DEVELOPMENT AND EVALUATION OF PATTERN RECOGNITION HABITAT MODELS FOR THE RUFFED GROUSE, GRAY SQUIRREL, AND FOX SQUIRREL IN MISSOURI

A Thesis

Presented to

the Faculty of the Graduate School

University of Missouri-Columbia

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

---

by

MURRAY K. LAUBHAN

August 1987

The undersigned, appointed by the Dean of the Graduate Faculty, have examined a thesis entitled

DEVELOPMENT AND EVALUATION OF PATTERN RECOGNITION HABITAT MODELS FOR THE RUFFED GROUSE, GRAY SQUIRREL, AND FOX SQUIRREL IN MISSOURI

presented by Murray K. Laubhan

a candidate for the degree of Master of Science

and hereby certify that in their opinion it is worthy of acceptance.

signatures redacted

ABSTRACT

Pattern recognition (PATREC) models are single-species models that use habitat characteristics to arrive at an estimation of population abundance. Currently, personnel of the Mark Twain National Forest in Missouri are using this type of model as a basis for making management decisions on 13 management emphasis species. Before the outputs of these models can be used with confidence, however, relational functions that support the models must be explored and quantified by research. The primary purpose of my study was to develop and evaluate PATREC models for the ruffed grouse (*Bonasa umbellus*), gray squirrel (*Sciurus carolinensis*), and fox squirel (*Sciurus niger*) in Missouri. I measured vegetative structure and population abundance of ruffed grouse and both squirrel species on 13 and 14 study areas, respectively, to identify habitat features asociated with high and low densities of each species. Six habitat parameters were determined to be related to ruffed grouse density. Areas with high spring densities (> 13.0/405 ha) had significantly ($P < 0.01$) greater amounts of disturbed forest habitats and lower amounts of upland sawtimber than areas with low densities. Structural characteristics influencing the quality of disturbed cover included basal area, woody stem density, and canopy closure. Woody stem density was also an important habitat condition of the upland sawtimber cover type. The PATREC model developed with these

6 parameters correctly classified 100% of the study areas into either high or low density classes. Based upon model outputs, areas with low densities were deficient in either the percent occurrence or structural characteristics of the disturbed cover type indicating that management for ruffed grouse in Missouri should be directed toward providing more of this habitat type. Population estimates of squirrels concurred with 2 years of poor acorn mast production. During and immediately following poor mast years, it appears that both fox squirrels and gray squirrels use areas where timber is interspersed with crops and old fields. These areas may provide a source of supplemental food. In contrast, both species were negatively correlated with the occurrence of the hardwood sawtimber cover type. However, the horizontal density of vegetation from 0.0 to 1.5 m in height and overstory canopy closure of shagbark hickory (*Carya ovata*) within the hardwood sawtimber cover type exhibited positive relationships with the abundance of both species. During periods of poor mast, both species also appear to be positively influenced by the combined effects of increased dominance of hickory and soft mast producing tree and shrub species. Management programs that facilitate the maintenance of openings and crop fields, an abundance of ground cover, and a variety of dominant and subdominant trees should not only improve habitats for year-round use by squirrels but also during periods of low mast availability.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

During the 1970's, legislation such as the Endangered Species Act of 1973, Forest and Rangeland Renewable Resources and Planning Act of 1976, and the Federal Land Policy and Management Act of 1976 forced resource management agencies to consider wildlife and habitat values in their management decisions. Realizing that traditional methods of inventory and analysis were inadequate for assessing values for wildlife habitat (Schamberger and Krohn 1982), state, federal, and private organizations initiated development of professionally acceptable and reasonably uniform methods of yielding these values (Farmer et al. 1982, Hamor 1970, Daniel and Lamaire 1974).

The pattern recognition (PATREC) model, a single-species model, is one type of habitat-based model that was developed. Currently, personnel of the Mark Twain National Forest, which comprises approximately 849,860 ha of timber within Missouri, are using PATREC models as a basis for making management decisions for 13 wildlife species considered to be indicators of forest habitat conditions. Before the outputs of these models can be used with confidence, however, the relational functions that support the models must be thoroughly explored and quantified by research. For most species-models such research data are lacking and the resultant models are based on partial data sets, reasonable assumptions by species authorities, and natural history literature. Attempts of several investigators to determine whether models accurately estimate the potential of an area for a given species have been largely inconclusive (Seitz et al. 1982, Marcot et al. 1983).

The primary purpose of my study was to develop and evaluate PATREC modelse for the ruffed grouse, gray squirrel, and fox squirrel in Missouri. The specific objectives were to (1) determine densities of ruffed grouse, gray squirrels, and fox squirrels on areas that support high and low densities of each species, (2) determine the specific condition of habitat parameters of potential importance on those areas where densities were determined, and (3) develop and evaluate a PATREC model for ruffed grouse, gray squirrel, and fox squirrel based upon the comparison of the model's predicted density versus the measured density.

ACKNOWLEDGEMENTS

I would like to express appreciation to my advisor, Dr. Ernie P. Wiggers, and Mr. David Hamilton, wildlife research biologist, Missouri Conservation Department, for their continued support, guidance, and advice throughout the study. Their interest in modeling species-habitat relationships gave the project increased meaning and made it enjoyable.

I would also like to thank Dr. Wiggers, Dr. Fritzell, and Dr. Krause for reviewing this manuscript.

I am also grateful to my summer field assistants, Mark Reed, Gary Zenitsky, and Eric Brunson, for their work in collecting the vegetation data needed to construct and drive the models. I would also like to thank Bill Dijak of the USFS North Central Experiment Station for collecting the vegetation data on the Carman Springs Refuge. I am indebted to over 40 University of Missouri, U. S. Forest Service, and Missouri Conservation Department personnel who diligently assisted in the grouse and squirrel surveys on 17 study areas during the two year project. Without them a project of this magnitude would not be possible. Special thanks are due to the managers of the state wildlife areas, personnel of the Forestry Division in the Conservation Department, and the Forest Service wildlife biologists who provided the necessary maps and timber inventory data needed to establish sampling points for vegetation collection and delineation of study area boundaries. Finally, I would like to thank my parents and brother for their support throughout my college education.

Funding was provided principally by the Missouri Department of Conservation-Federal Aid W-13-R, with additional support provided by the Missouri Cooperative Wildlife Research Unit (United States Fish and Wildlife Service, Missouri Department of Conservation, Wildlife Management Institute, and the University of Missouri cooperating), the Missouri Agricultural Experiment Station, and the E. Sidney Stephens Fellowship.

REVIEW OF THE LITERATURE

Pattern Recognition Models

The pattern recognition approach is based on pattern recognition theory (the ability to assign a classification to a perceived combination of events or characteristics) and medical diagnostic tools used to reduce uncertainty and risk concerning the outcome of patient surgery (Williams et al. 1977). Prior to the mid-1960's the main body of pattern recognition research was in the interdisciplinary area known as 'systems communications', which includes psychology, physiology, mathematics, and engineering (Uhr 1964). It was not until the early 1970's that wildlife researchers began adapting the concepts of pattern recognition for use in evaluating wildlife habitat.

Pattern recognition can be subdivided into three steps: (1) perception, (2) interpretation, and (3) decision-making (Williams et al. 1977). Mathematically, the model incorporates Bayesian statistical inference to produce a measure of habitat suitability. The Bayesian technique involves estimation of an initial probability distribution that some condition or set of conditions exists, collection of sample data, and the use of the sample results to revise the initial probability estimates into a final, decision-making distribution. Specifically, pattern recognition (PATREC) models consist of high and low density standards, high and low prior probabilities, and high and low conditional probabilities. The density standards represent the upper and lower bounds of model predictions. The model will produce estimates only within these standards. Therefore, they must be appropriate for the range, for instance a state, in which the model will be applied.

The 2 prior probabilities are determined based upon previous knowledge concerning the relative abundance of the species within the range of the model. The likelihood that a randomly selected area, within the range of the model, will support a high density population is the prior probabilitiy for a high density. Conversely, the probability that the same area supports a low density population represents the prior probability for a low population density. These 2 probability values must sum to 1.0.

The conditional probabilities of PATREC models are linked to the habitat parameters associated with high and low population densities of a wildlife species. For each parameter, a set of categories (ranges of parameter values) is established that best separates high from low population densities. The frequency with which high and low density areas occur within each category of a parameter constitutes the high and low conditional probabilities of that parameter, respectively. For example, if 40 to 60% canopy closure in pole stands occurred in 7 of 10 high density areas the conditional probability is 0.70 (70%) that the population density is high (regardless of other environmental factors) where pole stand canopy coverage is between 40 and 60%.

Conversely, if the pole stand canopy coverage is between 40 and 60% in 2 of 10 areas where population densities are low the conditional probability is 0.20 (20%) that the population density is low where pole stand canopy coverage is between 40 and 60%. Within each parameter, the probabilities must sum to 1.0 for both the high and low values. Detailed instructions pertaining to the use of PATREC models are presented in Appendix A.

PATREC models can be used as a tool to increase the probability of accurate decisions concerning a course of action that may affect the welfare of wildlife. They do not predict changes in ecological processes nor do they necessarily address cause and effect.

A distinct advantage of PATREC models over other habitat models is that actual estimates of animal density, or more correctly, potential carrying capacity, can be estimated. The step from probabilities to animal numbers requires additional assumptions and, therefore, yields more variable results. However, it is a step often required of land managers. In addition, the conditional probabilities can be used to identify courses for management action and prioritize these actions in order of importance. This is extremely important to state and federal agencies which must make the most efficient and effective use of available funds. Further, because it is possible to estimate potential carrying capacities under both present habitat conditions and future conditions, if they are predictable, the resultant

PATREC outputs can be used to evaluate alternative management plans for a given species and develop sound multiple-use programs.

A major disadvantage of PATREC models results from the use of discrete variables. Therefore, population probabilities may indicate no change as the level of a habitat characteristic increases or decreases until that change is great enough to cross an imaginary boundary into another probability class (Sweeney 1984). Another drawback of PATREC models results from the variables incorporated within the model structure. The variables normally included are those which can be (1) readily measured (2) altered by management decisions, and (3) predicted under future conditions. The omission of factors such as predation, hunting and competition which, in some cases, are important proximate causes in determining population levels detracts from the sensitivity and realism of the model. PATREC models are, therefore, a simplified version of the natural forces governing a species success in a given area. Nevertheless, a validated PATREC model allows resource managers and conservationists to discuss current and proposed management plans in terms of habitat conditions they are capable of manipulating. As a result, when factors not under human control are favorable, the species in question will respond favorably.

Ruffed Grouse

Geographic Range

The ruffed grouse is the most widely distributed non-migratory game bird on the continent, occurring naturally through 34 degrees of latitude and from the Atlantic to the Pacific Oceans (Bump et al. 1947). The species has also been successfully introduced outside its original range into Newfoundland and northeastern Nevada (Johnsgard 1973). Aldrich (1963) described 13 subspecies of ruffed grouse whose ranges encompassed 38 states and 13 Canadian provinces. The subspecies native to Missouri is the midwestern ruffed grouse (*B. umbellus medianus*), but the Appalachian ruffed grouse (*B. umbellus monticola*) has been reintroduced by the Missouri Department of Conservation (Hunyadi 1984).

History in Missouri

Missouri represents the southwestern border of the grouse range and grouse originally inhabited most of the forested area of the state (Korschgen 1966). Population size before the time of settlement is unknown but has been estimated in the hundreds of thousands (Bennitt and Nagel 1937). Following settlement, numbers declined rapidly to the point of near extirpation in the early 1900's, probably in response to habitat destruction caused by repeated burning and grazing (Lewis et al. 1968). According to Bennitt and Nagel (1937) ruffed grouse probably totaled fewer than 100 birds by the early 1930's and their distribution within the state was reduced to nine counties.

Efforts were made to reestablish ruffed grouse in some of its former range in Missouri from 1940-1943 through the release of grouse on 3 refuges in the southern Ozark Region (Lewis 1971). These birds persisted for a short period of time and then disappeared. In 1959, the Missouri Conservation Department initiated another program with the first releases being made on the Ashland Wildlife Research Area and the Daniel Boone Memorial Forest in the central portion of the state (Lewis et al. 1968). From 1959 to 1986 a total of 4,444 wild-trapped grouse from Ohio, Indiana, Minnesota, Kentucky, Michigan, and Wisconsin were released on 69 areas throughout Missouri (Missouri Department of Conservation 1986). Based upon stable numbers of drumming males and evidence of reproduction, these restocking efforts have been successful in establishing populations throughout portions of Missouri (Hunyadi 1984).

Habitat Requirements

General

Ruffed grouse are associated primarily with deciduous hardwood forests in various stages of succession (Johnsgard 1973, Edminster 1954). Ruffed grouse can be characterized as a transitional habitat species that is closely associated with disturbed forests. (Gullion 1977, Bump et al. 1947). Cover requirements of grouse change seasonally with the birds activities and prevailing environmental conditions. Edminster (1954) stated that young hardwood stands, slashings, overgrown woodlands, and open lands were the cover types most important to grouse on an annual basis. Bump (1938) reported that conifers and edge types were also seasonally important to grouse in New York. The importance of adequate interspersion and juxtaposition of these cover types to ruffed grouse has also been documented by Bump et al. (1947) in New York, and Kubisiak (1985) and Dorney (1959) in Wisconsin. King (1937) stated that the types need not be extensive but their interspersion is important. He further concluded that, in most cases, the cover pattern is more important than the plant species involved.

Drumming Habitat

The typical drumming stage used by male ruffed grouse is a fallen log but any object which permits the bird to stand above surrounding terrain may be used (Gullion 1967). The height of the drumming stage is normally a minimum of 15 cm above the ground and the bird assumes a position from which it can survey most of the ground for a distance of 14 to 18 m (Gullion et al. 1962). According to Boag and Sumanik (1969) the physical characteristics of the drumming platform are generally not considered important if the platform is elevated and level. Gullion (1984a) stated that the lack of suitable drumming surfaces is seldom a limiting factor of grouse abundance where other habitat qualities are present.

Throughout the range of the ruffed grouse, physical attributes of the forest are the most important criterion determining suitable drumming habitat. In most cases, the species composition of the vegetation surrounding the drumming site does not appear to be as important as its structure (Rusch and Keith 1971, Gullion 1984b) although Kubisiak (1985) and Palmer (1963) reported that drumming sites in Wisconsin and Michigan were concentrated around certain shrub species.

Kubisiak (1985) regarded vertical cover as a primary factor in the selection of drumming sites by grouse since this component determines the degree to which grouse are protected and influences their ability to efficiently detect ground predators (Boag and Sumanik 1969). In Minnesota, aspen regeneration cuts with woody stem densities ranging from 12,000-42,000 stems/ha were considered suitable drumming habitat (Gullion 1984a) but 14,000-20,000 stems/ha were classified as optimum (Gullion 1977). The selection of drumming sites with areas of high stem densities has also been reported in Ohio (Stoll et al. 1979), Michigan (Palmer 1963), Indiana (Backs 1984), southern Alberta (Boag 1976), and Missouri (Hunyadi 1984, Thompson et al. in press). In addition to high stem densities, suitable drumming habitat also contains overhead shrub cover and an open ground layer with little slash or horizontal debris (Hale et al. 1982, Gullion et al. 1962, Titus 1976, Kurzejeski 1979, Stauffer and Peterson 1985).

Several investigators have indicated that topographical features may be important in the selection of drumming sites within habitats containing suitable structure. In Missouri and Ohio, grouse occupied logs located at higher elevations (Titus 1976, Lewis et al. 1968, Stoll et al. 1979). Hungerford (1951) concluded that preferred drumming sites in Idaho were located along ridges due to the warmer microclimate. However, in Georgia, Hale et al. (1982) stated that drumming sites occurred randomly over the entire range of slopes, aspects, and elevations although there appeared to be a maximum slope above which grouse found conditions unsuitable.

Nesting Habitat

Qualitative information regarding nesting habitat of ruffed grouse is limited largely because of the difficulty associated with the location of nests. Grouse do not conceal their nests but rely mainly on cryptic coloration and the habit of 'sitting tight' for nest protection (Bump et al. 1947). Preferred nest sites tend to be in stands of second growth hardwoods with an open understory and little coniferous vegetation (Bump 1938) and are usually near some type of opening which will provide summer foods for broods (Bump et al. 1947). Similar findings have been reported for nests located in Iowa (Polderboer 1942), Missouri (Freiling 1985), and Minnesota (Gullion 1977, Maxson 1978).

The nest itself is normally placed near some object which will provide some protection from the rear while allowing an unobstructed view to the front (Edminster 1954). The most commonly used object is the base of a tree or stump, but nests have also been located under logs, tangles, or piles of brush (Bump et al. 1947, Freiling 1985, Talmadge 1957).

Brood Habitat

Brood cover has been suggested as the most important component of grouse habitat because it satisfies many of the annual requirements of adults as well as provides the elements necessary for brood survival (Berner and Gysel 1969). Hungerford (1957) reported that good brood habitat contains suitable roosting cover, adequate nesting and loafing cover, and a good source of summer food. Ideal brood habitat was described by King (1937) as having an abundance and variety of insects and succulent vegetation. Kimmel and Samuel (1984) found that grouse chicks rely on insects as the main component of their diet and gradually shift to a predominantly plant diet at about 8 weeks. They concluded the vegetative structure of the forest, as it affects the availability of invertebrate food, can significantly influence chick survival.

Due to the need for luxuriant vegetation where insects are also available, Bump et al. (1947) concluded that broods are normally found where crown cover is sparse. In Iowa, Porath and Vohs (1972) reported that most brood sightings occurred in hardwood stands 10 to 50 years of age which contained frequent openings with brush borders. They concluded that these stands provided the necessary interspersion of food and shelter for young chicks. Brood use of openings with moderately dense ground cover such as woods roads, forest edges, spot-lumbered areas, and regeneration cuts have also been reported in New York (Bump 1938), Idaho (Stauffer and Peterson 1985), Iowa (Polderboer 1942), Missouri (Hunyadi 1978, Kurzejeski 1979), Virginia (Stewart 1956), and Wisconsin (Kubisiak 1985).

Grouse broods tend to shift from lowland habitats early in the brood period to upland sites in late summer (Berner and Gysel 1969, Stewart 1956). This may be in response to the ripening fruits of various upland shrubs since, according to Bump et al. (1947), food is the most important factor governing brood movements. In contrast, Hungerford (1951) found that late summer broods used small ravines because they probably provided a cool, more favorable microenvironment. Polderboer (1942) also observed broods using brushy ravines during August.

Winter Habitat

With the onset of cold weather, ruffed grouse shift to cover-types which afford the best protection against environmental conditions. Johnsgard (1975) characterized suitable winter cover as providing adequate roosting sites in close proximity to a reliable food source. In Michigan, cover suitable for drumming males is also considered adequate fall to spring cover (Berner and Gysel 1969). The use of areas with high stem densities from late fall through winter was also reported in Tennessee (Gudlin and Dimmick 1984), and Idaho (Stauffer and Peterson 1985).

In New York, Bump (1938) concluded that the presence of conifers is the most important characteristic of ruffed grouse winter habitat. Birds in Indiana preferred pine plantations (*Pinus spp.*) as well as old-field associations from late fall through winter (Backs 1984). In some areas there appears to be selective use of coniferous vegetation under certain conditions. King (1937) reported that snow roosts provide adequate protection from climatic extremes but, in the absence of adequate snow depth, grouse roost among cedars (*Juniperus virginiana*), spruce (*Picea* spp.), or balsam (*Abies balsamea*). In Minnesota, Pietz and Tester (1982) observed an increase in grouse use of upland conifers during periods of snow cover. In contrast, Gullion and Marshall (1968) stated that conifers are not essential for wintering cover and may even be a detrimental component of the habitat.

Food

Ruffed grouse are primarily browsers, subsisting on buds, twigs, leaves, seeds, and fruits of various trees, shrubs, and herbs (Gullion 1984a). Foods consumed vary seasonally and from area to area depending upon the plant species locally available (Gullion 1966). The greatest regional disparity in foods consumed appears to occur in the fall and winter. During the spring and summer seasons, however, the same general foods (i.e. berries, fruits, leaves) are consumed although the individual species differ.

Results of several studies conducted in the northern and eastern portions of the grouse range show that the principal fall and winter foods of adult grouse include the buds and catkins of aspen (Populus spp.), birch (Betula spp.), beech, willow (Salix spp.), and poplar (Populus spp.) (Doerr et al. 1974, McGowan 1973, Brown 1946, Svoboda and Gullion 1974). During the spring and summer months, grouse in the same region consume leafy plant materials, insects, fruits, berries, and seeds as they become available and the buds of aspen, birch, and willow (Johnsgard 1975, Gullion 1984c, Brown 1946, Bump et al. 1947, Johnson 1928, King 1969).

In the southern areas of grouse range, however, many of the above staple food items are only sparsely distributed and they have been replaced in the diet by more locally abundant foods. In southwest Virginia, soft and hard fruits comprised the bulk of foods consumed during the fall and winter while leaves of herbaceous plants were the principal foods in spring and summer (Norman and Kirkpatrick 1984). Fruits were also important in the fall and winter diet of grouse in Tennessee and together with green leafy plants accounted for the majority of the foods taken during this period (Stafford and Dimmick 1979). In central Missouri, Korschgen (1966) reported that the buds and catkins of hop hornbeam (Ostrya virginiana), fruits, seeds, acorns, rose hips, insects, and green plant materials represented the major food items taken throughout the year as they became available.

