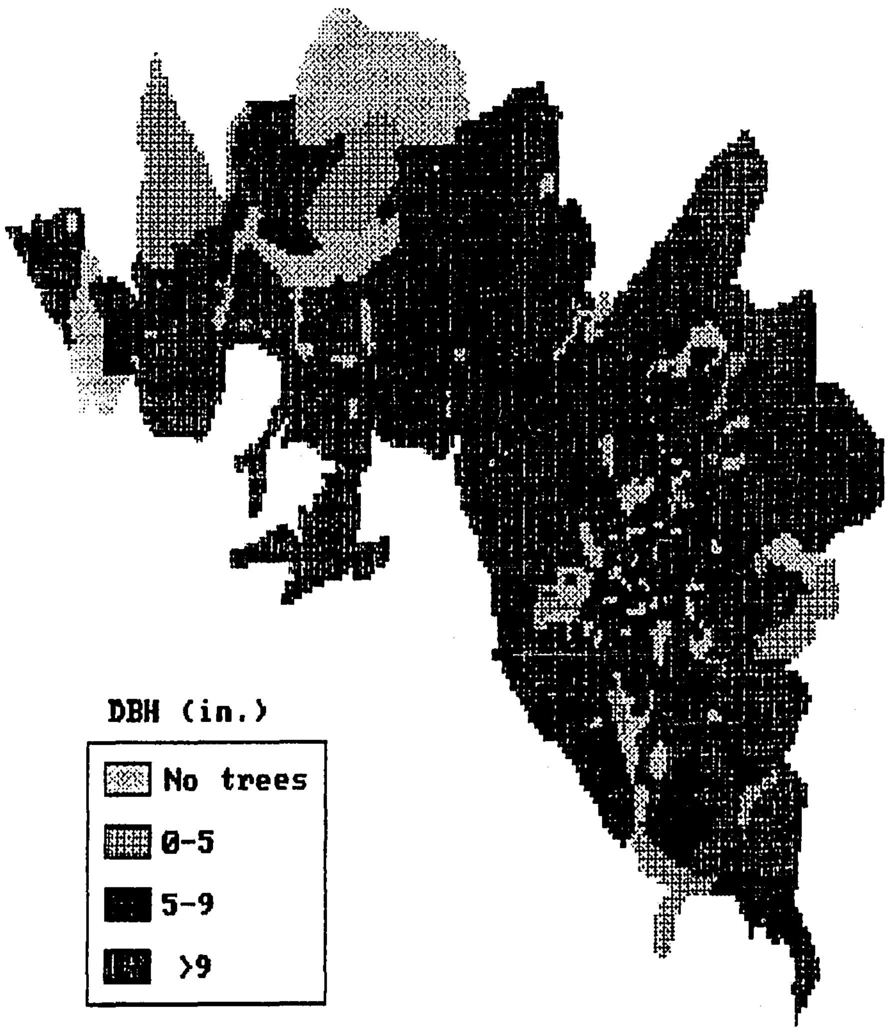

ELEVATION (ft.)
6520-6999
9000-9499
7000-7499
9500-9999
7500-7999
10000-10499
8000-8499
10500-10720
8500-8999

