ence or absence, based on a series of environmental and locational descriptor variables. We hypothesized that these variables could explain the spatial patterns of red squirrel habitat use as observed in the U.S. Forest Service's 1986/87 winter survey. It was assumed that probability of squirrel presence could be taken as a measure of habitat suitability, and that habitat losses would be used as a proxy indicator of potential population losses.

The Habitat Evaluation Procedures/Habitat Suitability Indices (HEP/HSI) (U.S. Fish and Wildlife Service, 1980,1981), a structured framework for habitat evaluation developed in the mid-1970s by the U.S. Fish and Wildlife Service, was used in the analysis. Lancia *et al.* (1982) remark that HEP/HSI models are often left untested, or are tested with inappropriate criteria. One of the most frequently used validation methods relies on consulting with experts on the species of concern, who are asked to examine model predictions and judge whether they are satisfactory. Because these models are usually built in a deductive manner, based also on expert knowledge, the entire process becomes highly circular. Multivariate statistical models, being inductive, empirical models, when appropriately tested against real habitat use data (Schamberger and O'Neil, 1986) offer the potential to minimize validation problems and were therefore the approach selected for the present study.

BACKGROUND

Red Squirrel Ecology

The Mt. Graham red squirrel study area, as designated by the U.S. Forest Service (U.S. Forest Service, 1988), covers approximately 6460 hectares of the upper part of the mountain. This site ranges in elevation from 2275 m to 3278 m and is characterized by a series of rolling areas surrounded by steep edges and narrow canyons, especially along the northern and eastern edges. Major land-cover types are conifer forests (spruce-fir, mixed, and ponderosa pine), small patches of aspen, meadows, cienegas, and rock outcrops (U.S. Forest Service, 1986). The relationships between the endangered red squirrel and its environment are primarily shaped by the need for appropriate food sources and cover conditions.

The Mt. Graham red squirrel's diet is not well known, except for the importance of conifer seeds from closed cones and limited evidence indicating that at least eight species of mushrooms are also consumed (U.S. Forest Service, 1988). Seed productivity of Mt. Graham conifers was ranked by Jones (1974), with Douglas-fir as the most productive species, followed by Engelmann spruce, corkbark fir, and lastly Ponderosa pine and White pine. Engelmann spruce and corkbark fir are considered the main suppliers of food to the red squirrel (U.S. Forest Service, 1988).

Red squirrels are territorial animals, very aggressive toward both conspecifics and other species of tree squirrels (Flyger and Gates, 1982). Size estimates of the average activity area vary between 0.5 and 1.0 hectares. Territoriality is expressed as central place foraging behavior, meaning that harvested cones are carried to a central place of the territory or activity area, where they are piled up or buried for winter and the following year's supply (U.S. Forest Service, 1988). These piles, or middens, consist not only of cones but also scales, cone cores, and sometimes needles (Hoffmeister, 1986). It is critical that cones remain humid; otherwise, they crack open and the seeds become susceptible to theft by other animals. Therefore, red squirrels look for damp, shaded spots (Rothwell, 1979), requirements that make obvious the role of tree cover and topography in habitat selection.

Favorable environmental conditions are especially necessary for the Mt. Graham sub-species because the Pinaleno Mountains, located at 32° N latitude, are the southernmost situation for both a continuous spruce-fir forest and a red squirrel population in North America. Therefore, more solar radiation reaches the top of the canopy layer here than anywhere else on the red squirrel's distribution range, and good habitat at the forest floor level can only be created when tree crowns intercept a large part of the incoming radiation. This seems to be in agreement with observations that the Mt. Graham red squirrel is very selective in choosing locations, not only for midden placement but also for general activity areas (U.S. Forest Service, 1988).

GIS in Wildlife Habitat Studies

Given the explicit importance of spatial habitat parameters in the Mt. Graham red squirrel ecology, it was decided to use Geographical Information Systems (GIS) technology as an aid to data management and analysis. A brief review of applications of GIS in wildlife habitat analysis work is provided, in order to set this paper in the broader context of a rapidly growing research field.

Lancia *et al.* (1986), Davis and DeLain (1986), and Ormsby and Lunetta (1987) used GIS in wildlife habitat studies, following the U.S. Fish and Wildlife Service Habitat Evaluation Procedures/Habitat Suitability Indices framework. Lancia *et al.* (1986) developed spatial models to assess habitat quality for three bird species, using georeferenced environmental data to create habitat suitability maps. These maps were validated by comparison with maps of observed frequency of habitat use. Better results were obtained for common, range restricted, or more specialized species, than for rare, wide-ranging, and/or more generalized forms.

Davis and DeLain (1986) used a GIS database as the key element to linkup wildlife habitat models with the ECOSYM forest planning system. They developed arithmetic HSI for the spotted owl in two spatial databases, and included habitat suitability maps in a cost-benefit analysis of timber management alternatives.

Lyon *et al.* (1987) presented three spatial habitat analysis models, one of which was supported by a multiple variable GIS database. They analyzed habitat suitability for the wood duck (Aix sponsa) in a forested wetland using topographic, vegetation, hydrologic, and infrastructure data. Model calibration, verification, and parameter sensitivity analysis are emphasized as necessary requirements of habitat modeling. These tasks are performed for a kestrel falcon non-GIS habitat model, whose performance was evaluated by comparison with both expert opinions and field habitat use and population data.

Ormsby and Lunetta (1987) developed whitetail deer food availability maps from Thematic Mapper land-cover digital data. These data were integrated with other cartographic information in a GIS and provided input to an arithmetic, expert-based habitat suitability model. Palmeirim (1988) used Landsat TM remote sensing data and a geographic information system to map avian species habitat, considering not only land-cover types but also habitat spatial characteristics, such as minimum patch size and distance to edge. These data were combined with bird counts to automatically generate distribution, suitability, and density maps, and to produce estimates of population size.

Broschart *et al.* (1989) used a stepwise multiple regression model to predict the density of beaver colonies in boreal landscapes, by relating vegetative and hydrologic landscape patches resulting from beaver impoundments with beaver presence/absence. They emphasize the usefulness of their results to estimate beaver abundance and determine historical and present population trends.

Hodgson *et al.* (1988) inventoried and analyzed availability of wetland foraging habitat for the wood stork, and its variability between wet and dry years.