Gray Squirrel and Fox Squirrel

Geographic Range

The geographic ranges of the fox squirrel and eastern gray squirrel are mainly sympatric (Hall 1981). In North America, the gray squirrel is found throughout the eastern one-half of the United States and the southern portions of Saskatchewan, Manitoba, Ontario, and Quebec. The North American distribution of the fox squirrel extends slightly farther west and not as far north as that of the gray squirrel. It includes only the southernmost portion of Ontario to the southern one-half of Pennsylvania (Schwartz and Schwartz 1981). Both species are found throughout most of Missouri but gray squirrels predominate in portions of the state where contiguous large tracts of timber occur, while the fox squirrel is more prevalent in prairie and agricultural land (Schwartz and Schwartz 1981).

Armitage and Harris (1982), using home ranges and activity patterns, concluded that in sympatric populations neither species excluded the other from any part of the habitat nor is either territorial. They further noted that while home ranges overlap, conspecifics tend to be grouped.

Home Range and Social Structure

Both fox and gray squirrels are considered sedentary species (Brown and Yeager 1945) but, at times, individuals are subject to occassional mass movements (Allen 1942). These movements seem to be in response to a failure of the mast crop. Under normal conditions, the home range size of both species depends upon the suitability of the habitat and the age and sex of the individual. Among fox squirrels the mean home ranges of males (7.6 ha) average roughly twice those of females (3.6 ha) and yearlings have significantly larger home ranges than adults (Adams 1976). In addition to age and sex, home range sizes of fox squirrels also appear to be positively related to the size of the woodlot they occupy. Flyger (1960) found that the average home ranges of adult male gray squirrels (0.8 ha) was larger than those of adult females (0.5 ha) and the average adult home range (0.6 ha) was larger than that of immatures (0.4 ha). Doebel and McGinnes (1974) found the same relationships, but stated that only the size between sexes was significantly different. In British Columbia, male gray squirrels moved over an area of at least 20.3 ha whereas the maximum movement of adult females was only 6.0 ha (Robinson and Cowan 1954).

Both species are basically solitary animals but not strictly territorial with individuals occupying overlapping home ranges. Mutual avoidance behavior tends to distribute squirrels spatially at feeding stations and during mating chases. In these situations, a social ranking, termed linear right heirarchy, manifests itself (Flyger 1955). This heirarchy is extremely stable among both species with physical battles rarely occurring (Pack et al. 1967, Benson 1980). The ranking of an individual is dependent upon its sex and age with males normally dominating females and immatures subordinate to adults.

Habitat

Although the geographic ranges of the fox and gray squirrel overlap to a large extent they often occupy different habitat types. Many investigators attribute this segregation to the characteristics of the understory vegetation (Nixon et al. 1978, Taylor 1974, Allen 1943, Brown and Yeager 1945). Their studies have shown gray squirrels prefer habitats with a high density of understory trees whereas fox squirrels prefer more open understory conditions. Brown and Batzli (1984) found no relationship between density of understory vegetation and habitat preference of either species. Instead, they suggested that separation may be linked to the extent of forestation with gray squirrels appearing to favor large forested tracts of land while the fox squirrel prefers fragmented timber interspersed with agricultural lands.

Allen (1943) described optimal fox squirrel habitat in Michigan as consisting of patches of oak-hickory (Quercus spp.-Carya spp.) woodlands interspersed with croplands and Baumgartner (1943) stated that fox squirrels in Ohio preferred small farm woodlots but also occurred along forest edges and open ridgetops in heavily forested regions. In Missouri, fox squirrels inhabit the higher ridges in forested areas while in the prairie regions they occupy farm woodlots, osage-orange (Maclura pomifera) hedge fences, and timbered fencerows and draws (Schwartz and Schwartz 1981). Welldrained bottomlands and solid stands of oak-hickory are considered temporary habitats for fox squirrels because they do not contain a sufficient annual food base (Goodrum 1937, Baumgartner 1943).

Optimal gray squirrel habitat in Illinois is a closed canopy forest coupled with an understory that is well-developed (Nixon et al. 1978). Gray squirrels in Missouri occupy dense hardwood forests and prefer those with a brushy understory located along river bottoms or river bluffs (Schwartz and Schwartz 1981). The quality of both fox squirrel and gray squirrel habitats are potentially affected by silvicultural prescriptions. This is an important concern since a high percentage of the oak-hickory forests in the central states are in need of regeneration (Nixon et al. 1968). Even-aged management consisting of clearcutting followed by intermediate thinnings and harvest clear-cutting could prove detrimental to some tree species important to squirrels. Nixon et al. (1968) recommended that 0.7 to 1.4 m^2/ha of fruiting hickories (<u>Carya</u> spp.) and beech (<u>Fagus</u> spp.) plus an additional 0.23 to 0.46 m^2/ha of elm (<u>Ulmus</u> spp.), maple (<u>Acer</u> spp.), and buckeye (<u>Aesculus</u> spp.) be retained in clearcuts to provide a food source for squirrels. The size and shape of clearcuts are also important in determining the degree to which squirrel populations are adversely affected. Nixon et al. (1980a) reported gray squirrels were less affected when cuts were small, narrow, and 40 to 60% of the area was in a seed-producing stage.

They recommended that the size of the cut be determined by the home range size of the females since they are the most sedentary portion of the population.

Selection or diameter-limit cutting tends to reduce the availability of food and shelter for squirrels but Nixon et al. (1980a) concluded that a 55% basal area removal of trees greater than 77.5 cm resulted in a temporary reduction of females but did not critically affect the quality of squirrel habitat. Therefore, 55% basal area removal may be near the maximum for retaining suitable squirrel habitat.

Food

The diets of gray and fox squirrels are essentially the same (Schwartz and Schwartz 1981) as are their daily energy requirements (Husband 1976, Ludwick et al. 1969). In order to meet these energy demands squirrels exploit a diverse food base, have a high efficiency of food utilization, and consume foods with high energy digestabilities (Montgomery et al. 1975). Their diets are normally composed of a few staple foods supplemented with an assortment of items which are seasonally available. This is substantiated by Nixon et al. (1968) and Brown and Yeager (1945) who concluded that fox squirrel stomachs usually contain only 1 or 2 food items.

The most important food source in the diet of both species is mast. The availability and quality of this food item has been suggested as the major cause in fluctuations of population abundance (Christisen and Korschgen 1955, Nixon and McClain 1969, Baker 1944). Although nuts and acorns are consumed throughout the year they are relied upon most heavily during the fall and winter (Nixon et al. 1968). During these seasons mast normally constitutes over 90% of the available energy in squirrel habitats (Montgomery et al. 1975). Hickory nuts, especially those of shagbark hickory (C. ovata), appear to be the most preferred form of mast, being consumed disproportionately to their occurrence (Nixon et al. 1968, Korschgen 1981). Lewis (1982) concluded this preferance was due to their high energy density which permits squirrels to forage less frequently thereby reducing thermoregulatory costs during inclement weather as well as minimize predation risk.

Mast production varies by species and age of tree as well as soil and weather conditions (Smith 1962). However, weather is unlikely to have a major impact in squirrel habitats where there are an assortment of mast-bearing trees since their flowering times are variable. Therefore, a variety of mast producing species should be present to minimize the chances of a complete crop failure. Nixon et al. (1975) concluded that at least 147.3 kg/ha of sound seed was needed to sustain reasonably high squirrel densities and stated that a minimum basal area of 8.0 to 9.2 m^2/ha of mast trees, of which 2.5 to 3.4 m^2/ha were hickories, would meet this requirement.

According to Short (1976), mast supplies squirrels with adequate energy but does not satisfy their metabolic requirements of some nutrients. Supplemental fall and winter foods, which may help meet these requirements, include the buds, seeds, and persistent fruits of various trees and shrubs (Allen 1943, Korschgen 1981). Corn is also considered an important winter food source, especially for fox squirrels, when mast crops are below average. Under normal conditions, however, it does not appear to be an adequate supplemental food (Havera and Smith 1979, Havera and Nixon 1980).

During spring and summer the diets of both species shift depending upon the extent to which the mast of the preceding year has been consumed. In Missouri, Korschgen (1981) identified 67 food items eaten by both species between March and May. Seventeen of these items accounted for 88% of the total food volume. Among the most important were black walnuts (Juglans nigra) and the buds and flowers of elm. Montgomery et al. (1975) also concluded that during spring the buds and flowers of such trees as oaks, hickories, and sugar maple (A. saccharum) were heavily used in addition to any remaining acorns and nuts. The most preferred foods during the summer months include fungi, forbs, grasses, green plants, green hickory nuts, and the fleshy fruits of various shrubs, vines, and trees (Allen 1943 Nixon et al. 1968). Insects also serve as a summer food source (Hamilton 1943 Nixon 1970) but are not considered a staple food item.

Water

Free water does not appear to be a habitat requirement of the fox squirrel (Allen 1982a). Succulent plants, berries, and fruits found in the uplands they inhabit adequately fulfill their moisture demands under normal conditions. During periods of drought, however, fox squirrels have been observed to gather at sources of surface water (Terrill 1941, Schwartz and Schwartz 1981).

Eastern gray squirrels can also satisfy water needs through consumption of succulent vegetation but pregnant and lactating females often use free water (Allen 1982b). In Illinois, Brown and Yeager (1945) found that gray squirrels were never far from water and, at least in summer, consumed water daily. Based on these reports, a source of free water may be a necessary component of gray squirrel habitat.

Reproduction

A suitable nest site is a critical reproductive requirement of squirrels. Both leaf nests and tree cavities are used by fox squirrels to rear young (Baumgartner 1943) although cavities are preferred (Allen 1942). In contrast, gray squirrels almost exclusively use tree cavities to rear their young (Allen 1982b).

In Illinois and Ohio, leaf nests were located in hickories, white oak (*Q. alba*), and scarlet oak (*Q. coccinea*) more frequently than they were available in the forest (Sanderson et al. 1980), whereas black oaks (*Q. velutina*) were selected in Michigan (Allen 1942). Sanderson et al.

(1980) also found leaf nests occurred more frequently in trees that contained grapevines (*Vitis spp.*) and suggested that 2 to 4/ha and 4 to 6/ha canopy-reaching grapevines would provide a sufficient number of nest anchors for gray and fox squirrels, respectively. Trees containing leaf nests had an average diameter breast height of 26.2 cm in Michigan (Allen 1942) and 35.8 cm in Ohio (Baumgartner 1939).

Suitable tree cavities have been located in numerous tree species across the range of squirrel habitats. Based on relative abundance, Nixon et al. (1980b) concluded that beech, sugar maple, sassafrass (*Sassafras albidum*), and elm contained the most tree cavities in Illinois while cavities in ash (*Fraxinus* spp.), elm, oaks, hickories, sassafras, basswood (*Tilia* spp.), beech, and sycamores (*Platanus occidentalis*) were utilized to the greatest extent in the eastern United States (Goodrum 1937, Nixon et al. 1968 in Allen 1982b). The average diameter breast height of den trees ranged from 38.1 cm in Texas (Baker 1944) to 53.8 cm in Ohio (Baumgartner 1938). Sanderson et al. (1975) concluded that one den/0.8 ha was necessary to provide winter shelter for gray squirrels and Brown and Yeager (1945) stated that 5 to 12 dens/ha were optimum.

STUDY AREAS

A total of 17 study areas were used throughout the course of the project (Fig 1). Of these, 13 were used in the grouse segment and 14 in the squirrel segment of the study (Table 1). Ten areas served as sites for both species. With the exception of Horton Burn, grouse have been reintroduced on each of the ruffed grouse study areas, but no releases occurred in the 3 years before the beginning of this project. All areas employed in the squirrel study were 102 ha in size while areas designated as grouse sites ranged in size from 154 ha to 530 ha. On those areas serving as study sites for both species, the squirrel area was located within the boundaries of the grouse area.

The study areas occurred in 6 physiographic regions of Missouri based upon the major soil types and topography (Krusekopf 1962). A general description of the areas by region follows.

1. River Hills Region - The Edward A. Anderson Wildlife Management Area (WMA), Ashland Wildlife Research Area (AWRA), and the Daniel Boone Memorial Forest lie in the band of river hills bordering the Mississippi and Missouri Rivers. The topography of these areas consists of deep hollows with narrow ridges and steep slopes. The major soils are of the Menfro type which are derived from loess and are characteristically brown in color and silty in texture. The inherent fertility of the soils is good, but the productivity may be low because of the generally low organic matter.

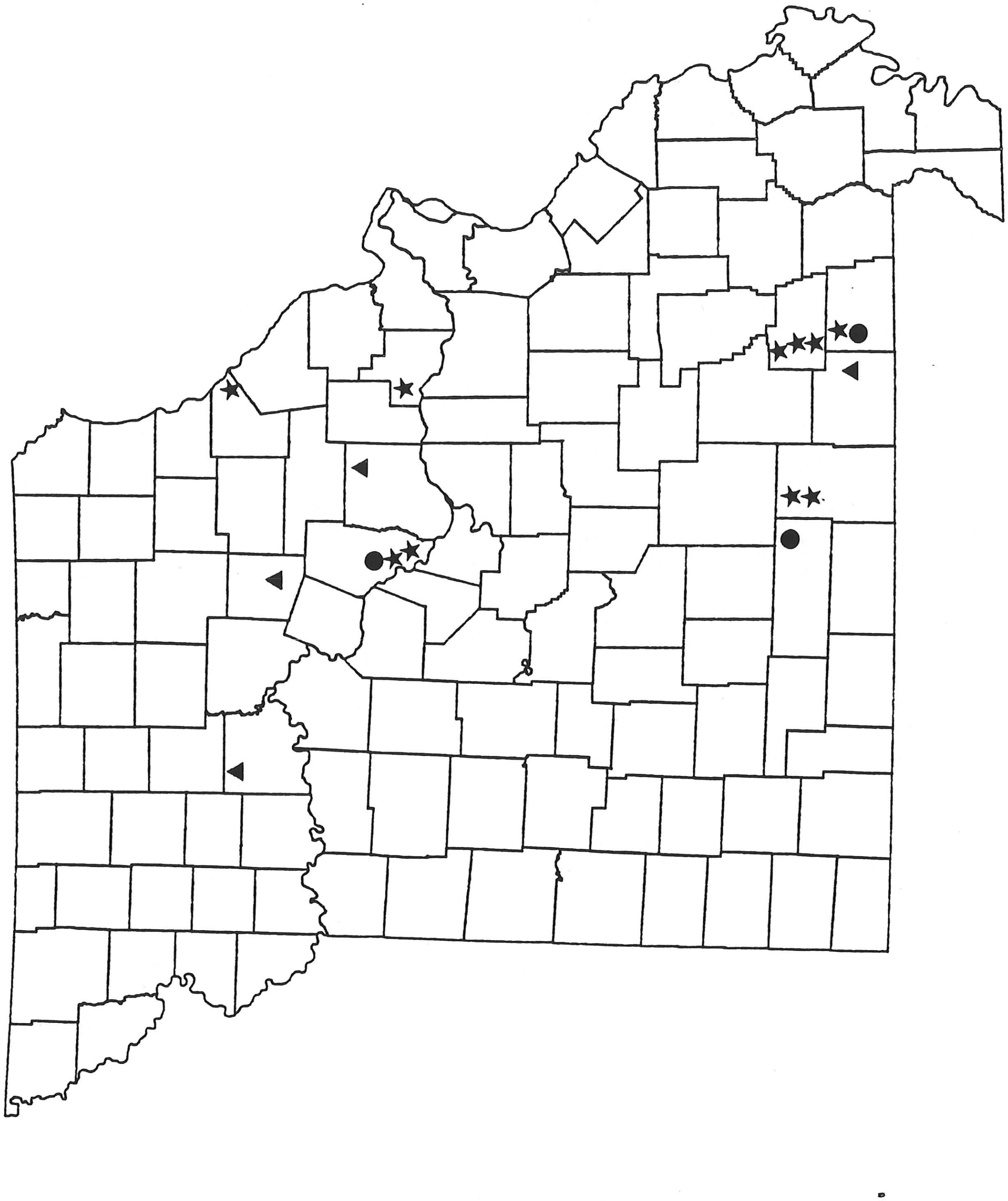


Table 1. Names, county and physiographic location, and ownership of areas used in the study to develop and refine PATREC models for the fox squirrel, gray squirrel, and ruffed grouse in Missouri.

Area	County	Area Type	Region	Ownership
Bunch Hollow WMA	Carroll	squirrel	Dark Prairie	MDC
Ashland Area Compartment 1	Boone	squirrel grouse	River Hills	UMC
Ashland Area Compartment 2	Boone	squirrel grouse	River Hills	UMC
Ashland Area Compartment 5	Boone	grouse	River Hills	UMC
Daniel Boone Forest	Warren	squirrel grouse	River Hills	MDC
Panther Spring Hollow	Oregon	squirrel	Ozark	USFS
Peck Ranch WMA	Carter	squirrel grouse	Ozark	MDC
Whetstone Creek WMA	Callaway	squirrel	Rolling Forest	MDC
Anderson WMA	Pike, Ralls	squirrel grouse	River Hills	MDC
Rudolph Bennitt WMA	Randolph	squirrel	Level Prairie	MDC
White Oak Hollow	Carter	squirrel grouse	Ozark	USFS
Compton Creek	Ripley	squirrel grouse	Ozark	USFS
Sleuter Hollow	Ripley	grouse	Ozark	USFS
Cowards Hollow	Carter	squirrel grouse	Ozark	USFS
Horton Burn	Douglas	grouse	Ozark	USFS
Carman Springs South	Howell	squirrel grouse	Ozark Plateau	USFS
Carman Springs North	Howell	squirrel grouse	Ozark Plateau	USFS

Elevations are similar ranging from 140.0 m above sea level on the Anderson WMA to 280.0 m above sea level on Boone Forest. Both Boone Forest and the Anderson WMA are comprised primarily of oak-hickory stands in various successional stages of development which are interspersed with small openings. The oak-hickory type also predominates on the AWRA but is intermixed with a variety of other types including different aged stands of eastern red cedar.

2. Rolling Forest Region - The Whetstone Creek WMA is located within this region which is characterized by gently rolling, narrow ridges with gentle to steep slopes. The ridges are intersected by permanent, intermittent, and ephemeral streams. Ponds and small lakes are common. The soils were formed from glacial-till and are of the Lindley type. The dominant surface soil is a gray-brown loam or silt loam and the subsoil a sandy clay loam. Elevations range from 198.1 to 243.8 m. The study area is comprised solely of oak-hickory timber of all size classes interspersed with cropfields located atop the major ridges.

3. Ozark Plateau Region - The land comprising the managed and unmanaged areas on the Carman Springs Wildlife Refuge is located within this region. Both areas lie in the drainages of Noblett and Spring Creeks. The topography features are moderately hilly plateaus with deep hollows and moderate to steep slopes. Elevations range from 274.3 to 365.8 m above sea level. The soils are of the Clarksville-Lebanon series. The surface soil is gray to light brown in

color and intermixed with chert stones in many areas. On relatively flat areas a fragipan has developed at a depth of 61.0 to 76.2 cm. Pine, oak-pine, oak-hickory, and bottomland hardwood cover types are found on both areas but the unmanaged area contains only timber in the sawtimber size class.

4. Ozark Region - Soils of the Clarksville type predominate over the highly dissected Ozark Region. The soils were derived from limestone and chert stones, 5.1 to 10.2 cm in diameter, are almost universally present and make up 20 to 60% of the soil mass. They were formed under forests and are low in organic matter and many minerals. The topography varies from narrow to relatively broad ridges with steep slopes near the larger streams. White Oak Hollow, Compton Creek, Peck Ranch, Panther Spring Hollow, Sleuter Hollow, Cowards Hollow, and the Horton Burn areas are located within this region. All areas are extensively forested with openings representing less than 6% of any area. Timber types are similar to those in the Ozark Plateau Region with oak-hickory sawtimber predominating on every area.

5. Level Prairie Region - The Rudolf Bennitt WMA is located on the western border of the Level Prairie Region which extends as a serrated plain almost to the Mississippi River. The Putnam-Mexico soils are characterized by a silt loam surface soil varying from 25.4 to 30.5 cm in depth and a subsoil which is classified as a claypan. Narrow bands of Lindley soil occur along the small streams. Elevations on

the area range from 228.6 to 259.1 m. Typical of the level prairies, the physiographic features are broad ridges with gentle to moderate slopes. The ridges on the area have been seeded with a mixture of forb and grass species while the remainder of the area is comprised of oak-hickory timber.

6. Dark Prairie Region - The Bunch Hollow WMA is located in this region which represents one of the largest and most productive soil areas in the state. The Marshall-Grundy soils are derived from loess and have a silt loam texture. The surface soils, which are highly productive, are dark brown to black and 25.4 to 38.1 cm in depth. The topography of the area consists of gently rolling hills with moderately wide bottomlands. Twenty-four percent of the area is under cultivation with the balance in deciduous forest, consisting of oak-hickory pole and sawtimber stands.

METHODS AND MATERIALS

Census Techniques

Ruffed Grouse

Ruffed grouse were censused by utilizing complete area counts of drumming males. This method should provide an accurate estimate of population size assuming that few non-drumming males are present and sex ratios are balanced (Hunyadi 1984). Thirteen areas were censused during the course of the project with 2 years of census information collected on ten of these areas while 3 areas were censused in only 1 year. Counts were conducted throughout April which corresponds to the peak drumming period in Missouri (Thompson pers. comm.). Walking routes were established that allowed all possible drumming activity to be heard throughout each area. These routes were normally located atop ridges or in hollows such that drumming was audible at the greatest possible distance and in as many directions as possible. Observers traversed these routes at a slow pace and paused for 4 minutes at approximately 183 m intervals. During each pause the observer would listen for drumming activity. When a grouse was heard an attempt was made to find the exact position of the bird and mark the location on a stand map of the area. If the bird was flushed or drumming ceased before the exact drumming location could be ascertained the approximate position of the bird was noted.