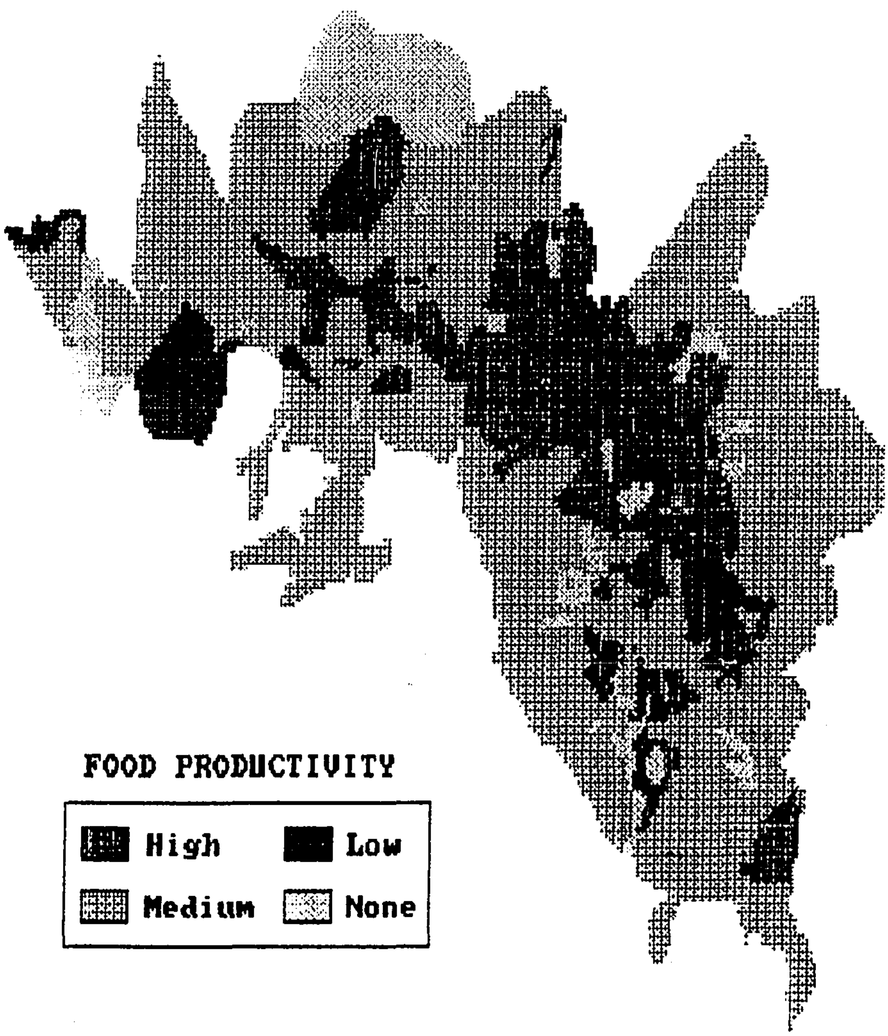

SLOPE (%)
0-20
61-80
21-40
81-100
41-60
>100

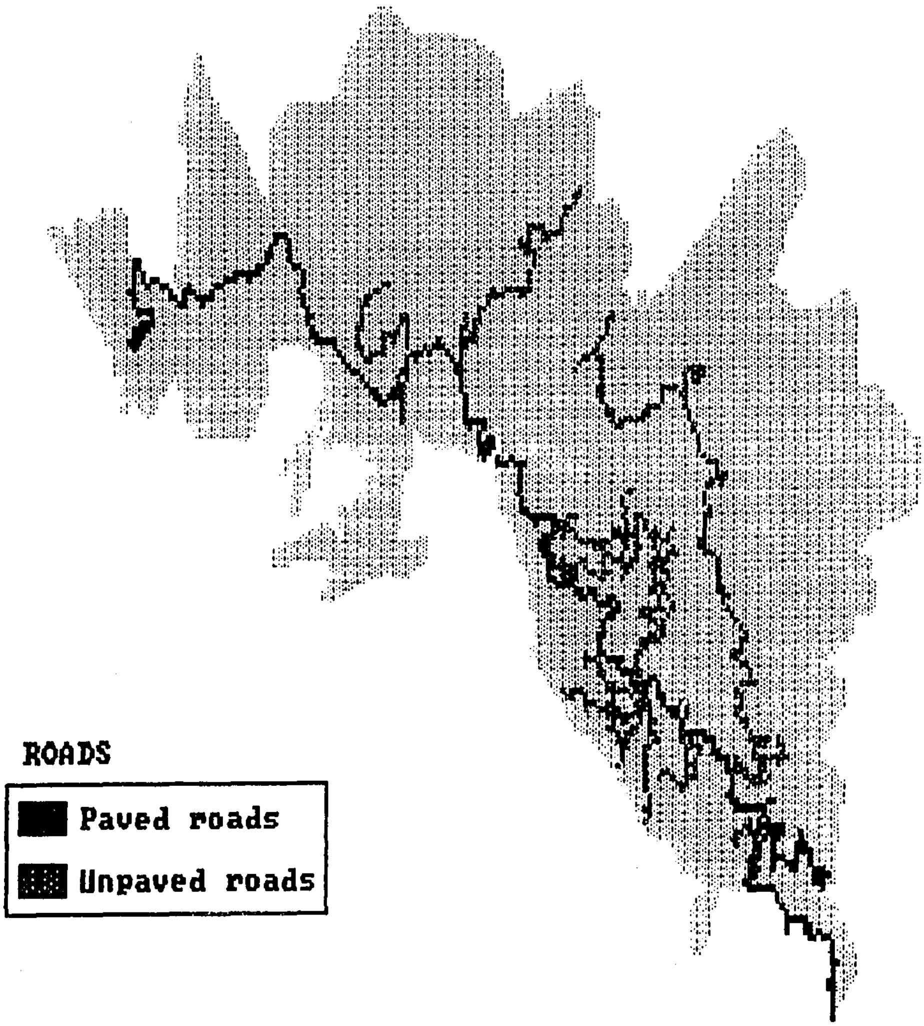

ASPECT
Flat
North
Northeast
East
Southeast
South