Counts began 30 minutes before sunrise and continued for at least 4 hours to overlap the peak period of drumming activity (Bump et al. 1947). Counts were not conducted in the presence of rain or winds above 15 km/h due to a reduction in both drumming activity and observer ability to detect grouse under these conditions (Gullion 1966). Because of variation in individual drumming behavior, counts were repeated a minimum of 3 times on each area.

Density estimates were calculated based upon the assumption of a 1:1 sex ratio of drumming males to females (Bezdek 1944). Therefore, the total number of adult grouse on an area was determined as twice the number of distinct drummers located throughout the entire count period.

For the purpose of model development, each area was also classified as containing either a high or low density population. The class into which each area was placed was determined by comparing the density of the area with the mean of the highest and lowest densities on the areas used in the study. All areas with densities below the mean were considered to have low populations while areas that had densities greater than the mean were classed as containing high populations.

Fox Squirrels and Gray Squirrels

Both fox squirrels and gray squirrels were censused using time-area counts as described by Goodrum (1940) and Bouffard and Hein (1978). Using a grid system, 20 time-area stations were established systematically throughout each study area. This spacing resulted in a density of 1 station/5.1 ha on each area. Each station was flagged in order that it could be readily relocated by the observer. One count consisted of visiting all 20 stations on an area.

Time-area counts were performed in March and June because of possible variation in squirrel activity. Census information was collected for 2 years on 10 areas while 4 areas were censused in only 1 year. Counts were conducted from 30 minutes before sunrise and continued for approximately 4 hours since both Hicks (1949) and Brown and Yeager (1945) found squirrels to be most active between the hours of 0600 and 1000 in the morning. Counts were not conducted during moderate to high winds (> 24 km/h) or rain since squirrels tend to be less active under these weather conditions (Baker 1944, Allen 1942). Each station was visited for 20 minutes. Upon arriving at a station the observer would become motionless, and after a 5 minute period to allow squirrel activity to resume, all squirrels seen were recorded by species. In addition, the distance at which each squirrel was first sighted was determined using a rangefinder and recorded. Due to the 4 hour time interval, 2 days (8 man-hours) were required to complete one count. To reduce inaccuracy in the results caused by variable squirrel activity, counts were repeated 3 times during both census periods. The highest single count during each period was considered the best estimate of squirrel abundance. Estimates are reported as numbers of squirrels observed since it was not possible to determine the proportion of each area accurately sampled. The estimates may be comparable, however, because each area was 102 ha in size.

Vegetation Analysis

General

Study areas for both species of squirrel and ruffed grouse were stratified to ensure that habitat characteristics of each cover type within an area were adequately sampled. Criteria used to delineate cover types included stand type and diameter of dominant trees. When available, animal habitat codes contained within the Wildlife Management Information System (WMIS) of the Mark Twain National Forest were also used to further refine the classification of cover types. A total of 10 unique cover types were identified within the grouse study areas (Table 2) and 7 were recognized within the smaller squirrel areas (Table 3).

The number of sample plots located in a cover type was in direct proportion to the percentage of the area comprised of that type. A minimum of 3 samples were collected in each type regardless of its percentage occurrence unless it represented less than 5. In those cases, only 1 sample was taken.

The location of plots was determined using a random numbers table to select individual stands within each type. Placement of plots within stands was determined by selecting 2 additional random numbers to represent (1) the distance traveled into the stand and (2) the distance traversed

Table 2. Cover type description of ruffed grouse study areas.

Cover Type	Description
Upland Sawtimber	timber greater than 22.9 cm dbh[A] with Quercus spp. and Carya spp. comprising greater than 50% of the dominant vegetation
Upland Poletimber	timber between 10.2 and 22.9 cm dbh with Quercus spp. and Carya spp. comprising greater than 50% of the dominant vegetation
Bottomland Hardwood Sawtimber	timber greater than 22.9 cm dbh with Betula spp., Acer spp., Juglans spp., Fraxinus spp., and Populus spp. comprising the dominant vegetation
Bottomland Hardwood Poletimber	timber between 10.2 and 22.9 cm dbh with Betula spp., Acer spp., Juglans spp., Fraxinus spp., and Populus spp. comprising the dominant vegetation
Pine Sawtimber	timber greater than 22.9 cm dbh with Pinus spp. comprising greater than 50% of the dominant vegetation
Pine Poletimber	timber between 10.2 and 22.9 cm dbh with Pinus spp. comprising greater than 50% of the dominant vegetation
Open	grassland savannas, food plots, crop fields, glades
Regeneration	clearcuts less than 5 years of age
Disturbed	clearcuts between 5 and 15 years of age, cedar stands, and WMIS[B] animal habitat codes 2, 13, and 16
Sapling	clearcuts over 15 years of age with the dominant vegetation less than 10.2 cm dbh

[A] diameter at breast height

[B] Wildlife Management Information System, USFS Mark Twain National Forest (animal habitat codes 2, 13, and 16 include brushy borders around pones, shrub-fruiting tree openings, and shrub-fruiting tree savannas).

Table 3. Cover type description of fox squirrel and gray squirrel study areas.

Cover Type	Description
Hardwood Sawtimber	timber greater than 22.9 cm dbh with hardwood timber comprising greater than 50% of the dominant vegetation
Hardwood Poletimber	timber between 10.2 and 22.9 cm dbh with hardwood timber comprising greater than 50% of the dominant vegetation
Pine Sawtimber	timber greater than 22.9 cm dbh with *Pinus* spp. comprising greater than 50% of the dominant vegetation
Regeneration	all clearcuts with dominant vegetation less than 10.2 cm dbh
Open	old fields, fields not in agricultural production
Crop Fields	agricultural cropland
Cedar	timber with *Juniperus* spp. as the dominant vegetation

perpendicular to the line of entry. The methods and equipment utilized to measure habitat conditions in the field were those recommended by Chambers and Brown (1983), Knight (1978), and Allen (1982a and b). At each sample point, data were collected within a 0.02-ha circular plot and along a line-transect 30 m in length. Scientific and common names of plants follow that of Steyermark (1963).

Ruffed Grouse

Data collected within the circular plot included aspect, slope, basal area, total canopy closure, maximum and minimum canopy height of dominant and codominant trees, number of deciduous and coniferous stems with a diameter less than 2.54 cm dbh and greater than 1 m in height, 6 measures of horizontal density, and the diameter of all woody vegetation greater than 2.54 cm dbh by species (Table 4).

Shrub crown closure and ground cover were sampled using the line-intercept method (Table 4). A 30 m line-transect was placed across slope with the midpoint at the center of the circular plot. Shrub crown closure was measured by recording the distance of canopy intercepts along the transect. Dominant ground cover was recorded at each 0.5 m interval along the transect.

Fox Squirrel and Gray Squirrel

The same field measurements collected in grouse habitats were also recorded in squirrel habitats. In addition, the number of canopy reaching grapevines in the circular plot and crown closure of canopy and subcanopy trees along the 30 m line-transect were also measured (Table 5).

To compare the contribution of a tree species to the composition of each cover type, an importance value was calculated. Importance value (IV) is defined as the sum of the relative values for dominance (basal area), frequency, and density of individual tree species and is derived as follow:

$$\text{dominance} = \frac{\text{dominance (basal area) of a species}}{\text{dominance of all species}} \times 100$$

$$\text{frequency} = \frac{\text{plots in which a species occurs}}{\text{total number of plots}} \times 100$$

$$\text{density} = \frac{\text{number of individuals of a species}}{\text{total number of individuals}} \times 100$$

IV = relative dominance + relative frequency + relative density.

The maximum IV for a species is 300, which would indicate a monotypic cover type.

Table 4. Definitions and methods of measuring habitat variables collected within ruffed grouse study areas during 1985 and 1986.

Habitat Characteristic	Variable	Definition	Method of Collection
Physiography	slope (%)	maximum slope within plot	clinometer
	aspect (degrees)	recorded from plot center	compass
Woody Vegetation	basal area (m^2/ha)	all woody vegetation greater than 2.54 cm dbh	10 BAF prism
	deciduous stems/ha coniferous stems/ha total woody stems/ha	less than 2.54 cm in diameter and greater than 1 m in height	4 belt transects: 1 m height, 2 m width and 8 m length
	horizontal structure (%)	density of vegetaion at 0.25 m intervals from ground level to 1.5 m in height	density board
Canopy Cover	shrub canopy closure (%)	woody vegetation between 1 and 5 m in height	30 m line transect
	total canopy closure	all vegetation greater than 1.5 m in height	spherical densiometer
Canopy Height	maximum canopy height (m) minimum canopy height (m)	maximum and minimum height of dominant trees within plot	haga altimeter clinometer
Ground Cover	forb (%) rock (%) bare ground (%) woody vine (%) woody sprout (%) litter (%) legume (%) grass (%) moss and lichen (%)	vegetation less than 1 m in height	30 m line transect

Table 5. Definitions and methods of measuring habitat variables collected within fox squirrel and gray squirrel study areas during 1985 and 1986.

Habitat Characteristic	Variable	Definition	Method of Collection
Physiography	slope (%)	maximum slope within plot	clinometer
	aspect (degrees)	recorded from plot center	compass
Woody Vegetation	basal area (m^2/ha)	all woody vegetation greater than 2.54 cm dbh	10 BAF prism
	deciduous stems/ha coniferous stems/ha total woody stems/ha	less than 2.54 cm in diameter and greater than 1 m in height	4 belt transects: 1 m height, 2 m width and 8 m length
	horizontal structure (%)	density of vegetaion at 0.25 m intervals from ground level to 1.5 m in height	density board
	grapevines (#/ha)	secure canopy-reaching grapevines	visual observation
Overhead Cover	overstory canopy closure by species (%)	dominant and codominant trees	30 m line transect
	understory canopy closure by species (%)	subdominant trees greater than 5 m in height	30 m line transect
	shrub canopy closure (%)	woody vegetation between 1 and 5 m in height	30 m line transect
	total canopy closure (%)	all vegetation greater than 1.5 m in height	spherical densiometer
Canopy Height	maximum canopy height (m) minimum canopy height (m)	maximum and minimum height of dominant trees within plot	haga altimeter, clinometer
Ground Cover	percent coverage of rock, bare ground, woody vine, woody sprout, litter, forb, grass, legume, moss	vegetation less than 1 m in height	30 m line transect

DATA ANALYSIS

Ruffed Grouse

Vegetation data collected on sample plots located within the grouse study areas was coded to permit analysis of 10 cover types which differed in their structure and vegetative communities. The mean values of the vegetative variables within each type were calculated for each area, used in all subsequent analyses, and in the construction of the ruffed grouse PATREC model.

The selection of variables (parameters) to be incorporated into the model was based on 2 separate, but related analyses of the vegetation data. First, the relationships between the occurrence (%) of individual cover types and grouse density were analyzed using correlation analysis and scatter diagrams. Those cover types correlated with grouse density were retained for further analysis. Second, the variables related to the structure and composition of the important cover types were analyzed in the same manner to detect differences that would alter the potential of a cover type to support ruffed grouse. I assumed that differences in the qualitative characteristics of these cover types would alter the capability of the entire study area to support grouse. The variables important in distinguishing these differences in cover type suitability (structure, composition) were also considered for inclusion into the model as parameters. It was also assumed that the habitat features of those cover types whose occurrence was neither beneficial nor detrimental types whose occurrence was neither beneficial nor detrimental would not significantly change the overall potential of an area to support grouse. Therefore, variables related to the structure of these cover types were not considered as potential PATREC parameters. The final selection of variables to be incorporated into the PATREC model was based upon scatter diagrams, principal components analysis, and discriminant function analysis.

For each model parameter, categories were selected that were biologically meaningful and delineated areas with different grouse densities. These categories were determined using scatter diagrams depicting changes in grouse density with changing values of the parameter. Because each study area represented an observation, the sample size consisted of 13 data points. As a result, general trends were evident but the exact relationship (linear, quadratic, sigmoid) between grouse density and some of the parameters could not be conclusively determined.

Conditional probabilities were assigned to each category in a parameter based on the frequency with which high density areas and low density areas were associated with each category. In some instances, only one type of area (high or low) was present within a category. When this occurred, the probability value for the missing type was set at either 0.05 or 0.10, depending on the importance of the parameter. This was necessary because the overall PATREC estimate is determined using multiplicative equations and, as a result, only positive numbers greater than 0.0 can be incorporated into the model.

Grouse densities predicted by the ruffed grouse PATREC model developed by the Missouri Department of Conservation (MDC) were compared with those observed on the study areas to verify this model. Evaluation was limited to 4 areas, however, due to the lack of adequate habitat data needed to drive the model.

Fox Squirrel and Gray Squirrel

Vegetation data collected on sample plots located within the squirrel study areas were coded to permit analysis of 7 cover types which differed in their structure and vegetative communities. Mean values of the vegetative variables within each type were calculated for each area and used in all subsequent analyses. As a result of the 2 worst mast crops (1983 and 1984) in the past 31 years (Christisen 1983 and 1984), populations of both fox squirrels and gray squirrels were extremely low during the 1984 and 1985 census periods. I beleive the population estimates derived from the time-area counts did not accurately reflect the carrying capacity of the study areas for either squirrel species. Therefore, pattern recognition models were not constructed for either species. Instead, the data were analyzed using several linear techniques to determine the amounts and specific habitat conditions (structure and composition) of those cover types important to fox and gray squirrels when mast crop failures occur. As a result, this analysis does not necessarily reflect those habitat conditions that would be of primary importance in determining habitat suitability for either species under normal conditions.

RESULTS AND DISCUSSION

Ruffed Grouse

Population Estimates

In 1985, 47 activity centers were located on 10 areas representing 3,374 ha. Assuming an equal sex ratio, densities on individual areas ranged from 0 on Carman Springs South to 21.7 grouse/405 ha on White Oak Hollow (Table 6).

In 1986, drumming counts were repeated on the 10 areas censused in 1985 and on 3 additional areas. A total of 75 activity centers were located on 4,766 ha. Densities on individual areas, assuming a balanced sex ratio, ranged from 0 on Carman Springs South and the Anderson WMA to 29.5/405 ha on White Oak Hollow (Table 6).

For model evaluation, mean grouse densities for the 10 areas on which 2 years of census information was collected and single year drumming data on the remaining 3 areas were used. Therefore, calculated densities ranged from 0.0 on Carman Springs South to 26.0/405 ha (1000 ac) on White Oak Hollow (Table 6).

Development of PATREC Model

The mean of the highest and lowest densities on the study areas was 13/405 ha. This resulted in 7 of the areas being classed as containing high populations whereas the populations on the remaining 6 areas were classified as low (Table 6). The high density standard for the model was set equivalent to 26/405 ha, which is the highest recorded

Table 6. Ruffed grouse population estimates for 13 study areas in Missouri during 1985 and 1986.

Area	Area Size (ha)	Grouse Density (birds/405 ha)		
		1985	1986	$\overline{X}$
Anderson WMA	325	2.5	0	1.2
Ashland Area Compartment 1	199	4.1	12.2	8.2
Ashland Area Compartment 2	175	18.5	13.9	16.2
Ashland Area Compartment 5	154	15.7	26.2	20.9
Daniel Boone Forest	378	10.7	19.3	15.0
Carman Springs North	322	2.5	2.5	2.5
Carman Springs South	357	0	0	0
Compton Creek	514	15.8	11.0	13.4
Cowards Hollow *	444	------	16.4	------
Horton Burn *	415	------	5.9	------
Peck Ranch WMA	528	10.7	9.2	10.0
Sleuter Hollow *	433	------	18.8	------
White Oak Hollow	522	21.7	29.5	26.0

* Areas censused in 1986 only

density in the state. The low density standard was set at 2/405 ha.

Prior probabilities for the ruffed grouse PATREC model were the same as those used in the previous model developed for this species by the Missouri Department of Conservation (MDC) (Table 7). The prior probabilities of an area supporting a high and low population density were estblished at 0.20 (20%) and 0.80 (80%), respectively.

Cover Type Occurrence

Correlation analysis indicated that the percent occurrence of 3 types (disturbed, upland-sawlog, and open) were related to grouse density. Scatter diagrams were also examined but non-linear relationships between cover types and grouse density were not detected. Grouse density exhibited a positive correlation with the percent occurrence of disturbed cover on an area ($r = 0.80$ $P < 0.01$). Discriminant function analysis (DFA) correctly classified 85% of the high density areas and 100% of the low density areas based solely on the relative occurrence of this type. This was expected because disturbed sites serve as the primary drumming habitat for ruffed grouse. Fifty-three percent of all activity centers located during the course of this study were in disturbed cover. Bump et al. (1947) and Edminster (1954) also considered disturbed forest habitat as an essential habitat component and its use as both drumming and winter habitat by grouse has been well documented in other states (Gullion 1977, Stauffer and Peterson 1985, Rusch and Keith 1971, Bump

Table 7. PATREC model for the ruffed grouse developed by the Missouri Department of Conservation.

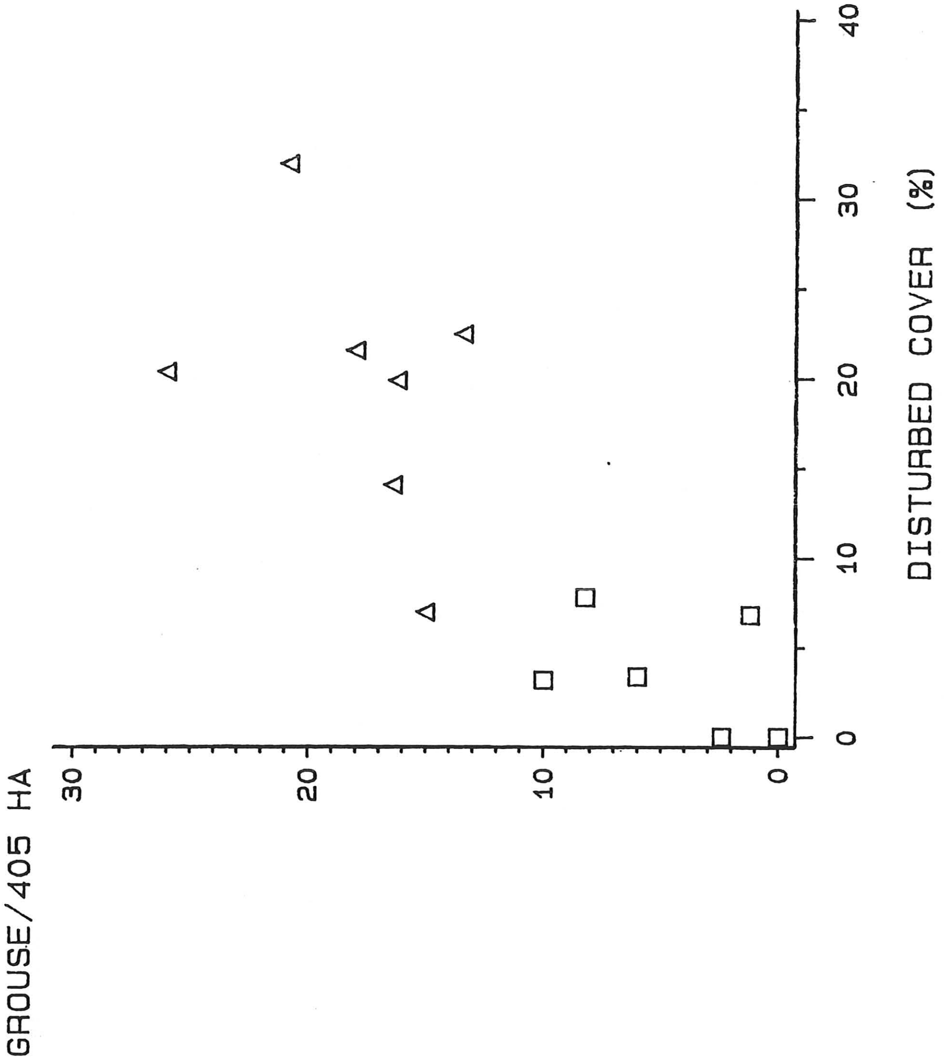
	High	Low
Prior Probabilities:	High: 0.20	Low: 0.80
Population Density Standards (birds/405 ha):	High: 30	Low: 10
PARAMETER	High	Low
I. Percent of area in North and Northeast aspects and colluvial benches (ELT's 7, 18, 25, 51, 52) with site index ≥ 60		
a. ≥30	.60	.10
b. 20-30	.30	.30
c. <20	.10	.60
II. Percent of area with age class ≤ 20 years and animal habitats 12, 13, 15 and 16 on ELT's 7, 18, 25, 51, 52		
a. ≥15	.70	.10
b. 5-14	.20	.20
c. <5	.10	.70
III. Percent area in ELT's 1, 2 and 3		
a. ≥5	.60	.10
b. 2-5	.30	.30
c. ≤2	.10	.60
IV. Percent area in ELT's 4, 5 and 6		
a. ≥10	.60	.10
b. 5-10	.30	.30
c. ≤5	.10	.60
V. Percent of area in ELT's 4, 5 and 6 with overstory crown closure ≥ 40 % (S-3) and sub-canopy ≥ 60% crown closure (S-4)		
a. >5	.60	.10
b. 1-5	.30	.30
c. <1	.10	.60
VI. Percent of area with understory component (S-6) Code 5 and 6 and sub-canopy (S-4) ≥ 40%		
a. ≥40	.70	.10
b. 15-40	.20	.20
c. <15	.10	.70

1938). Due to the direct positive relationship between disturbed cover and population density, the percent occurrence of disturbed cover was incorporated within the model as a parameter.

Disturbed cover ranged from 0% on Carman Springs South and Carman Springs North to 32.0% on compartment 5 of the AWRA (Table 8). Disturbed cover on the 3 areas located on the AWRA was comprised entirely of cedar stands interspersed with hardwood poletimber whereas sapling stands dominated this cover type on the remaining study areas. Categories established for the disturbed cover parameter were a) < 5%, b) 5-15%, and c) > 15%. Seventy-one percent of the areas with high populations contained greater than 15% of disturbed cover while the remaining 20% had between 5 and 15%. In contrast, 34% of low population areas contained between 5 and 15% disturbed cover and 66% had less than 5%. The high and low conditional probabilities were 0.05 and 0.60, 0.30 and 0.30, and 0.65 and 0.10 for each category. Only 1 grouse was detected on the 2 areas where disturbed cover was absent. A level at which the proportion of disturbed cover on an area did not increase its value for ruffed grouse was not detected (Fig 2). In Wisconsin, however, Kubisiak (1985) recommended that 30 to 35% of the aspen type be present in sapling stands under 26 years of age when management goals are directed towards grouse. Gullion (1972) stated that higher sustained grouse densities in Minnesota occurred on areas where aspen

Table 8. Occurrence of cover types correlated with ruffed grouse density on 13 study areas in Missouri during 1985 and 1986.

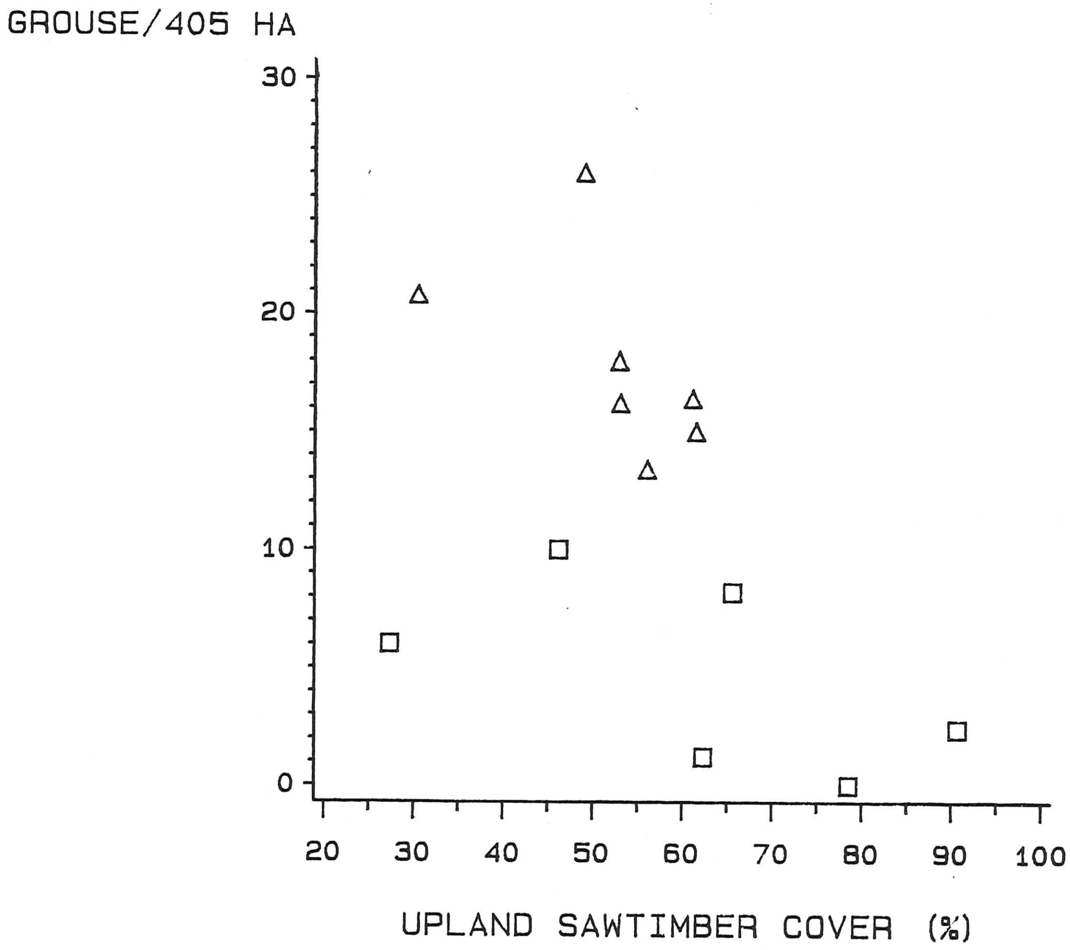
Area	Disturbed		Upland Sawtimber		Open	
	Ha	%	Ha	%	Ha	%
Anderson WMA	22	6.8	202	62.3	13	3.9
Ashland Area Compartment 1	15	7.8	131	65.6	8	4.2
Ashland Area Compartment 2	35	19.9	93	53.0	5	2.8
Ashland Area Compartment 5	49	32.0	47	30.4	0	0
Daniel Boone Forest	26	7.0	232	61.5	6	1.7
Carman Springs North	0	0	293	90.7	4	1.4
Carman Springs South	0	0	280	78.5	11	2.9
Compton Creek	116	22.5	288	56.0	0	0
Cowards Hollow	63	14.1	271	61.1	0	0
Horton Burn	14	3.4	113	27.3	5	1.3
Peck Ranch WMA	17	3.2	244	46.2	28	5.2
Sleuter Hollow	93	21.6	229	52.9	0	0
White Oak Hollow	106	20.4	255	49.0	0	0


GROUSE/405 HA
30
20
10
0
0
10
20
30
40
DISTURBED COVER (%)

regeneration stands less than 20 years of age comprised at least 50% of the area.

Although the inclusion of the percent occurrence of upland-sawlog cover with the occurrence of disturbed cover did not alter the classification results of the discriminant function, it was included as a model parameter due to its negative relationship to grouse density (r= -0.50 P = 0.07). In Missouri, upland sawlog stands have been shown to provide both nesting habitat (Freiling 1985) and forage in the form of oak mast (Korschgen 1966). Therefore, its presence in small to moderate amounts is beneficial. However, the ability of an area to support grouse declines when a single cover type occupies a large portion of an area because grouse require forests in various successional stages and cover types for long-term survival (Johnsgard 1973, Edminster 1954). In this study, the upland-sawlog cover type exhibited this sort of influence on grouse density. The level at which the percent occurrence of upland sawtimber decreased the value of an area for grouse was 60 to 70% (Fig 3). Therefore, in association with disturbed cover, the occurrence of upland-sawlog cover helped delineate the optimum level of occurrence of these 2 important cover types for ruffed grouse.

The upland-sawlog cover type comprised from 27% of Horton Burn to 91% of Carman Springs North (Table 8). The categories established were a) < 55%, b) 55-70%, and c) > 70%. All high density areas contained less than 70% of the


GROUSE/405 HA
30
20
10
0
20
30
40
50
60
70
80
90
100
UPLAND SAWTIMBER COVER (%)

upland-sawlog cover type and 57% of these areas contained less than 55%. In contrast, low density areas exhibited equal occurrence in all 3 categories. Consequently, the high and low conditional probabilities were 0.55 and 0.30, 0.35 and 0.35, and 0.10 and 0.35 for each category, respectively. These results suggest that low density populations can occur on areas regardless of the amount of upland sawlog stands present but high density populations tend to occur on those areas with a smaller amount of this type.

The proportion of an area consisting of the open cover type was negatively correlated with grouse density ($r = -0.59$ $P = 0.03$). In contrast to this negative correlation, Bump (1938) and Edminster (1954) both reported that open land types enhance the value of adjacent woodlands by creating edges. Perhaps by using drumming males as indicators of density and, therefore habitat quality, the relationship between the open cover type and grouse density was obscured. Therefore, this cover type was not included in the PATREC model.

Cover Type Structure

Analysis of the structure and composition of vegetation within cover types was restricted to those variables that characterized specific vegetative conditions within the disturbed and upland sawlog cover types. Within the disturbed cover type, a subset of 3 variables identified as important by correlation analysis and scatter diagrams was selected from among the 30 variables measured in the disturbed cover type. These variables were the mean basal area of woody vegetation ≥ 2.54 cm dbh, mean density of woody stems < 2.54 cm in diameter and > 1 m in height, and the mean percent canopy closure of all vegetation over 1.5 m in height. Principal components analysis, which computes uncorrelated linear combinations of the original variables, also indicated that these 3 factors distinguished between structural differences in the disturbed cover type.

Based on DFA, each of these variables contributed to the correct classification of high density and low density areas but no single variable or combination of 2 variables classified all the areas correctly. When all 3 variables were combined, however, DFA correctly classified 100% of all areas. Therefore, all 3 variables were retained for use in the PATREC model.

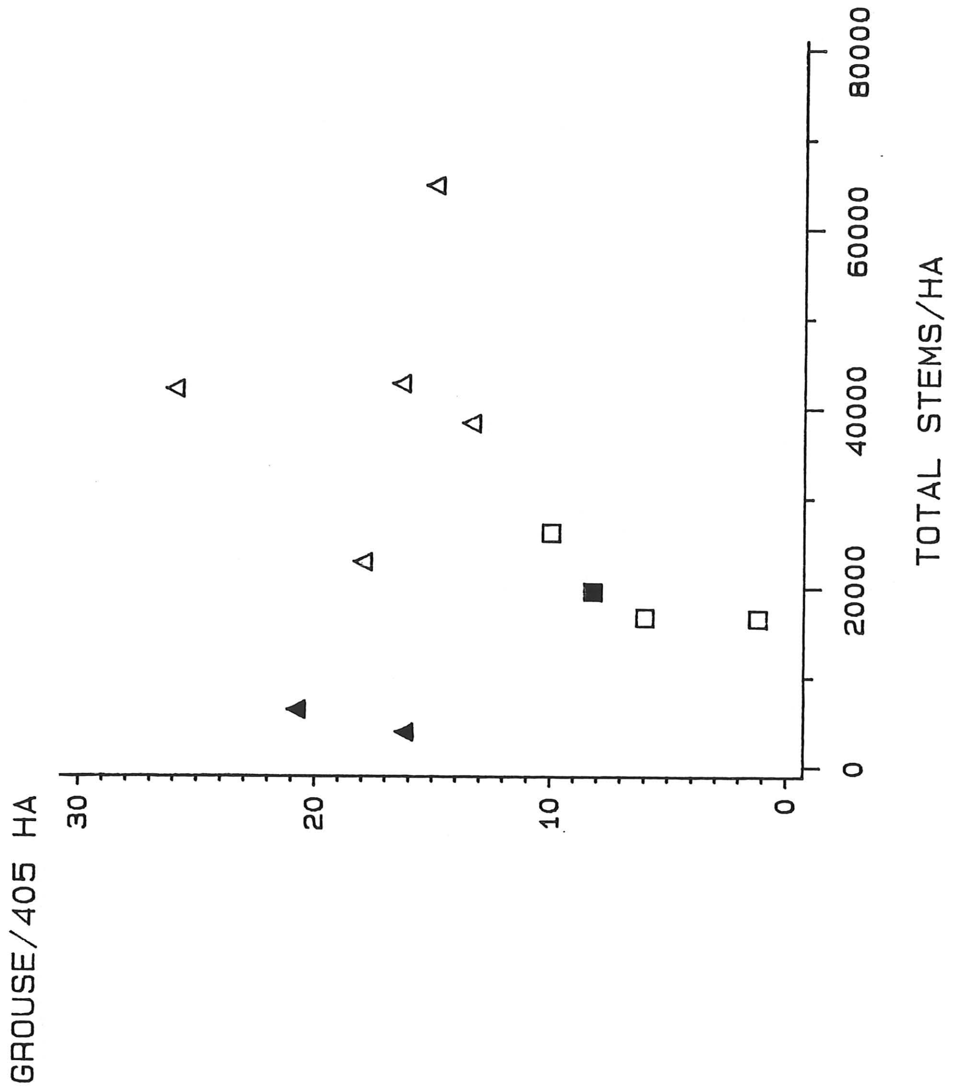
Woody stem density has been reported as an important factor affecting the selection of drumming sites within hardwood regeneration stands across the range of the ruffed grouse. Gullion (1977) reported that sites with stem densities ranging from 12,000 to 42,000/ha provided suitable drumming habitat in Minnesota. Palmer (1963) and Rusch and Keith (1971) stated that drumming males selected sites where stem densities are between 19,600 and 44,600/ha. In Missouri, previous studies on separate areas have shown that activity centers are established at sites where the density of woody stems is greater than the mean stem density of the entire area (Thompson et al. in press, Hunyadi 1978, Kurzejeski 1979, Titus 1976).

In this study, the mean density of woody stems < 2.54 cm dbh and > 1 m in height within disturbed cover ranged from 3,833/ha on compartment 2 of the AWRA to 64,792/ha on Boone Forest (Table 9). Both of these areas contained high density populations suggesting stem densities did not exert an influence on the quality of disturbed cover for ruffed grouse. This was due to the type of disturbed forest habitat on compartments 1, 2, and 5 of the AWRA. In these compartments, cedar stands interspersed with hardwood poletimber constituted disturbed cover. The brushy growth form, dense canopy, and evergreen nature of cedars within these stands restricted woody undergrowth and lower stem densities resulted. However, high grouse densities still occurred in compartments 2 and 5 because the cedar stands were well-stocked and cedar canopies remained near the ground.

In contrast, hardwood regeneration stands between the ages of 6 and 15 comprised the majority of disturbed cover on the remaining 10 areas. With respect to these areas, there was a curvilinear relationship between the density of small woody stems within disturbed cover and grouse density (Fig 4). When areas with low populations were compared to those with high populations a test of least significant differences (LSD) indicated that the mean density of woody stems within disturbed cover on low population areas (8,004/ha) was

Table 9. Means and standard errors of the mean for qualitative habitat parameters in the ruffed grouse PATREC model in Missouri.

	Disturbed Cover						Upland Sawtimber	
	stems/ha		basal area (m^2/ha)		canopy closure (%)		stems/ha	
Area	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
AWRA Compartment 1	19515.4	7781.5	13.7	2.6	54.9	8.5	8057.8	721.6
AWRA Compartment 2	3833.4	790.6	18.3	7.1	66.2	18.9	8066.7	1495.8
AWRA Compartment 5	6333.4	1593.7	21.8	5.6	63.9	15.2	6083.4	1060.0
Anderson WMA	16518.7	2836.6	6.1	1.4	49.1	13.5	5305.6	658.9
Daniel Boone Forest	64792.6	9843.7	18.6	5.3	74.8	18.1	4951.5	431.7
Compton Creek	38271.4	4269.8	19.2	2.2	89.3	4.9	5436.6	1219.5
Cowards Hollow	42708.9	5309.2	16.9	3.0	81.0	7.0	7328.2	785.0
Carman Springs North	-------	-------	-----	----	-----	-----	3439.9	339.4
Carman Springs South	-------	-------	-----	----	-----	-----	2647.7	255.5
Horton Burn	16666.9	.	12.8	.	99.0	.	4884.7	730.5
Peck Ranch WMA	26146.2	6737.1	18.7	3.3	93.8	2.2	3978.3	683.8
Sleuter Hollow	22820.8	5407.6	21.7	3.4	75.3	8.3	5022.8	934.1
White Oak Hollow	42094.3	10727.0	19.5	2.7	70.4	7.7	6420.4	1284.7


GROUSE/405 HA
30
20
10
0
0
20000
40000
60000
80000
TOTAL STEMS/HA

significantly ($P < 0.05$) lower than those within the same cover type on areas with high populations (17,053/ha).

The density of woody stems within the disturbed cover type was significantly ($P < 0.10$) higher than the mean stem density of the entire area on 8 of the 11 study areas with the disturbed cover component (Table 10). On areas where there was no significant difference, hardwood regeneration stands between 6 and 15 years of age comprised the disturbed cover component of only 1 area, Sleuter Hollow. Disturbed cover on the other 2 areas (compartment 2 and compartment 5 of the AWRA) consisted entirely of cedars whose canopies provide the protective and concealing characteristics of suitable drumming and winter habitat. These results further suggest that stem densities are an important factor determining the quality of habitat for ruffed grouse within hardwood cover types, but are not important within coniferous vegetation. In fact, the mean stem densities within disturbed cover (cedar) on compartments 2 and 5 of the AWRA were somewhat lower than the mean stem density of the entire area.

The range of stem densities was separated into 3 categories that best separated grouse densities: a) < 17,300/ha, b) 17,300-39,600/ha, and c) > 39,600/ha. Of the high population areas, 43% had stem densities greater 39,600/ha within disturbed cover, 28% had stem densities between 17,300 and 39,600/ha, and the remaining 29% had stem densities less than 17,300/ha. In contrast, 50% of low

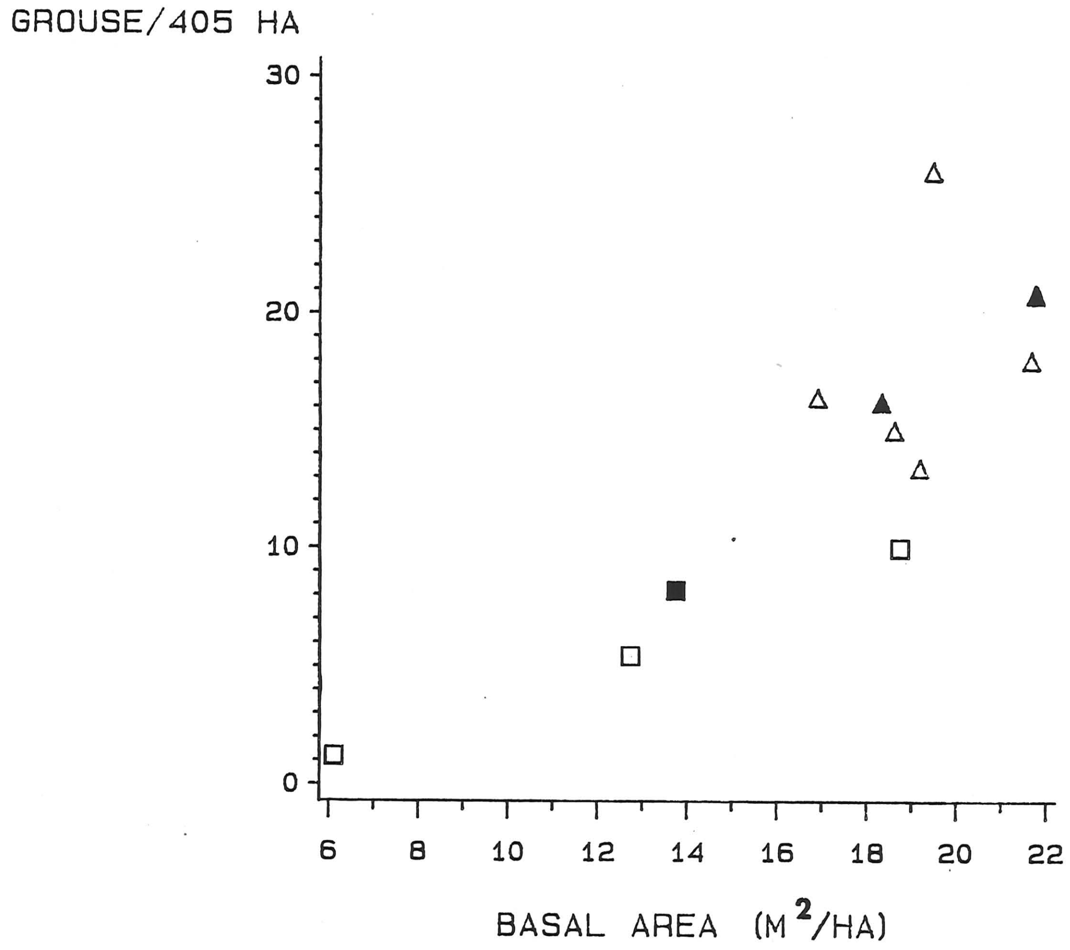
Table 10. Comparison of the mean density of woody stems less than 2.54 cm dbh in disturbed cover with the mean stem density of the entire area for 11 ruffed grouse study areas in Missouri.

Area	Disturbed Cover stems/ha	Entire Area stems/ha	P
Ashland Area Compartment 1	19,516	10,670	0.03
Ashland Area Compartment 2	3,833	7,025	0.08
Ashland Area Compartment 5	6,333	7,386	0.58
Anderson WMA	16,519	5,252	<0.01
Daniel Boone Forest	64,792	5,908	<0.01
Compton Creek	38,271	8,496	<0.01
Cowards Hollow	42,709	13,142	<0.01
Horton Burn	16,667	8,503	0.06
Peck Ranch WMA	26,146	6,472	<0.01
Sleuter Hollow	22,822	15,977	0.30
White Oak Hollow	42,093	6,246	0.01

population areas had stem densities between 39,600/ha and 17,300 and 50% had densities less than 17,300/ha. High and low conditional probabilities were 0.30 and 0.50, 0.30 and 0.40, and 0.40 and 0.10 for each category, respectively.