Southwest
West
Northwest

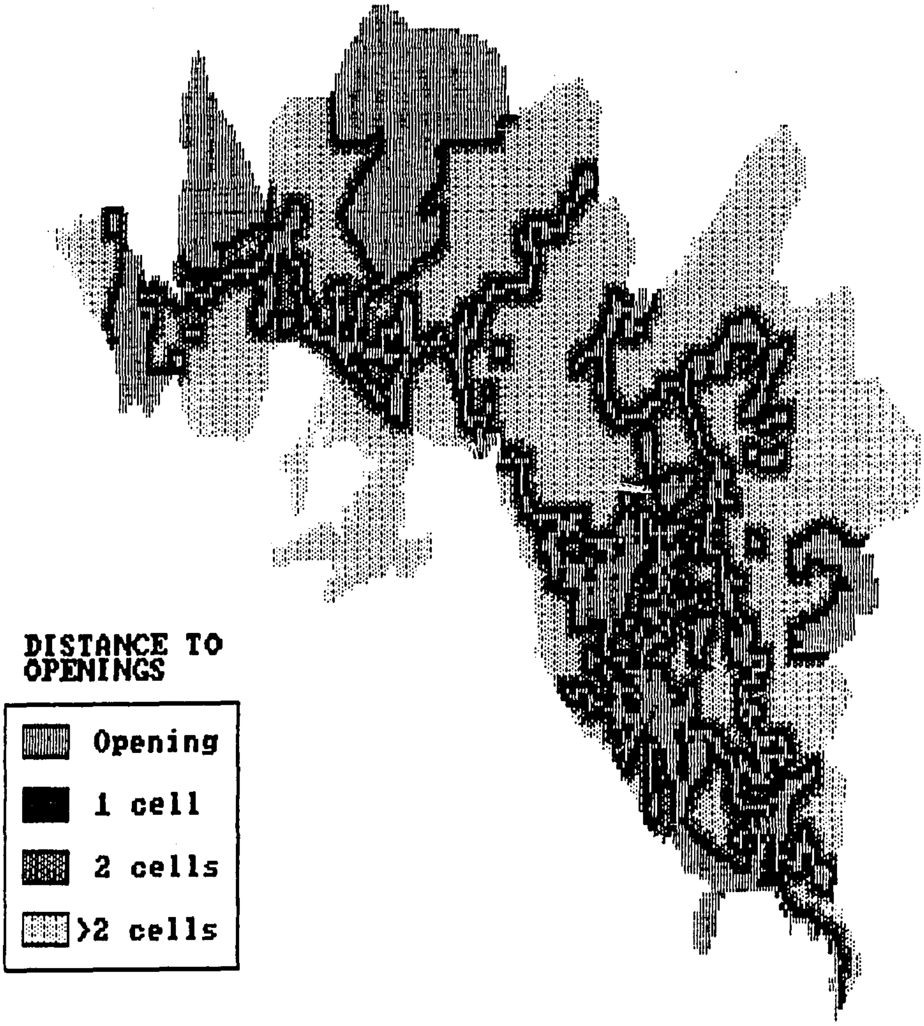

VEGETATION TYPES
Spruce-fir
Mixed conifer
Aspen
Barren ground
Ponderosa pine
Meadow/cienegas