The mean basal area of woody vegetation in disturbed cover exhibited a linear relationship with grouse density ($r = 0.81$ $P < 0.01$) (Fig 5). The mean basal area for low population areas (56.3 m^2/ha) was significantly ($P < 0.10$) lower than that of high population areas (84.9 m^2/ha). This variable is an especially important measure of the quality of disturbed cover for ruffed grouse because cedar stands may replace disturbed deciduous stands as the primary drumming and wintering habitat in central Missouri. As mentioned above, cedar stands and some old-fields are capable of providing suitable grouse cover if an area is largely wooded. As cedar trees become more sparsely distributed, basal area decreases as does the quality of cedar stands for grouse. This is reflected on the 3 AWRA study areas which had cedar stands as the disturbed cover component. Grouse densities on these areas decreased as basal area within disturbed cover decreased (Fig 5).

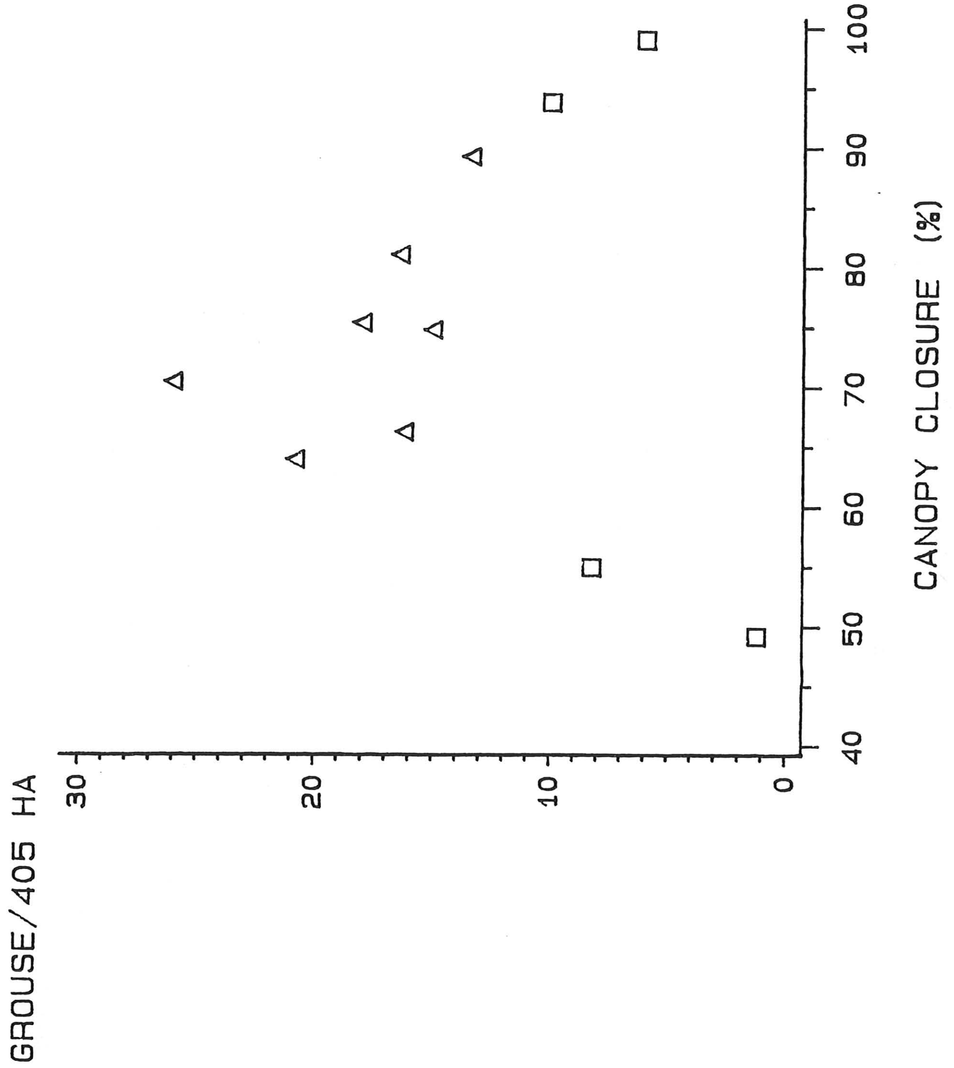
Basal area of woody vegetation is also an important component of hardwood regeneration stands. In addition to providing added vertical cover in the form of stems, the larger trees and shrubs included in this variable provide the overhead canopy closure that protects grouse from avian predation. This was substantiated by Moulton (1968) who


GROUSE/405 HA
30
20
10
0
6
8
10
12
14
16
18
20
22
BASAL AREA (M 2/HA)

reported that protective cover is provided primarily by the shrub and small sapling vegetation in Wisconsin. Boag (1976) also stated that the vegetation in the shrub layer was the most important factor in the selection of drumming sites.

Mean basal area values within disturbed cover ranged from 6 m^2/ha on the Anderson Area to 21.8 m^2/ha on compartment 5 of the AWRA (Table 9). Based on the scatter diagram, 3 categories were delineated for this parameter: a) < 17 m^2/ha, b) 17-20 m^2/ha, and c) > 20 m^2/ha. Fourteen percent of high density areas and 75% of the low density areas had mean basal areas less than 17 m^2/ha within disturbed cover. Forty-two percent of the high and 25% of the low density areas had mean basal areas ranging from 17 to 20 m^2/ha. In contrast, only high density areas (42%) had mean basal areas greater than 20 m^2/ha within this cover type. High and low conditional probabilities were 0.20 and 0.60, 0.40 and 0.30, and 0.40 and 0.10 for each category, respectively.

The degree of canopy closure within disturbed cover exhibited a curvilinear relationship with grouse density (Fig 6). As indicated previously, the presence of a canopy provides valuable protection from avian predation. This is particularly important in spring when males use disturbed sites as drumming habitat and are vulnerable to a greater extent than during any other season (Bump et al. 1947). Density of the smaller woody stems is equally important, however, in providing cover and protection near the ground.


GROUSE/405 HA
30
20
10
0
40
50
60
70
80
90
100
CANOPY CLOSURE (%)

Complete canopy closure, although rendering an almost inpenetrable barrier to avian predators, would tend to reduce woody stem densities below the optimum level needed for adequate cover. Therefore, a median canopy closure that affords some overhead protection but still allows adequate growth of woody stems represented the preferred structure of disturbed cover for grouse on the 11 study areas.

Within the disturbed cover type, mean canopy closure ranged from 49% on the Anderson Area to 99% on Horton Burn (Table 9). Grouse densities were lowest when the canopy closure in this type was either below 60% or above 85% while higher densities occurred within the range of 60 to 85%. The categories that best separated high from low densities were: a) < 70%, b) 70-85%, and c) > 85%. Only high density areas (57%) had disturbed cover with canopy closures between 70 and 85%. Fifteen percent of high and 50% of low density areas had closures greater than 85% wherease canopy closures less than 70% occurred on the remaining 28% and 50% of the high and low density areas, respectively. The high and low conditional probabilities were 0.30 and 0.50, 0.55 and 0.10, and 0.15 0.40 for each category, respectively.

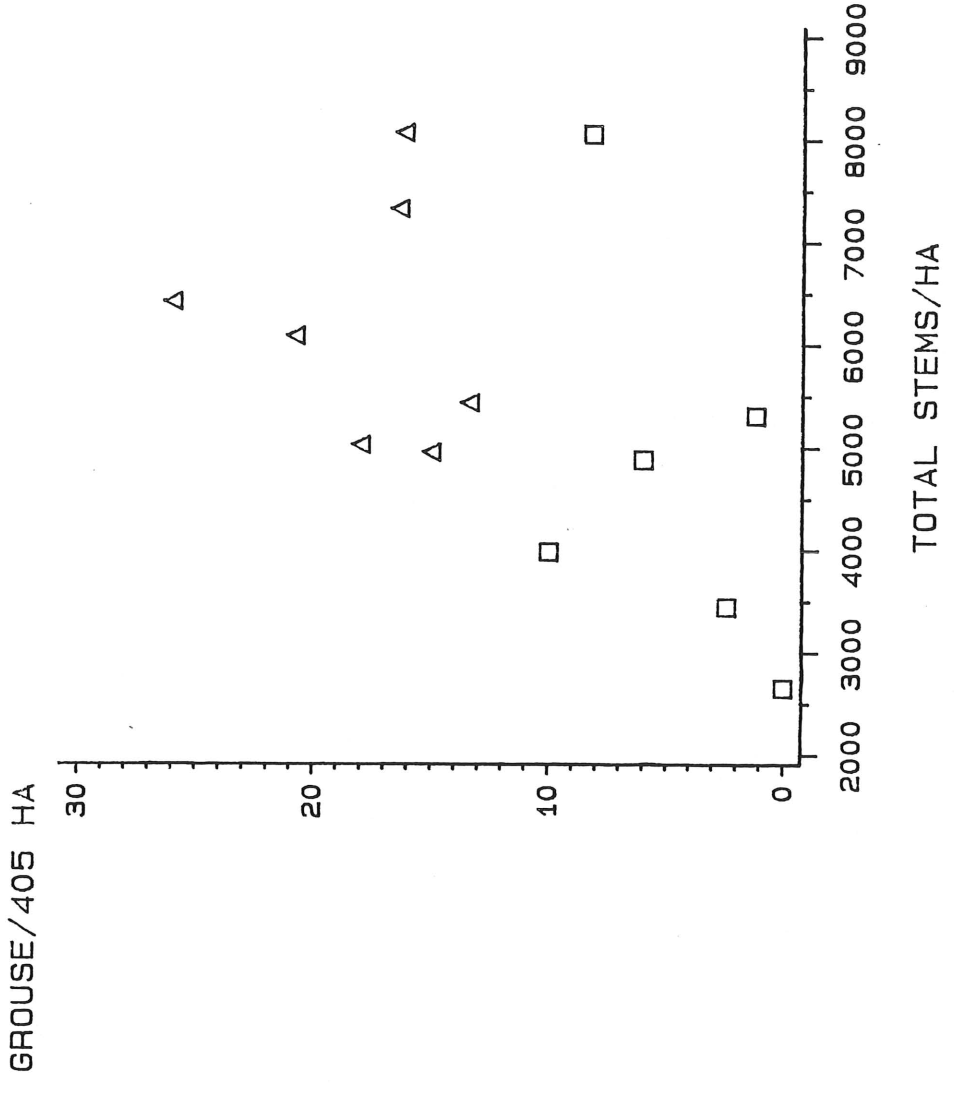
Two variables were identified by correlation analysis as important factors determining the quality of the upland sawtimber cover type for ruffed grouse. These variables were the mean basal area of woody vegetation ≥ 2.54 cm dbh and the mean density of woody stems < 2.54 cm in diameter and > 1 m in height. Using these 2 variables, DFA correctly classified

71% of high density areas and 83% of low density areas. Sequential removal of each variable from the analysis, however, indicated that both variables were not necessary. Based solely on the density of woody stems, DFA correctly classified 57% (N = 4) of high density and 83% (N = 5) of low density areas suggesting that this variable was an important qualitative component of upland sawlog stands. Using the same procedure, 57% (N = 4) of high density and only 67% (N = 4) of low density areas were correctly classified when mean basal area was substituted for stem densities. Scatter diagrams of these 2 variables also indicated that the density of woody stems separated high from low density areas better than mean basal area. An LSD test showed that the mean density of stems on low population areas (1,910/ha) was significantly ($P < 0.10$) lower than the mean density of stems on high population areas (2,504/ha). Therefore, only the density of woody stems was retained for use in the PATREC model.

Based on the location of drumming logs, it appeared that upland sawlog stands served as alternative sites for the establishment of activity centers in addition to providing food and nest sites. Thirty-three percent of all activity centers located during the study were within the upland-sawlog cover type.

Upland sawlog stands with broken canopies were present on most areas in the study. In addition, a scarlet oak-black oak die-off, which affected numerous sawlog stands, occurred in southern Missouri where 7 of the study areas were located. Small openings within these stands tended to have somewhat higher stem densities due to increased sunlight penetration and diminished competition for nutrients. Brood use of such openings with moderately dense cover near the ground has been reported in Iowa (Porath and Vohs 1972), Virginia (Stewart 1956), and Wisconsin (Kubisiak 1985). The positive correlations between grouse density and both basal area ($r = 0.55$ $P = 0.05$) and woody stem densities ($r = 0.55$ $P = 0.05$) tend to support the hypothesis that the relative importance of the upland sawlog cover type to grouse is at least partially determined by its structure near ground level.

Mean woody stem densities in the upland sawlog type ranged from 2,647/ha on Carman Springs South to 8,066/ha on compartment 2 of the AWRA (Table 9). The categories that best separated high from low densities were: a) < 5,200/ha, b) 5,200-6,200/ha, and c) > 6,200/ha. Of the low population areas, 68% had less than 5,200 stems/ha within the upland sawlog type, 16% had densities between 5,200 and 6,200/ha, and 16% had stem densities greater than 6,200/ha. With respect to upland sawlog stands on high population areas, 30% had stem densities that were less than 5,200/ha, 30% had densities between 5,200 and 6,200/ha, and 40% had stem densities greater than 6,200/ha (Fig 7). The high and low conditional probabilities were 0.30 and 0.70, 0.30 and 0.15, and 0.40 and 0.15 for each category, respectively.


GROUSE/405 HA
30
20
10
0
2000
3000
4000
5000
6000
7000
8000
9000
TOTAL STEMS/HA

Patrec Model Performance

The revised PATREC model consists of the 6 parameters discussed in the previous section (Table 11). Each of these parameters is mutually exclusive (uncorrelated) of the others in its relationship to ruffed grouse density. In combination, these variables characterized the habitat conditions that best quantified ruffed grouse density on the 13 areas used in the study.

The density estimates determined from both the PATREC model computations and spring drumming surveys are presented for each area in Table 12. Of the areas that contained high populations of grouse (> 13/405 ha), the largest diffence between potential (25/405 ha) and measured densities (18/405 ha) occurred on Sleuter Hollow. There were no significant differences between the habitat conditions on this area and those on White Oak Hollow, which had both an observed and predicted density of 26/405 ha. However, the observed density on Sleuter Hollow was 8 birds lower indicating that some factor other than habitat may be affecting the population on this area. Based on the location of activity centers within the area, drumming males occupied the disturbed cover surrounding the site where grouse were released in 1983. Additional drummers were detected in disturbed cover located adjacent to the study area but near the release site, suggesting that grouse were dispersing to suitable sites outside the study area boundary. Therefore, it is possible that grouse densities near the potential

Table 11. Revised PATREC model for ruffed grouse developed from habitat data and population estimates collected on 13 study areas in Missouri during 1985 and 1986.

Prior Probabilities:	High: 0.20	Low: 0.80
Population Density Standards (birds/405 ha):	High: 26	Low: 2
PARAMETER	High	Low
I. Percent of area in the disturbed cover type		
a. <5	.05	.60
b. 5-15	.30	.30
c. >15	.65	.10
II. Percent canopy closure in disturbed cover		
a. <70	.30	.50
b. 70-85	.55	.10
c. >85	.15	.40
III. Basal area (m^2/ha) in disturbed cover		
a. <17	.20	.60
b. 17-20	.40	.30
c. >20	.40	.10
IV. Total number of woody stems/ha (<2.54 cm diameter and >1 m in height) in disturbed cover		
a. <17,300	.10	.60
b. 17,300-39,600	.30	.30
c. >39,600	.60	.10
V. Percent of area in upland sawtimber		
a. <55	.55	.30
b. 55-70	.35	.35
c. >70	.10	.35
VI. Total number of stems/ha (<2.54 cm diameter and >1 m in height) in upland sawtimber		
a. <5,200	.30	.70
b. 5,200-6,200	.30	.15
c. >6,200	.40	.15

Table 12. Comparison of grouse densities predicted by the revised PATREC model with observed densities determined from complete area drumming counts in 1985 and 1986 on the 13 study areas in Missouri used to develop the revised PATREC model.

Area	Predicted Density (birds/405 ha)	Observed Density (birds/405 ha)	Difference
Ashland Area Compartment 1	4.0	8.0	4.0
Ashland Area Compartment 2	21.0	16.0	5.0
Ashland Area Compartment 5	23.0	21.0	2.0
Anderson WMA	2.0	1.0	1.0
Daniel Boone Forest	20.0	15.0	5.0
Compton Creek	15.0	13.0	2.0
Cowards Hollow	22.0	16.0	6.0
Carman Springs North	2.0	2.0	0.0
Carman Springs South	2.0	0.0	2.0
Horton Burn	2.0	6.0	4.0
Peck Ranch WMA	4.0	10.0	6.0
Sleuter Hollow	25.0	18.0	7.0
White Oak Hollow	26.0	26.0	0.0

predicted by the PATREC model will occur on Sleuter Hollow as grouse disperse throughout the surrounding area in future years.

The low potential density estimate (4/405 ha) for Peck Ranch was due largely to inaccurate information concerning the percent occurrence of the disturbed cover type. According to the current timber inventory, only 3.2% of the area is comprised of disturbed cover. During the course of conducting fieldwork, however, several disturbed stands were located that were not identified on the timber inventory. Following conversations with Peck Ranch personnel, it was suspected that disturbed cover may occupy as much as 15% of the study area but it was not possible to determine the actual value. Therefore, the initial value of 3.2% was used in calculating the potential density estimate of 4/405 ha. If disturbed cover does occupy over 15% of the area the potential density estimate computed by the PATREC model would become 10/405 ha, which is also the observed density determined by spring drumming counts.

Densities of $\leq$ 6 birds/405 ha separated the potential and actual estimates on the remaining 11 areas. Estimates on 6 of these areas differed by less than 3 birds/405 ha. The small diffences between the estimates could have been caused by several factors including the presence of non-drumming males that were undetected, yearly fluctuations in grouse numbers, or subtle habitat conditions to which the PATREC model is not sensitive. In addition, the potential density estimates may be slightly higher than the actual estimates on some areas because complete saturation and use of the available habitat has not yet occurred and the area can sustain more breeding pairs.

Based on the above comparisons, the PATREC model adequately estimates the potential grouse densities on the areas used to construct the model. These comparisons do not represent a true test of model validity because the model was developed using density and habitat data collected on these areas. However, the comparisons do show that the model is both sensitive and flexible in that different estimates were produced by the model as habitat conditions present on an area varied.

Comparison of Outputs Between the Original and the Revised PATREC Models

The ruffed grouse PATREC model developed by MDC was constructed for use with the data currently being collected by the U. S. Forest Service. The 6 parameters of the original model distinguish the grouse potential of an area based mainly on the occurrence of ecological land types (ELT), structure of the understory vegetation, and age classes (Table 7). Since these data were not collected during sampling, the information was obtained from the WMIS data base of the Mark Twain National Forest. However, collection of some of these data have started only recently. As a result, information was only available for Carman

Springs South and North, Compton Creek, and compartment 40 of White Oak Hollow.

The original model adequately estimated grouse densities on Carman Springs South and Carman Springs North but over-estimated the density on Compton Creek and under-estimated the density on compartment 40 of White Oak Hollow (Table 13). Because of similar potential density estimates, it was determined that the original PATREC model recognized no substantial differences between the habitat conditions for grouse on compartment 40 of White Oak Hollow and either Carman Springs area. However, 26% of White Oak Hollow is comprised of sapling stands that provide drumming and winter habitat whereas saplings were absent on both Carman Springs areas. In contrast, oak-hickory sawlog stands dominated both Carman Springs South (78%) and Carman Springs North (91%) but represented only 49% of White Oak Hollow. As result of these differences, which the original PATREC model did not recognize, the observed density of grouse on White Oak Hollow (15/405 ha) was much higher than that on either Carman Springs South (0) or Carman Springs North (2/405 ha).

The observed grouse density on Compton Creek (13/405 ha) and compartment 40 of White Oak Hollow (15/405 ha) were similar. However, the original PATREC model produced potential density esimates of 24/405 ha for Compton Creek and 3/405 ha for White Oak Hollow. These potential density estimates represent a difference of 21 birds/405 ha on 2 areas that contained similar numbers of grouse.

Table 13. Comparison of grouse densities predicted by the original PATREC model with observed densities determined from complete area drumming counts in 1985 and 1986 on 4 study areas in Missouri.

Area	Predicted Density (birds/405 ha)	Observed Density (birds/405 ha)	Difference
White Oak Hollow *	3.0	15.0 *	12.0
Compton Creek	24.0	13.0	11.0
Carman Springs North	2.0	2.0	0.0
Carman Springs South	2.0	0.0	2.0

* Density is based only on the number of drumming grouse in located in compartment 40 of White Oak Hollow

Based on these comparisons, the original PATREC model does not satisfactorally estimate the potential of an area for supporting grouse. The model parameters do not reflect either the quality or quantity of the cover types necessary for grouse survival. As a result, the model is not sensitive enough to distinguish differences between the suitability of habitat characteristics on different areas and assign appropriate density estimates.

Summary and Conclusions

The quantity of disturbed cover present on an area was identified as one of the most important characteristics distinguishing the potential of an area to support ruffed grouse. The predominant use of this cover type was likely for drumming and winter habitat but it is expected that broods also use these sites to feed. Areas on which disturbed cover was absent or represented only a small percentage of the total area had lower grouse densities than areas with larger amounts of this cover type. The best condition for grouse occurred on those areas where disturbed cover represented over 15% of the total acreage.

Although grouse used disturbed sites when present, the structure of the vegetation was important in determining the quality of this type. Variables related to the important structural characteristics were the mean basal area of woody vegetation $\geq$ 2.54 cm dbh, the mean density of woody stems < 2.54 cm in diameter and > 1 m in height, and mean percent canopy closure. Areas that contained disturbed cover with high woody stem densities, high basal areas, and a semi-closed canopy exhibited higher grouse densities than areas with comparable amounts of disturbed cover whose structure failed to meet all 3 criteria. As a result, when the quality of disturbed cover is low, a larger amount of disturbed cover is required to support an equal number of grouse.

Upland sawlog stands represented another important cover type determining the potential of an area for ruffed grouse. The mast produced by these stands is an important food source for ruffed grouse in Missouri. This cover type also provides both nesting habitat and alternative sites for the establishment of activity centers. However, large amounts (> 55%) of this cover type were detrimental to ruffed grouse habitat. As a result, a small amount of this type is beneficial but as its occurrence increased it began to limit the occurrence of other cover types, including disturbed cover, that are more important components of grouse habitat.

The mean density of woody stems < 2.54 cm in diameter and > 1 m in height was an important feature of the upland sawlog type. As stem densities increased the value of upland sawlog stands as grouse habitat also increased. Based on the location of activity centers, it appears that this relationship is due partially to the use of this type as drumming habitat. If disturbed cover was present in adequate amounts on these areas, the density of stems in sawlog stands may not have been an important factor determining spring grouse densities. However, in many portions of Missouri the upland-sawlog type is the dominant cover type, and stem densities that provide adequate cover will probably always be an important component of grouse habitat.

The PATREC model constructed for the ruffed grouse incorporated the 6 variables discussed above as the model parameters. In association with each other, they represented the habitat characteristics that best distinguished between the grouse densities on the 13 areas used in the study. With respect to ruffed grouse habitat requirements, the model was sensitive to different combinations of habitat conditions. The model produced potential density estimates within 6 birds/405 ha of observed densities on 11 of the 13 areas. Complete verification of the model, however, will require that it be tested on areas not used to develop the model. Due to the relatively small sample size of 13 observations, some of the conditional probabilities may have to be adjusted, but the model parameters should not change.

In contrast, the PATREC model for ruffed grouse developed by the MDC did not perform well on the 4 areas for which habitat data were available. These results indicate that the original model's parameters were not strongly related to key features of ruffed grouse habitat. The MDC model did appear to distinguish poor quality habitat but it also classified some of the best grouse habitat in Missouri as having a low potential for supporting a high density population.

Management Implications

Due to time and monetary constraints, the goal of habitat management for any wildlife species is to improve the habitat characteristics limiting the population. For each area, however, the limiting factor may be different making it difficult to manage multiple areas for the same species in a cost effective manner. One advantage of PATREC models is the ability to indicate which habitat component is limiting. This is accomplished by subtracting the low conditional probability value from the high conditional probability value of the correct category within each parameter. The parameter with the greatest negative value represents the habitat parameter limiting the population.

Habitat characteristics identified by some parameters in the PATREC model cannot be easily manipulated. These are identified by the 3 parameters (canopy closure, basal area, stem density) dealing with the structure of disturbed cover. When one of these parameters suggests that a habitat characteristic is limiting, it is an indication that this cover type could support more grouse if its quality were improved. Although silvicultural prescriptions to increase the quality of these sites are often not cost effective, this type of situation can be relieved to some extent by increasing the amount of disturbed cover on an area. Site quality within the disturbed cover type should be considered when planning timber harvests. Site index, soil, aspect, and pre-cut stocking density of stands should be considered to avoid poor quality sites where the density of stems and woody growth may be slow. This practice should help prevent the occurrence of disturbed cover that has poor structural qualities relative to ruffed grouse habitat requirements.

The remaining 3 parameters (canopy closure, percent occurrence of disturbed cover, and percent occurrence of upland sawlog stands) can be managed for directly. Regulations of many state and federal agencies, however, impose limitations on the amount of timber harvested within a compartment or other specified area during a given length of time. In addition, standards and guidelines established to enhance other resource concerns also limit the amount and location of timber harvesting efforts. As a result, there is an upper limit on the amount of disturbed cover present on an area. Therefore, the quality of disturbed cover is extremely important in determining the potential density of grouse on an area. In contrast, upland sawlog stands occupy a dominant proportion of most areas in Missouri. Due to restrictive cutting practices, this cover type will continue to dominate forests for many years and may be managed for grouse habitat as intensively as possible. The main consideration, based on this study, is to promote the occurrence of high stem densities and basal areas in as many stands as possible. This can be accomplished through silvicultural prescriptions that designate the group selection of large diameter trees along with the scattered removal of tall understory trees.

This will allow the growth of a moderately dense layer of vegetation within 5 m of the ground. Not only will such a prescription result in suitable drumming habitat but it will also provide brood habitat near suitable nesting sites. Currently, the Mark Twain National Forest has a prescription similar to that just mentioned but it is not utilized to a great extent.

Fox Squirrel and Gray Squirrel

Population Estimates

The highest spring (March) count on each area was selected for use in both the fox and gray squirrel analyses. Mean values of fox and gray squirrels observed were utilized for those 10 areas for which survey information from 2 years was available while single values were used on the 4 areas surveyed only in 1986. Fox squirrel estimates ranged from 0.0 on Boone Forest, Compton Creek, White Oak Hollow, and Cowards Hollow to 13.0 on Bunch Hollow WMA (Table 14). Gray squirrel estimates ranged from 0.0 on Peck Ranch to 9.0 on both Rudolf Bennitt WMA and Bunch Hollow WMA (Table 15).

Vegetation Analysis

Cover Type Occurrence

Fox squirrel numbers were negatively correlated with the percent occurrence of hardwood sawtimber ($r = -0.41$ $P = 0.13$) and positively correlated with the occurrence of crop fields ($r = 0.85$ $P < 0.01$). The number of gray squirrels on each area was also negatively correlated with hardwood sawtimber occurrence ($r = -0.46$ $P = 0.09$) and positively correlated with the occurrence of both the crop field ($r = 0.51$ $P = 0.06$) and open ($r = 0.47$ $P = 0.09$) cover types.

I believe the negative relationship between hardwood sawtimber occurrence and the numbers of both squirrel species was due to the 1983 and 1984 mast crops, which were the worst in Missouri during the past 31 years (Christisen 1983 and

Table 14. Maximum number of fox squirrels observed in a single count during March of 1985 and 1986 on 14 study areas in Missouri.

Area	Number of squirrels observed/102 ha		
	1985	1986	$\overline{X}$
Bunch Hollow WMA *	----	13.0	----
Ashland Area Compartment 1	0.0	2.0	1.0
Ashland Area Compartment 2	1.0	2.0	1.5
Daniel Boone Forest	0.0	0.0	0.0
Panther Spring Hollow	1.0	0.0	0.5
Peck Ranch WMA	0.0	2.0	1.0
Whetstone Creek WMA *	----	2.0	----
Anderson WMA	6.0	5.0	5.5
Rudolph Bennitt WMA *	----	6.0	----
White Oak Hollow	0.0	0.0	0.0
Compton Creek	0.0	0.0	0.0
Cowards Hollow *	----	0.0	----
Carman Springs South	0.0	1.0	0.5
Carman Springs North	0.0	1.0	0.5

* Areas surveyed only in 1986

Table 15. Maximum number of gray squirrels observed in a single count during March of 1985 and 1986 on 14 study areas in Missouri.

Area	Number of squirrels observed/102 ha		
	1985	1986	$\overline{X}$
Bunch Hollow WMA *	----	9.0	----
Ashland Area Compartment 1	1.0	4.0	2.5
Ashland Area Compartment 2	1.0	8.0	4.5
Daniel Boone Forest	2.0	1.0	1.5
Panther Spring Hollow	0.0	2.0	1.0
Peck Ranch WMA	0.0	0.0	0.0
Whetstone Creek WMA *	----	4.0	----
Anderson WMA	5.0	11.0	8.0
Rudolph Bennitt WMA *	----	9.0	----
White Oak Hollow	0.0	2.0	1.0
Compton Creek	2.0	6.0	4.0
Cowards Hollow *	----	3.0	----
Carman Springs South	0.0	1.0	0.5
Carman Springs North	0.0	2.0	1.0

* Areas surveyed only in 1986

1984). During normal years, mast in the form of acorns and hickory nuts represents a staple food item of both species. In fact, the availability and quality of mast has been suggested as the major cause in fluctuations of population abundance (Baker 1944, Nixon and McClain 1969). As a result, hardwood sawtimber is considered an essential component of squirrel habitat since the mature trees within these stands produce the majority of this mast and also provide suitable dens (Baumgartner 1938, Baker 1944). However, due to reduced mast production during the years of this study, the importance of sawlog stands as a food source and, therefore, as a component of squirrel habitat, decreased (Table 16).

The areas with the greatest squirrel numbers were those where crop fields and open areas were present within or near the study area. Fox squirrel numbers were more highly correlated with the occurrence of crops than gray squirrel numbers, but the latter species was also positively correlated with the occurrence of the open cover type. Crop fields consisted primarily of corn although a 2 ha bean field was also present on the Bunch Hollow WMA. In the absence of adequate mast supplies, crop field and open habitat types provided important food items that enabled areas to sustain slightly higher squirrel numbers than areas where these 2 types were absent.

Corn fields were located within the boundaries of only 2 areas, Whetstone Creek WMA and Bunch Hollow WMA, but were

Table 16. Occurrence of cover types correlated with fox squirrel and gray squirrel numbers following two years of oak mast failure in Missouri.

Area	Hardwood Sawtimber		Crop Fields		Open	
	Ha	%	Ha	%	Ha	%
Bunch Hollow WMA	43	42.5	24	24.0	0 *	0
Ashland Area Compartment 1	62	61.5	0	0	6	5.5
Ashland Area Compartment 2	54	53.3	0	0	5	4.8
Daniel Boone Forest	61	60.4	0	0	0	0
Panther Spring Hollow	72	70.6	0	0	0	0
Peck Ranch WMA	42	41.6	0	0	3	2.8
Whetstone Creek WMA	29	28.8	2	2.0	17	17.2
Anderson WMA	75	74.4	0 *	0	2	2.0
Rudolph Bennitt WMA	22	21.6	0 *	0	0	0
White Oak Hollow	62	61.2	0	0	0	0
Compton Creek	58	57.2	0	0	0	0
Cowards Hollow	82	80.6	0	0	0	0
Carman Springs South	77	76.0	0	0	2	2.0
Carman Springs North	91	90.4	0	0	0	0

* Cover type not present in study area but within 300 m of the study area boundary.

within 300 m of the Anderson WMA and Rudolf Bennitt WMA. These 4 areas had the highest fox squirrel numbers of the 14 areas used in the study (Table 16). Havera and Smith (1979) and Havera and Nixon (1980) have stated that corn can be an important winter food source, when mast crops are below average, especially for fox squirrels. However, Havera and Smith (1979) also concluded that this food did not appear to be an adequate supplemental food under normal conditions. This may explain why the 4 areas with corn fields had only slightly higher fox squirrel numbers than areas where corn was absent.

In contrast, 9 study areas contained the open cover type either on the area or within 200 m of its boundary (Table 16). Of the 4 areas where the most gray squirrels were observed, this cover type was present or within 200 m of the area boundaries. In addition, corn fields were present on or within 300 m of 3 of these areas. The tree species present within old fields included persimmon (Diospyros virginiana), sugar maple, american elm, and red elm. The buds, seeds, and persistant fruits of these trees, in addition to corn, may have provided sufficient food to sustain slightly higher gray squirrel numbers.

Cover Type Structure and Composition

Previous investigations have shown that gray squirrels select habitats with a high density of understory trees whereas fox squirrels select more open understory conditions

(Taylor 1974, Allen 1943, Brown and Yeager 1945). I found, however, the best structure of hardwood sawtimber stands for both species consisted of a moderately dense layer of vegetation near the ground. This was indicated by a positive correlation between the horizontal density of vegetation from 0.0 to 1.5 m in height and both fox squirrel ($r = 0.83$ $P < 0.01$) and gray squirrel ($r = 0.70$ $P = 0.01$) abundance. Bunch Hollow WMA and Rudolf Bennitt WMA, which had the greatest number of both species, had mean horizontal densities greater than 40% within the sawtimber cover type (Table 17). The amount of overstory canopy closure provided by shagbark hickory was also positively related to both fox squirrel ($r = 0.83$ $P < 0.01$) and gray squirrel ($r = 0.51$ $P = 0.06$) numbers. Canopy closure of this tree species within the sawtimber cover type exceeded 10% on Bunch Hollow WMA, which had the largest observed number of both fox squirrels and gray squirrels (Table 17). In contrast, the understory canopy closure of all oak species, which ranged from 0.0 to 40.0%, exhibited a negative correlation with both fox squirrels ($r = -0.50$ $P = 0.06$) and gray squirrels ($r = -0.62$ $P = 0.01$). In addition, gray squirrel numbers were also positively correlated with the degree of canopy closure by shrubs between 1 and 5 m in height.

With respect to ground cover within hardwood sawlog stands, fox squirrel abundance was positively correlated with the total number of stems/ha > 1 m in height and < 2.54 cm diameter ($r = 0.63$ $P = 0.01$) and woody sprouts ($r = 0.95$ $P <$

Table 17. Means and standard errors of the mean of important habitat variables within fox squirrel and gray squirrel habitats following two years of oak mast failure in Missouri.

Area	Stems/ha in hardwood sawtimber		Horizontal density (%) in hardwood sawtimber		Woody sprout ground cover in hardwood sawtimber (%)		Woody vine ground cover in hardwood sawtimber (%)	
	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE
AWRA Compartment 1	7678.7	853.3	32.8	2.7	10.3	1.3	10.1	2.5
AWRA Compartment 2	8309.6	2162.2	32.7	4.6	8.7	1.1	1.4	0.6
Anderson WMA	5416.7	664.3	24.7	2.7	19.4	3.8	19.9	4.6
Daniel Boone Forest	4551.3	494.1	25.2	2.4	10.9	1.5	6.4	2.1
Bunch Hollow WMA	11166.8	2790.7	53.9	7.2	28.9	3.8	10.5	1.9
Compton Creek	4257.6	759.6	21.7	4.5	9.1	1.6	8.0	3.5
Cowards Hollow	6774.6	830.0	22.1	2.9	12.1	1.2	0.9	0.4
Carman Springs North	4210.6	395.1	20.2	1.9	8.5	1.1	0.8	0.3
Carman Springs South	3460.8	360.3	21.7	1.9	10.0	1.5	0.8	0.5
Peck Ranch WMA	3819.5	777.6	29.9	3.8	9.0	1.8	3.8	1.6
Panther Spring Hollow	3738.1	504.5	24.3	3.3	8.4	1.2	9.1	3.0
Rudolf Bennitt WMA	7944.6	873.1	46.2	9.3	17.7	7.2	13.7	3.8
Whetstone Creek WMA	6444.5	2453.9	33.7	6.4	10.7	1.6	7.1	3.3
White Oak Hollow	8410.4	2018.5	26.9	4.4	4.7	0.7	10.1	3.5

Table 17 (cont.)

Area	Litter ground cover (%) in hardwood sawtimber		Shagbark canopy closure (%) in hardwood sawtimber		Understory closure (%) of oaks in hardwood sawtimber		Grass ground cover (%) in hardwood poletimber	
	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE
AWRA Compartment 1	47.0	3.4	1.1	0.9	8.6	2.7	9.8	6.7
AWRA Compartment 2	55.3	5.3	1.7	1.3	3.0	1.4	3.3	0.8
Anderson WMA	39.0	3.1	0	0	5.9	2.1	18.0	3.4
Daniel Boone Forest	65.6	3.0	0	0	11.7	3.2	1.6	0.7
Bunch Hollow WMA	37.9	1.7	11.0	6.6	7.2	3.8	14.1	6.5
Compton Creek	69.9	6.2	0	0	39.6	8.5	1.4	0.6
Cowards Hollow	70.6	3.8	0	0	22.7	3.9	5.5	3.9
Carman Springs North	76.4	5.5	0	0	24.6	4.6	----	----
Carman Springs South	77.1	2.5	0	0	27.5	5.3	1.6	1.2
Peck Ranch WMA	67.2	3.1	0	0	30.5	3.9	1.0	0.3
Panther Spring Hollow	72.6	3.8	0	0	36.3	4.9	1.4	0.8
Rudolf Bennitt WMA	27.3	6.3	0	0	0	0	9.5	2.1
Whetstone Creek WMA	41.8	9.3	0	0	4.9	2.5	8.6	2.3
White Oak Hollow	56.2	8.1	0	0	15.7	4.6	2.6	1.1

Table 17 (cont)

Area	Forb ground cover (%) in hardwood poletimber		Horizontal density (%) in hardwood poletimber		Litter ground cover (%) in hardwood poletimber		Understory closure (%) of oaks in hardwood poletimber	
	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE
AWRA Compartment 1	16.9	11.3	33.0	4.7	48.1	3.3	14.8	8.7
AWRA Compartment 2	10.5	4.0	26.4	2.7	53.4	7.7	16.5	6.7
Anderson WMA	25.0	6.1	28.5	5.4	26.6	9.3	0	0
Daniel Boone Forest	4.5	2.0	35.2	6.6	67.6	6.9	8.0	3.6
Bunch Hollow WMA	11.9	2.2	54.7	4.9	34.0	5.4	3.3	1.7
Compton Creek	0.9	0.5	18.9	3.6	86.0	2.6	27.7	9.9
Cowards Hollow	13.7	7.2	34.5	10.6	50.3	15.9	8.9	8.9
Carman Springs North	-----	-----	-----	-----	-----	-----	-----	-----
Carman Springs South	3.7	2.1	18.3	2.6	76.2	6.4	24.1	2.8
Peck Ranch WMA	3.3	1.2	32.4	7.7	62.5	6.2	15.5	6.8
Panther Spring Hollow	1.1	0.7	22.9	3.1	65.9	4.1	25.8	7.1
Rudolf Bennitt WMA	13.3	3.7	47.9	3.7	37.7	4.5	11.0	3.6
Whetstone Creek WMA	13.5	3.3	42.9	2.9	35.0	4.3	4.5	2.2
White Oak Hollow	8.4	3.0	15.2	5.3	74.5	4.0	17.6	6.1

0.01) but negatively correlated with litter ($r = -0.69$ $P < 0.01$). Gray squirrel abundance was also negatively correlated with litter ($r = -0.82$ $P < 0.01$) and positively correlated with both woody sprouts ($r = 0.83$ $P < 0.01$) and woody vines ($r = 0.62$ $P = 0.01$).

Although the percent occurrence of the hardwood poletimber cover type was not related to numbers of either squirrel species, there were structural attributes of this type that were correlated to squirrel abundance. The horizontal density of vegetation up to 1.5 m in height was again related to both fox squirrel ($r = 0.71$ $P < 0.01$) and gray squirrel ($r = 0.63$ $P = 0.02$) abundance. Horizontal densities greater than 45% occurred on Bunch Hollow WMA and Rudolf Bennitt WMA, the areas that had the most squirrels of both species (Table 17). As in sawtimber stands, the degree of understory canopy closure by oak trees was negatively correlated with both fox squirrels ($r = -0.56$ $P = 0.04$) and gray squirrels ($r = -0.57$ $P = 0.03$). In addition, fox squirrel numbers were correlated with the percent cover of litter ($r = -0.66$ $P = 0.01$) and grass ($r = 0.74$ $P < 0.01$) on the forest floor whereas gray squirrel numbers were correlated to the percent cover of forbs ($r = 0.61$ $P = 0.02$) as well as grass ($r = 0.80$ $P < 0.01$) and litter ($r = -0.73$ $P < 0.01$).

The predominant cover type on all study areas, regardless of size, was oak-hickory timber which constituted from 50.8% of Carman Springs North to 100% of Boone Forest.

This is found throughout Missouri, with oaks comprising over 60% of all the commercial timber (Settergren and McDermott 1972). Acorns and nuts produced by the trees in these stands represent the most important food items in the diet of both species, particularly in the fall and winter (Nixon et al. 1968). The poor mast crops observed on the study areas during 1983 and 1984 were likely because late spring frosts occurred from late March to early April, after several oak species had initiated flowering. Complete mast failures were not observed, however, due to the wide variety of mast bearing trees, whose flowering times are variable. The predominant oak species on the study areas were white oak and black oak, which flower in early April, and were probably among the most affected by the oak (Q. stellata), which occurred less frequently, normally initiate flowering in mid-April and were probably less affected by low temperatures. Of the hickories found in Missouri, shagbark, pignut (C. glabra), and mockernut (C. tomentosa) initiate flowering in mid-April whereas bitternut hickory (C. cordiformes) flowers in early April. Shagbark hickory occurred only on those study areas located north of the Missouri river while the other species occurred infrequently on all areas.

The positive correlation between the canopy closure of shagbark hickory in hardwood sawtimber and the number of both squirrel species may have resulted because nut production by this species was not totally affected by the frost that caused freeze damage at the time of black oak and white oak fruit set, the 2 largest mast producers (Nixon et al. 1975). On the areas where shagbark was present, the nuts provided a valuable food item for both squirrel species. Nixon et al. (1968) stated that the nuts of shagbark appear to be the most preferred form of mast and Lewis (1982) concluded this preference was due to their high energy density. In Missouri, Korschgen (1981) found that shagbark hickory nuts were the most used form of mast by both squirrel species.