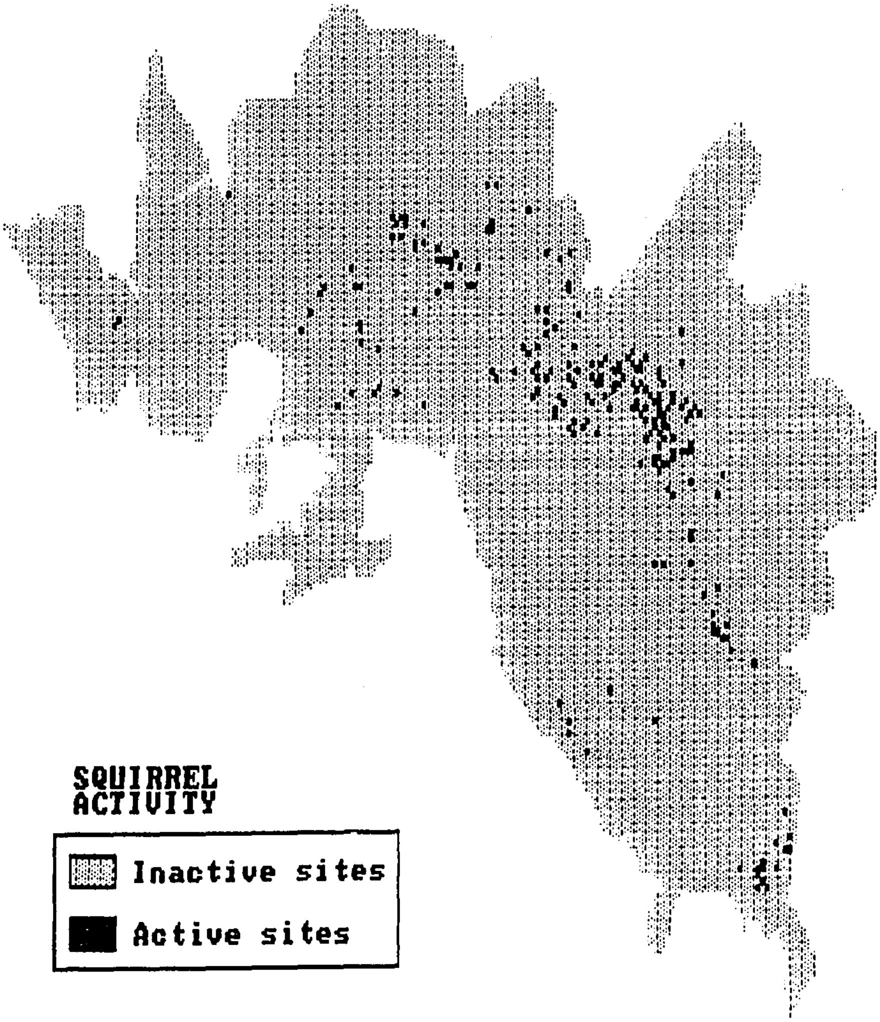

CANOPY
CLOSURE
No trees
10-40
40-70
70-100

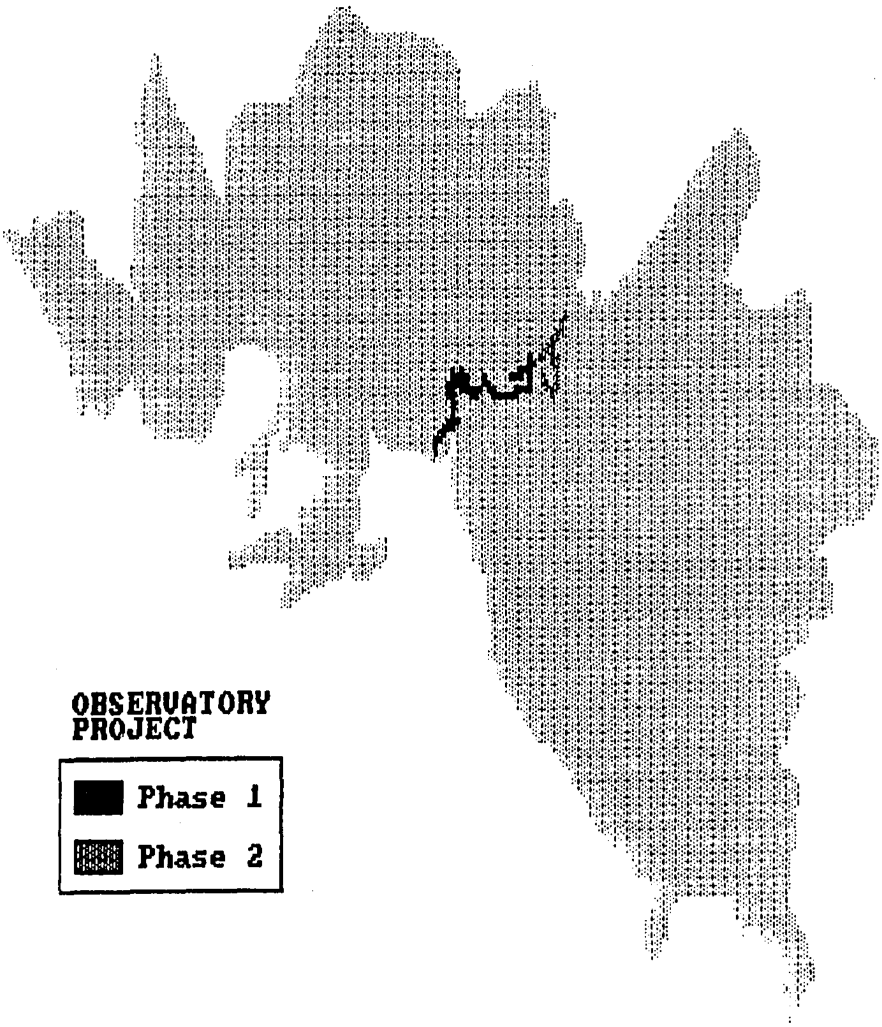

DBH (in.)
No trees
0-5
5-9
>9


FOOD PRODUCTIVITY
High
Low
Medium
None


ROADS
Paved roads
Unpaved roads


DISTANCE TO OPENINGS
Opening
1 cell
2 cells
>2 cells


SQUIRREL
ACTIVITY
Inactive sites
Active sites


OBSERVATORY
PROJECT
Phase 1
Phase 2

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