Due to the inability of mast to provide a sufficient fall and winter food base, both fox squirrels and gray squirrels were more dependent on items that are normally considered supplementary foods. In addition to corn and sorghum grain, identified by Korschgen (1981) as important winter foods in Missouri for fox squirrels and gray squirrels, respectively, the reproductive structures of shrubs and understory trees may have provided an additional source of food. Within the hardwood sawtimber cover type, correlation analysis indicated that there was a positive relationship between gray squirrel numbers and the importance value (IV) of black gum (Nyssa sylvatica), cherry (Prunus spp.) green ash (Fraxinus pennsylvanica), red elm, and red mulberry (Morus rubra), whereas a negative relationship existed between gray squirrels and dogwood (Cornus spp.) (Table 18). Similar associations occurred between gray squirrels and the IV of tree species in hardwood poletimber. A positive correlation existed with redbud (Cercis

Table 18. Tree species greater than 2.54 cm dbh whose importance values (IV) were correlated with gray squirrel numbers on 14 study areas in Missouri in 1985 and 1986.

Tree Species	Cover Type	r	P
	Hardwood Sawtimber		
black gum		0.78	0.03
cherry		0.82	<0.01
green ash		0.82	0.04
red elm		0.83	<0.01
red mulberry		0.75	0.08
dogwood		-0.78	<0.01
	Hardwood Poletimber		
redbud		0.74	0.08
black oak		-0.77	<0.01

canadensis) and a negative correlation with black oak (Table 18). All of the tree species exhibiting positive relationships with gray squirrels are common subcanopy and shrub species. The seed, buds, and fruits of many of these species have been reported as foods consumed by gray squirrels in Missouri (Korschgen 1981). In contrast, dogwood and black oak, the 2 species negatively associated with gray squirrels, may not have represented important food trees during this study.

Similarly, some of the trees in the hardwood sawtimber and poletimber cover types that are normally considered as important food components of the habitat had an IV that was negatively associated with fox squirrel numbers (Table 19). These included scarlet oak, black oak, mockernut hickory, and white oak. In contrast, many trees considered to provide only supplementary food exhibited positive relationships. Within this group were red elm, redbud, cherry, green ash, and white ash.

These correlations suggest that the abundance of both species was influenced to some extent by the combined effects of relative dominance, density, and frequency of subcanopy and shrub layer vegetation. The negative correlation of subcanopy oak closure with squirrel numbers also tends to indicate that tree species other than the oaks are important during years of poor mast. Because most analyses of squirrel food habits have been conducted during years of fair to good mast production, there is little information concerning the

Table 19. Tree species greater than 2.54 cm dbh whose importance values (IV) were correlated with gray squirrel numbers on 14 study areas in Missouri in 1985 and 1986.

Tree Species	Cover Type	r	P
	Hardwood Sawtimber		
black gum		-0.91	<0.01
cherry		0.86	<0.01
green ash		0.78	0.06
red elm		0.94	<0.01
bitternut hickory		0.76	0.04
dogwood		-0.66	<0.01
redbud		0.85	<0.01
scarlet oak		-0.60	0.11
shagbark hickory		0.69	0.05
white ash		0.70	0.03
	Hardwood Poletimber		
redbud		0.81	0.04
black oak		-0.71	<0.01
mockernut hickory		-0.53	0.07
post oak		0.67	0.04
red elm		0.65	0.10
scarlet oak		-0.62	0.09
white oak		-0.51	0.07

importance of subcanopy trees and shrubs during fall and winter. From this study, however, it appears that the persistent parts of trees in these 2 vegetative layers may provide an important food source not only in spring and summer but also into fall and early winter.

During spring and summer the diet of both species shift depending upon the extent to which the mast of the preceding year has been consumed. During this study, however, there was very low availability of mast and squirrels may have consumed most mast by early spring. This may explain the slightly higher number of both squirrel species on areas where sawtimber and poletimber stands are characterized by moderately dense horizontal structure near the ground and a large occurrence of the woody vine, woody sprout, forb, and grass ground cover types (Table 17). The positive correlations between these variables and squirrel numbers may be in response to the heavy exploitation of this vegetation as a food source during these 2 seasons. This is in agreement with Korschgen (1981), Allen (1943), and Nixon et al. (1968), who stated that the most preferred foods during spring and summer includes grasses, forbs, green plants, green hickory nuts, fleshy fruits, and the leaves, buds, and flowers of various trees.

<u>Fox Squirrel Linear Model</u>

Of the variables correlated with fox squirrel numbers, principal components analysis (PCA) indicated that a subset of 6 variables characterized the habitat conditions preferred by this species (Table 20). When this subset was subjected to an all-possible-subsets regression analysis, the best linear model consisted of the percent occurrence of crop fields (CF), horizontal density (HD) within the sawtimber cover type, and the percent occurrence of litter (LITTER) as ground cover within the poletimber cover type. This model had an adjusted R^2 value of 0.84 ($F = 23.4$ $P < 0.01$). However, residual plots indicated that the latter 2 variables (HD, LITTER) were actually quadratic expressions. When these transformations were performed, the adjusted R^2 value of the 5 variable model

$$\text{Fox Squirrel Number} = 18.62 + 0.12CF - 8.54HD + 0.01HD^2 - 0.31LITTER + 0.0002LITTER^2$$

increased to 0.93 ($F = 32.95$ $P < 0.01$).

Based on the number of fox sqiurrels observed, cluster analysis separated the 14 study areas into 3 groups: high, medium, and low. Bunch Hollow WMA (13) was the only high area whereas Rudolf Bennitt WMA (6) and the Anderson WMA (5.5) comprised the medium areas. The remaining 11 areas, which had observed numbers of less than 2 fox squirrels, comprised the low areas.

The mean values of the 4 qualitative model variables (HD, HD^2, LITTER, and $LITTER^2$) were calculated for each class and compared using LSD tests with a type I error rate of 0.10. For all 4 variables, there were significant

Table 20. Habitat variables identified by principal components analysis as the most important in characterizing fox squirrel habitat following two years of oak mast failure in Missouri.

Cover Type	Variable
Crop Field	occurrence (%)
Hardwood Sawtimber	occurrence (%)
	horizontal density (%)
	overstory canopy closure of shagbark hickory (%)
Hardwood Poletimber	litter ground cover (%)
	understory oak canopy closure (%)

differences between the high and medium classes and high and low classes but not between the medium and low classes (Table 21).

Gray Squirrel Linear Model

PCA indicated that 5 of the 14 variables correlated with gray squirrel numbers best characterized the habitat of this species (Table 22). The best model, as indicated by all-possible-subset and linear regression, consisted of 3 variables: the percent occurrence of the old field (OF) and crop field (CF) cover types and the percentage of ground cover comprised of litter (LITTER) within the poletimber cover type. These variables resulted in the following linear equation

$$\text{Gray Squirrel Number} = 7.15 + 0.18\text{CF} + 0.1\text{OF} - 0.08\text{LITTER}$$

that had an adjusted R^2 value of 0.56 ($F = 6.1$ $P = 0.015$).

Based on the number of gray squirrels observed, the 14 study areas were separated by cluster analysis into 2 groups, high and low. High areas consisted of Bunch Hollow WMA (9), Rudolf Bennitt WMA (9), and the Anderson WMA (8). The remaining 11 areas, all of which had observed numbers of less than 5 squirrels, were considered as low areas. An LSD test showed the mean value of litter ground cover in pole stands on high areas (32.8%) was significantly lower than the mean value (61.7%) on low areas ($P < 0.10$).

Table 21. Means and standard error of the means for the qualitative variables placed in the fox squirrel linear model.

	Class					
	High		Medium		Low	
Variable	$\overline{X}$	SE *	$\overline{X}$	SE	$\overline{X}$	SE
Horizontal Density	53.9	.	35.4	10.8	26.5	1.5
Horizontal Density^2	3269.7	.	1504.7	802.4	872.0	95.0
Litter	34.1	.	32.2	5.5	61.9	4.8
Litter^2	1361.5	.	1277.3	308.3	4213.0	577.1

* Only Bunch Hollow WMA in high class

Table 22. Habitat variables identified by principal components analysis as the most important in characterizing gray squirrel habitat following two years of oak mast failure in Missouri.

Cover Type	Variable
Crop Field	occurrence (%)
Open	occurrence (%)
Hardwood Sawtimber	overstory canopy closure of shagbark hickory (%)
	horizontal density (%)
Hardwood Poletimber	litter ground cover (%)

<u>Summary and Conclusions</u>

In Missouri, Schwartz and Schwartz (1981) found that gray squirrels predominate in the southern and eastern portions of the state where contiguous large tracts of timber occur, while the fox squirrel is more prevalent in the northern and western prairie and agricultural land. During and immediately following poor mast years, however, it appears that the occurrence of both species is slightly higher in areas where timber is interspersed with crops and old fields that provide a source of additional food. Furthermore, the importance of the oak-hickory forest type is lessened to a large extent during these periods. This is exemplified by the small, but significant, negative correlations that existed between the occurence of the hardwood sawtimber cover type and the abundance of both species of squirrels. Nor was there a significant positive relationship between the IV of the oak species within this type and squirrel numbers.

Korschgen (1981) stated that the feeding habits of gray and fox squirrels in Missouri were similar, but the use of foods reflected differences in habitats and foraging behavior. He also stated that gray squirrels occupy dense forest with nearly closed canopies and abundant ground cover, and relied more heavily upon oak and hickory food sources than fox squirrels. In contrast, fox squirrels commonly inhabited more open forest, forest edges, and woodlots, where they supplement oak and hickory mast with important amounts of corn, osage orange, wheat, and other foods that commonly occur in open habitats.

During my study, however, the abundance of both species were correlated to similar habitat conditions indicating that the areas most favorable for fox squirrels during poor mast years also represented the best habitat for gray squirrels. The specific conditions of the timber on these areas include an abundance of ground cover, a high density of vegetation within 1.5 m of the ground, a small amount of understory oak canopy, and a variety of trees that are normally considered to provide only supplemental foods. Based on importance values, preferred trees included shagbark hickory, red mulberry, red elm, redbud, white ash, green ash, and cherry. With the exception of the ashes and shagbark hickory, these trees are mainly understory, or subdominant, trees.

In conclusion, it is difficult to reliably interpret the relationships between habitat conditions and each squirrel species due to the low number of squirrels observed on all areas. However, it is evident that the populations of both species are severely reduced when mast crops are poor in successive years. During these periods, food is likely the limiting factor, particularly winter food. Under these conditions, the welfare of both species appears to be enhanced by the presence of crop fields, old fields, abundant ground cover, and a variety of dominant and subdominant trees that not only includes oak and hickory but also species that normally provide supplemental foods. Management programs that preserve or increase these species will not only improve habitats for year-round use by squirrels but also during periods of low mast availability.

LITERATURE CITED

Adams, C. E. 1976. Measurements and characteristics of fox squirrel home ranges. Am. Midl. Nat. 95:211-215.

Aldrich, J. W. 1963. Geographic orientation of American Tetraonidae. J. Wildl. Manage. 27:528-545.

Allen, A. W. 1982a. Habitat suitability index models: fox squirrels. U. S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.18. 11 pp.

_____. 1982b. Habitat suitability index models: gray squirrel. U. S. Dept. Int., Fish Wildl. Serv. FWS/OBS- 82/10.19. 11 pp.

Allen, D. L. 1942. Populations and habits of the fox squirrel in Allegen County, Michigan. Am Midl. Nat. 27:338-379.

_____. 1943. Michigan fox squirrel management. Mich. Dept. Cons. Game Div. Publ. 100. 404pp.

Armitage, K. B. and K. S. Harris. 1982. Spatial patterning in sympatric populations of fox and gray squirrels. Am. Midl. Nat. 108:389-397.

Backs, S. E. 1984. Ruffed grouse restoration in Indiana. Pp. 37-58 in W. L. Robinson (Ed.), Ruffed grouse management: state-of-the-art in the early 1980's. Proc. Symp. 45th Midwest Fish and Wildlife Conf. St. Louis, MO. 181 pp.

Baker, R. H. 1944. An ecological study of tree squirrels in eastern Texas. J. Mammal. 25:8-24.

Baumgartner, L. L. 1938. Population studies of the fox squirrel in Ohio. Trans. N. Am. Wildl. and Nat. Resour. Conf. 3:685-689.

_____. 1939. Fox squirrel dens. J. Mammal. 20:456-465.

_____. 1943. Fox squirrels in Ohio. J. Wildl. Manage. 7:193-202.

Bennitt, R. and W. O. Nagel. 1937. A survey of the resident game and furbearers of Missouri. Univ. Missouri Stud. 12:1-25.

Benson, B. N. 1980. Dominance relationships, mating behavior, and scent marking in fox squirrels (Sciurus niger). Mammalia 44:143-160.

Berner, A. and L. W. Gysel. 1969. Habitat analysis and management considerations for ruffed grouse for a multiple use area in Michigan. J. Wild. Manage. 33:769-778.

Bezdek, H. 1944. Sex ratios and color phases in two races of ruffed grouse. J. Wildl. Manage. 8:85-88.

Boag, D. A. 1976. Influence of changing grouse density and forest attributes on the occupancy of a series of potential territories by male ruffed grouse. Can J. Zool. 54:1727-1736.

_____. and K. M. Sumanik. 1969. Characteristics of drumming sites selected by ruffed grouse in Alberta. J. Wildl. Manage. 33:621-628.

Bouffard, S. H. and D. Hein. 1978. Census methods for eastern gray squirrels. J. Wildl. Manage. 42: 550-557.

Brown, B. W. and G. O. Batzli. 1984. Habitat selection by fox and gray squirrels: a multivariate analysis. J. Wildl. Manage. 48:616-621.

Brown, C. P. 1946. Food of Maine ruffed grouse by season and cover types. J. Wildl. Manage. 10:17-28.

Brown, L. G. and L. E. Yeager. 1945. Fox squirrels and gray squirrels in Illinois. Illinois Nat. Hist. Surv. Bull. 23:449-536.

Bump, G. 1938. Analysis of certain cover requirements of the ruffed grouse in New York State. Trans. N. Am. Wildl. Conf. 3:818-824.

_____., R. W. Darrow, F. C. Edminster, and W. F. Crissey. 1947. Ruffed grouse: life hisory-propagation-management. New York Conserv. Dept., Albany. 915pp.

Chambers, J. C. and R. W. Brown. 1983. Methods for vegetation sampling and analysis on revegetated mine lands. U. S. Dept. of Agric. Intermountain Forest and Range Expt. Stn. Gen. Tech. Rep. INT-151.

Christisen, D. M. 1983. Mast yields in Missouri. Perf. Rep. Surveys Invest. Projs. Mo. Dep. Conserv. 11 pp.

_____. 1984. Mast yields in Missouri. Perf. Rep. Surveys Invest. Projs. Mo. Dep. Conserv. 11 pp.

_____. and L. J. Korschgen. 1955. Acorn yields and wildlife usage in Missouri. Trans. N. Am. Wildl. and Nat. Resour. Conf. 20:337-357.

Daniel, C. and R. Lamaire. 1974. Evaluating effects of water resource developments on wildlife habitats. Wildl. Soc. Bull. 2:114-118.

Doebel, J. H. and B. S. McGinnes. 1974. Home range and activity of a gray squirrel population. J. Wildl. Manage. 38:860-867.

Doerr, P. D., L. B. Keith, D. H. Rusch, and C. A. Fischer. 1974. Characteristics of winter feeding aggregations of ruffed grouse in Alberta. J. Wildl. Manage. 38:601-615.

Dorney, R. S. 1959. Relationship of ruffed grouse to forest cover types in Wisconsin. Wisconsin Conserv. Dept. Tech. Bull. No. 18. 32pp.

Edminster, F. C. 1954. The ruffed grouse (it's life story, ecology, and management). Macmillan Co., New York. 385pp.

Farmer, A. H., M. J. Armbruster, J. W. Terrell, and R. L. Schroeder. 1982. Habitat models for land use planning: assumptions and strategies for development. Trans. N. Am. Wildl. and Nat. Resour. Conf. 47:47-56.

Flyger, V. 1955. Implications of social behavior in gray squirrel management. Trans. N. Am. Wildl. Conf. 20:381-389.

_____. 1960. Movements and home range of the gray squirrel in Maryland woodlots. Ecology 41:365-369.

Freiling, D. A. 1985. Ruffed grouse brood and nesting habitat. M. S. Thesis, Univ. Missouri, Columbia. 57 pp.

Goodrum, P. 1937. Notes on gray and fox squirrels of eastern Texas. Trans. N. Am. Wildl. and Nat. Resour. Conf. 2:499-504.

_____. 1940. A population study of the gray squirrel in eastern Texas. Texas Agric. Exp. Stn. Bull. 591. 34pp.

Gudlin, M. J. and R. W. Dimmick. 1984. Habitat utilization by ruffed grouse from Wisconsin to West Tennessee. Pp. 75-88 in W. L. Robinson (Ed.), Ruffed grouse management: state-of-the-art in the 1980's. Proc. Symp. 45th Midwest Fish and Wildlife Conf. St. Louis, MO. 181 pp.

Gullion, G. W. 1966. A viewpoint concerning the significance of studies of game bird food habits. Condor 68:372-376.

_____. 1967. Selection and use of drumming sites by male ruffed grouse. Auk 84:87-112.

_____. 1977. Forest manipulation for ruffed grouse. Trans. N. Am. Wildl. and Nat. Resour. Conf. 42:449-458.

_____. 1984a. Managing northern forests for wildlife. Minnesota Agr. Expt. Stn. Publ. No. 13442. 72pp.

_____. 1984b. Ruffed grouse management-where do we stand in the eighties? Pp. 169-181 in W. L. Robinson (Ed.), Ruffed grouse management: state-of-the art in the early 1980's. Proc. Symp. 45th Midwest Fish and Wildlife Conf. St. Louis, MO. 181 pp.

_____. 1984c. Grouse of the North Shore. Willow Creek Press, Oshkosh, WI. 144pp.

_____., R. T. King, and W. H. Marshall. 1962. Male ruffed grouse and thirty years of forest management on the Cloquet Forest Research Center, Minnesota. J. For. 60:617-622.

_____. and W. H. Marshall. 1968. Survival of ruffed grouse in a boreal forest. The Living Bird:7:117-167.

Hale, P. E., A. S. Johnson, and J. L. Landers. 1982. Characteristics of ruffed grouse drumming sites in Georgia. J. Wildl. Manage. 46:115-123.

Hall, E. R. 1981. The mammals of North America. 2nd ed. John Wiley and Sons, Inc., New York. 1177 pp.

Hamilton, W. J., Jr. 1943. Caterpillars as food of the gray squirrel. J. Mammal. 24:104.

Hamor, W. H. 1970. Guide for evaluating the impact of water and related land resource development projects on fish and wildlife habitat. U.S.D.A. Soil Conserv. Serv., Lincoln, Nebraska. 25pp.

Havera, S. P. and K. E. Smith. 1979. A nutritional comparison of selected fox squirrel foods. J. Wildl. Manage. 43:691-704.

_____. and C. M. Nixon. 1980. Winter feeding of fox and gray squirrel populations. J. Wildl. Manage. 44L41-55.

Hicks, E. A. 1949. Ecological factors affecting the activity of western fox squirrels, Sciurus niger rufiventer. Ecol. Monogr. 19:287-302.

Hungerford, K. E. 1951. Ruffed grouse populations and cover use in northern Idaho. Trans. N. Am. Wildl. Conf. 16:216-224.

_____. 1957. Evaluating ruffed grouse foods for habitat improvement. Trans. N. Am. Wildl. and Nat. Resour. Conf. 22:380-395.

Hunyadi, B. W. 1978. Analysis of ruffed grouse habitat in central Missouri. M. S. Thesis. Univ. of Missouri, Columbia. 145 pp.

_____. 1984. Ruffed grouse restoration in Missouri. Pp. in W. L. Robinson (Ed.), Ruffed grouse management: state-of-the-art in the early 1980's. Proc. Symp. 45th Midwest Fish and Wildlife Conf. St. Louis, MO. 181 pp.

Husband, T. P. 1976. Energy metabolism and body composition of the fox squirrel. J. Wildl. Manage. 40:255-263.

Johnsgard, P. A. 1973. Grouse and quail of North America. Univ. Nebraska Press, Lincoln. 553pp.

_____. 1975. North American game birds of upland and shore. Univ. of Nebraska Press, Lincoln. 183pp.

Johnson, R. A. 1928. The fall food habits of the ruffed grouse in the Syracuse area of New York. Auk 45: 330-333.

Kimmel, R. O. and D. E. Samuel. 1984. Implications of ruffed grouse brood habitat studies in West Virginia. Pp. 389-108 in W. L. Robinson (Ed.), Ruffed grouse management: state-of-the-art in the early 1980's. Proc. Symp. 45th Midwest Fish and Wildlife Conf. St. Louis, MO. 181 pp.

King, R. T. 1937. Ruffed grouse management. J. For. 35:523-532.

_____. 1969. Spring and summer foods of ruffed grouse on Vancouver Island. J. Wildl. Manage. 33:440-442.

Knight, D. H. 1978. Methods for sampling vegetation. Univ. of Wyoming, Dept. of Botany, Ark Industries. 87pp.

Korschgen, L. J. 1966. Food and nutrition of ruffed grouse in Missouri. J. Wildl. Manage. 30:86-100.

_____. 1981. Foods of fox and gray squirrels in Missouri. J. Wildl. Manage. 45:260-266.

Krusekopf, H. H. 1962. Major soil areas of Missouri. Univ. of Missouri Agr. Expt. Stn., Columbia. 25pp.

Kubisiak, J. F. 1985. Ruffed grouse habitat relationships in aspen and oak forests of central Wisconsin. Wisconsin Dept. Nat. Resour. Tech. Bull. No. 151. 22pp.

Kurzejeski, E. W. 1979. Habitat utilization and survival of male ruffed grouse. M. S. Thesis. Univ. of Missouri, Columbia. 151pp.

Lewis, A. R. 1982. Selection of nuts by gray squirrels and optimal foraging theory. Am. Midl. Nat. 107: 250-257.

Lewis, J. B. 1971. Ruffed grouse: an indicator of environmental change. Trans. N. Am. Wildl. and Nat. Resour. Conf. 35:196-204.

_____, J. B., J. P. McGowan, and T. S. Baskett. 1968. Evaluating ruffed grouse reintroduction in Missouri. J. Wildl. Manage. 32:17-28.

Ludwick, R. L. J. P. Fontenot, and H. S. Mosby. 1969. Energy metabolism of the eastern gray squirrel. J. Wildl. Manage. 33:569-575.

Marcot, B. G., M. G. Raphael, and K. H. Berry. 1983. Monitoring wildlife habitat and validation of wildlife-habitat relationships models. Trans. N. Am. Wildl. and Nat. Resour. Conf. 48:315-329.

Maxson, S. J. 1978. Spring home range and habitat use by female ruffed grouse. J. Wildl. Manage. 42:61-71.

McGowan, J. D. 1973. Fall and winter foods of ruffed grouse in interior Alaska. Auk 90:636-640.

Missouri Department of Conservation. 1986. Species management plan for the ruffed grouse in Missouri. Jefferson City, MO. 31 pp.

Montgomery, S. D., J. B. Whelan, and H. S. Mosby. 1975. Bioenergetics of a woodlot gray squirrel population. J. Wildl. Manage. 39:709-717.

Moulton, J. C. 1968. Ruffed grouse habitat requirements and management opportunities. Res. Rep. No. 36. Wisconsin Dept. Nat. Reour. 32pp.

Nixon, C. M. 1970. Insects as food for juvenile gray squirrels. Am. Midl. Nat. 84:283.

______., D. M. Worley, and M. W. McClain. 1968. Food habits of squirrels in southeast Ohio. J. Wildl. Manage. 32:294-305.

______., C. M., S. P. Havera, and R. E. Greenburg. 1978. Distribution and abundance of the gray squirrel in Illinois. Ill. Nat. Surv. Biol. Notes. 105. 55 pp.

______. and M. W. McClain. 1969. Squirrel population decline following a late spring frost. J. Wildl. Manage. 33:353-357.

______., M. W. McClain, and R. W. Donohoe. 1975. Effects of hunting and mast crops on a squirrel population. J. Wildl. Manage. 39:1-25.

______., M. W. McClain, and R. W. Donohoe. 1980a. Effect of clearcutting on gray squirrels. J. Wildl. Manage. 44:403-412.

______., S. P. Havera, and L. P. Hansen. 1980b. Initial response of squirrels to forest changes associated with selection cutting. Wildl. Soc. Bull. 8:298-306.

Norman, G. W. and R. L. Kirkpatrick. 1984. Foods, nutrition, and condition of ruffed grouse in southwestern Virginia. J. Wildl. Manage 48:183-187.

Pack, C. J., H. S. Mosby, and P. B. Siegel. 1967. Influence of social heirarchy on gray squirrel behavior. J. Wildl. Manage. 31:720-728.

Palmer, W. L. 1963. Ruffed grouse drumming sites in northern Michigan. J. Wildl. Manage. 27:656-663.

Pietz, P. J. and J. R. Tester. 1982. Habitat selection by sympatric spruce and ruffed grouse in north central Minnesota. J. Wildl. Manage. 46:391-403.

Polderboer, E. B. 1942. Cover requirements of the eastern ruffed grouse in northeast Iowa. Iowa Bird Life 12:50-55.

Porath, W. R. and P. A. Vohs. 1972. Population ecology of ruffed grouse in northeastern Iowa. J. Wildl. Manage. 36:793-802.

Robinson, D. T. and I. Cowan. 1954. An introduced population of the gray squirrel in British Columbia. Can. J. Zool. 32:261-282.

Rusch, D. H. and L. B. Keith. 1971. Ruffed grouse-vegetaion relationships in central Alberta. J. Wildl. Manage. 35:417- 429.

Sanderson, H. R., C. M. Nixon, R. W. Donohoe, and L. P. Hansen. 1980. Grapevines--an important components of gray and fox squirrel habitat. Wildl. Soc. Bull. 8:307-310.

_____., W. M. Healy, J. C. Pack, J. D. Gill, and J. W. Thomas. 1975. Gray squirrel habitat and nest nest tree preference. Proc. Southeastern Assoc. Game and Fish Comms. 29:609-616.

Schamberger, M. and W. B. Krohn. 1982. Status of the habitat evaluations procedures. Trans. N. Am. Wildl. and Nat. Resour. Conf. 47:154-164.

Schwartz, C. W. and E. R. Schwartz. 1981. The wild mammals of Missouri. Rev. ed. Univ. of Missouri Press and Missouri Department of Conservation. Columbia, MO. 356 pp.

Seitz, W. K., C. L. Kling, and A. H. Farmer. 1982. Habitat evaluation: a comparison of three approaches on the northern great plains. Trans. N. Am. Wildl. and Nat. Resour. Conf. 47:82-94.

Settergren, C. and R. E. McDermott. 1972. Trees of Missouri. Univ. Mo. Agr. Expt. Stn., Columbia. 123 pp.

Short, H. L. 1976. Composition and squirrel use of acorns and black and white oak groups. J. Wildl. Manage. 40:479-483.

Smith, D. 1962. The practice of silviculture. 7th ed. John Wiley and Sons, Inc., New York. 578 pp.

Stafford, S. K., and R. W. Dimmick. 1979. Autumn and winter foods of ruffed grouse in the southern Appalachians. J. Wildl. Manage. 43:121-127.

Stauffer, D. F. and S. R. Peterson. 1985. Seasonal micro-habitat relationships of ruffed grouse in southeastern Idaho. J. Wildl. Manage. 49:604-610.

_____ and _____. 1985. Ruffed and blue grouse habitat use in southeastern Idaho. J. Wildl. Manage. 49:459-466.

Stewart, R. E. 1956. Ecological study of ruffed grouse broods in Virginia. Auk 73:33-41.

Steyermark, J. A. 1963. Flora of Missouri. Iowa State Univ. Press, Ames. 1725pp.

Stoll, R. J., Jr., M. W. Milford, P. L. Boston, and G. P. Hanchur. 1979. Ruffed grouse drumming site characteristics in Ohio. J. Wildl. Manage. 43: 324-333.

Svoboda, F. J. and G. W. Gullion. 1974. Preferential use of aspen by ruffed grouse. in southern Appalachia. J. Wildl. Manage. 36:1166-1180.

Sweeney, J. M. 1984. Estimating wildlife production with habitat models. Paper presented at the annual joint meeting of the Western Section of The Wildlife Society and Western Division of the American Fisheries Society, Sacramento, Calif. 12pp.

Talmadge, R. R. 1957. Nesting of ruffed grouse in California. Condor 59:67-68.

Taylor, G. J. 1974. Present status and habitat survey of the Delmarva fox squirrel with a discussion of reasons for its decline. Proc. Southeastern Assoc. Gam and Fish Comms. 27:278-289.

Terrill, H. V. 1941. A preliminary investivation of the fox squirrel. M. S. Thesis. Univ. of Missouri, Columbia. 164 pp.

Thompson, III, F. R., D. A. Freiling, and E. K. Fritzell. 1987. Drumming, nesting, and brood habitats of ruffed grouse in an oak-hickory forest. J. Wildl. Manage. 51:in press.

Titus, R. R. 1976. Habitat utilization by grouse in the Missouri Ozarks. M. S. Thesis. Univ. Missouri, Columbia. 118pp.

Uhr, L. 1964. Pattern Recognition. IBM Med. Symp. 6:305-323

Williams, G. L., K. R. Russell, and W. K. Seitz. 1977. Pattern Recognition as a tool in the ecological analysis of habitat. Pp. 521-531 in Classification, inventory and analysis of fish and wildlife habitat-the proceedings of a national symposium. U. S. Fish and Wildl. Serv., Office of biological Services, Washington, D. C. 604pp.

APPENDIX A

Instructions On the Use of PATREC Models

Appendix A provides an example of the calculations associated with a PATREC model for determining an estimate of potential population density. The PATREC model developed by the Missouri Department of Conservation is used as the example model. The following steps are in reference to the PATREC model worksheet (Table A1).

Step 1. Record the prior probabilities from the ruffed grouse PATREC model (Table A2) in the appropriate labeled 'probability high' and 'probability low'.

Step 2. Record the habitat estimates and corresponding category for each parameter in the 'habitat estimate' and 'parameter category' columns, respectively.

Step 3. Record the appropriate high conditional probability value and low conditional probability value for each habitat estimate.

Step 4. Sequentially multiply all the probabilities in the probability high column and record product at 13H.

Step 5. Sequentially multiply all the probabilities in the probability low column and record producuct at 13L.

Step 6. Sum the products in 13H and 13L and record the answer as the denominator in equations (1) and (2).

Step 7. Record the product of the high probability values (13H) as the numerator in the probability high density equation (1).

Step 8. Record the product of the low probability values (13L) as the numerator in the probability low density equation (2).

Step 9. Perform the division operations as shown in density probability equations (1) and (2).

These values are the respective probabilities that the tract of land has the potential to support high and low population densities.

Step 10. Record the high (C) and low (D) density standards provided in the model (Table A2) at equation (3).

Step 11. Record the probability high (PH) value and high density standard (HDS) value, and the probability low (PL) value and low density standard (LDS) value as indicated in equation (4). Perform the arithmetic operations.

This value is the estimated density potential as based upon the habitat conditions present on the tract of land.

Step 12. Record the tract size (in the same units as used to identify the density standards) and the potential density estimate (DE) in equation (5). The product is the potential population size on this tract of land based upon the habitat conditions.

Table A1. Worksheet for computing potential density estimates from PATREC models.

Species: Ruffed Grouse   Tract Name: Big Barren Creek   Tract Size: 2000 ha

Parameter	Parameter Number	Habitat Estimate	Parameter Category	Prob. High	Prob. Low
Prior Probabilities				0.20	0.80
Percent of area in north and northeast aspects	1	20%	20-30%	0.30	0.30
Percent of area with age class ≤ 20 years	2	10%	5-14%	0.20	0.20
Percent of area in ELT's 1, 2, and 3	3	1%	≤ 2%	0.10	0.60
Percent of area in ELT's 4, 5, and 6	4	8%	5-10%	0.30	0.30
Percent of area in ELT's 4, 5, and 6 with overstory closure ≥ 40%	5	3%	1-5%	0.30	0.30
Percent of area with understory component Codes 5 and 6	6	20%	15-40%	0.20	0.20

13H: 0.0000216   13L: 0.0005184

$$\text{Probability High (PH)} = \left[\frac{13H}{13L + 13H}\right] = \underline{\ 0.04\ } \quad (1)$$

$$\text{Probability Low (PL)} = \left[\frac{13L}{13L + 13H}\right] = \underline{\ 0.96\ } \quad (2)$$

Density Standards: High Density Standard (DSH) = 1/14 ha
Low Density Standard (LSH) = 1/50 ha   (3)

Density Estimates (DE) = PH * DSH + PL * DSL   (4)
= 0.04 * (1/14) + 0.96 * (1/50)
= 0.022/ha

Population potential = Tract size * DE   (5)
= 2,000 ha * 0.022/ha
= 44

Table A2. PATREC model for the ruffed grouse developed by the Missouri Department of Conservation used as an example in the calculation of potential density estimates.

Prior Probabilities:	High: 0.20	Low: 0.80
Population Density Standards (birds/405 ha):	High: 30	Low: 10

PARAMETER	High	Low
I. Percent of area in North and Northeast aspects and colluvial benches (ELT's 7, 18, 25, 51, 52) with site index ≥ 60		
a. ≥30	.60	.10
* b. 20-30	.30	.30
c. <20	.10	.60
II. Percent of area with age class ≤ 20 years and animal habitats 12, 13, 15 and 16 on ELT's 7, 18, 25, 51, 52		
a. ≥15	.70	.10
* b. 5-14	.20	.20
c. <5	.10	.70
III. Percent area in ELT's 1, 2 and 3		
a. ≥5	.60	.10
b. 2-5	.30	.30
* c. ≤2	.10	.60
IV. Percent area in ELT's 4, 5 and 6		
a. ≥10	.60	.10
* b. 5-10	.30	.30
c. ≤5	.10	.60
V. Percent of area in ELT's 4, 5 and 6 with overstory crown closure ≥ 40 % (S-3) and sub-canopy ≥ 60% crown closure (S-4)		
a. >5	.60	.10
* b. 1-5	.30	.30
c. <1	.10	.60
VI. Percent of area with understory component (S-6) Code 5 and 6 and sub-canopy (S-4) ≥ 40%		
a. ≥40	.70	.10
* b. 15-40	.20	.20
c. <15	.10	.70

* hypothetical habitat conditions present on a tract of land being evaluated

Appendix B. Codes for study area names, cover types, and descriptive habitat variables on 13 ruffed grouse study areas in Missouri.

Study Area		Cover Type		Habitat Variables	
Name	Code	Cover Type	Code	Variable	Code
AWRA Compartment 1	AA1	Bottomland Hardwood Sawtimber	BHDW_S	Percent occurrence of cover types	OCCUR
AWRA Compartment 2	AA2	Bottomland Hardwood Poletimber	BHDW_P	Mean canopy height of dominant and codominant trees (m)	CANMN
AWRA Compartment 5	AA5	Upland Sawtimber	ULND_S	Canopy closure of all vegetation greater than 1.5 m in height (%)	CC
Anderson WMA	AND	Upland Poletimber	ULND_P	Horizontal density of vegetation from 0.0 to 1.5 m in height (%)	HDEN
Daniel Boone Forest	BNF	Pine Sawtimber	PINE_S	Woody stems/ha	TSTEM
Compton Creek	CCR	Pine Poletimber	PINE_P	Basal area (m^2/ha)	BA
Cowards Hollow	COH	Open	OPEN	Mean dbh	DBH
Carman Springs North	CSN	Regeneration	REGEN	Trees/ha	TREES
Carman Springs South	CSS	Disturbed	DISTB		
Horton Burn	HBN	Sapling	SAPLIN		
Peck Ranch WMA	PCK				
Sleuter Hollow	SLH				
White Oak Hollow	WOH				

Appendix C. Means and standard errors of the mean for descriptive habitat variables in 10 cover types on 13 ruffed grouse study areas in Missouri during 1985 and 1986.

AREA	COVER_TP	OCCUR	CANMN	SE	CC	SE	HDEN	SE	TSTEM	SE	BA	SE	DBH	SE	TREES	SE
AA1	BHDW_S	2.3	14.1	1.8	92.0	2.3	27.5	2.5	11125.2	767.9	29.2	2.9	19.8	2.0	300.0	54.0
AA1	REGEN	2.5	0.5	0.5	5.0	2.7	62.1	4.8	23667.0	7228.5	1.9	1.2	12.0	.	50.0	.
AA1	DISTB	7.8	6.0	0.6	54.9	8.5	53.4	5.1	19515.4	7781.5	13.7	2.6	18.2	1.0	222.7	53.7
AA1	OPEN	4.2	1.5	1.5	6.0	6.0	56.4	11.2	5000.1	1000.0	3.4	3.4	18.0	3.4	300.0	.
AA1	ULND_P	14.5	11.0	0.7	93.3	1.1	30.5	3.2	5666.7	713.6	31.5	3.1	15.5	0.4	991.7	126.1
AA1	ULND_S	65.6	13.3	0.5	93.5	1.0	33.4	2.0	8057.8	721.6	26.2	1.1	23.6	0.7	378.8	29.8
AA1	PINE_S	2.9	13.0	0.6	83.8	3.2	40.8	6.2	15583.5	4248.5	44.5	5.6	21.6	0.5	875.0	79.3
AA2	BHDW_S	7.6	20.5	4.5	98.5	0.5	35.1	7.4	7166.8	1271.1	35.5	3.5	22.4	1.5	625.0	85.4
AA2	DISTB	19.9	4.0	1.3	66.2	18.9	56.4	11.0	3833.4	790.6	18.3	7.1	16.9	0.6	587.5	156.0
AA2	OPEN	2.8	0.0	0.0	0.0	0.0	52.5	9.6	4000.1	4000.1	0.0	0.0	.	.	.	.
AA2	ULND_P	16.7	12.5	0.8	95.6	1.0	30.1	3.7	4833.4	606.4	32.9	4.0	20.4	0.9	664.3	81.4
AA2	ULND_S	53.0	13.6	0.7	97.0	0.4	34.0	3.4	8066.8	1495.8	32.3	1.6	23.2	0.7	487.5	34.2
AA5	BHDW_S	4.2	15.1	1.3	98.0	0.6	25.9	6.3	4777.8	1528.6	25.2	0.7	19.1	1.5	516.7	44.1
AA5	REGEN	6.6	5.8	5.8	19.0	13.9	59.2	5.9	7166.8	3404.8	6.9	4.8	29.0	7.5	150.0	.
AA5	DISTB	32.0	5.7	1.3	63.9	15.2	50.8	9.3	6333.4	1593.7	21.8	5.6	17.5	0.7	542.9	105.5
AA5	ULND_P	18.6	10.7	0.5	95.5	1.0	34.4	10.4	5833.4	1778.2	37.2	3.1	17.6	0.7	875.0	85.4
AA5	ULND_S	30.4	13.0	1.1	95.3	1.8	34.7	9.9	6083.4	1060.0	31.7	2.9	19.7	1.1	525.0	140.7
AA5	PINE_S	8.1	6.3	2.9	37.3	28.8	65.9	17.3	14889.1	8352.5	19.8	11.4	22.6	1.6	466.7	159.0
AND	REGEN	10.7	17.0	.	62.0	.	69.5	.	14500.2	.	13.7	.	40.0	8.0	100.0	.
AND	DISTB	6.8	7.2	1.7	49.1	13.5	69.2	8.3	16518.7	2836.6	6.1	1.4	20.4	3.1	133.3	16.7
AND	OPEN	3.9	3.6	2.2	3.4	3.4	38.0	8.4	533.3	343.2	0.5	0.5	14.0	.	50.0	.
AND	ULND_P	16.3	10.2	1.2	85.1	4.7	23.1	4.1	7119.1	1016.9	10.3	2.1	15.9	0.6	475.0	113.8
AND	ULND_S	62.3	15.1	0.8	92.8	1.0	19.9	2.3	5305.6	658.9	19.8	1.0	26.5	1.0	258.3	19.7
BNF	REGEN	7.5	1.5	0.1	6.0	4.6	94.3	3.6	25555.9	5710.2	5.7	1.7	32.0	12.0	100.0	.
BNF	DISTB	7.0	2.4	0.4	74.8	18.1	98.2	0.5	64792.6	9843.7	18.6	5.3	15.0	.	50.0	.
BNF	OPEN	1.7	1.5	1.5	5.8	4.8	43.8	14.5	3333.4	2660.6	1.7	1.7	17.8	2.4	250.0	.
BNF	ULND_P	22.8	13.4	0.9	97.1	0.4	31.5	4.6	3041.7	598.2	26.3	2.2	18.3	0.6	550.0	56.7
BNF	ULND_S	61.5	14.6	0.5	94.7	0.8	31.0	2.8	4951.5	431.7	25.8	1.2	22.6	0.6	395.8	29.8
BNF	PINE_P	.	8.8	.	97.0	.	44.4	.	3166.7	.	36.6	.	19.5	1.5	700.0	.
CCR	DISTB	22.5	4.7	0.3	89.3	4.9	77.6	3.7	38271.4	4269.8	19.2	2.2	15.9	1.5	95.0	24.1
CCR	ULND_P	17.4	14.9	0.9	95.7	0.7	25.2	4.9	4486.2	1700.4	28.2	1.8	17.7	0.6	584.6	84.6
CCR	ULND_S	56.0	19.0	0.8	96.1	0.6	23.6	3.9	5436.6	1219.5	27.0	1.4	21.0	0.7	461.9	34.3
CCR	PINE_P	0.7	11.9	0.5	96.0	0.6	46.7	12.5	48056.2	26113.1	46.2	6.4	17.9	0.4	1133.3	88.2
CCR	PINE_S	3.4	24.6	2.7	96.7	0.7	22.2	1.3	6389.0	2575.4	39.7	1.4	24.6	1.5	466.7	83.3
COH	REGEN	13.2	1.8	0.5	30.8	17.2	84.5	12.1	55267.4	14752.5	4.1	1.2	18.0	0.4	150.0	50.0
COH	DISTB	14.1	4.5	0.7	81.0	7.0	73.4	13.3	42708.9	5309.2	16.9	3.0	14.1	0.5	466.7	202.8
COH	ULND_P	11.6	14.9	0.6	95.6	0.6	25.3	4.1	10407.5	1809.7	27.2	2.4	17.0	0.4	1222.2	139.2
COH	ULND_S	61.1	16.4	0.4	91.8	0.9	25.7	2.7	7328.2	785.0	25.5	1.3	19.6	0.3	1103.3	106.4
CSN	BHDW_S	4.9	19.3	2.0	98.3	0.3	43.2	8.8	2416.7	493.0	20.3	3.8	21.7	1.5	475.0	126.7
CSN	OPEN	1.4	3.1	3.1	38.0	27.3	62.3	8.9	5444.5	4028.1	3.1	3.1	14.3	1.7	200.0	.
CSN	ULND_S	90.7	17.6	0.8	97.2	0.5	24.9	2.1	3439.9	339.4	31.4	1.5	20.8	0.4	648.6	35.3
CSN	PINE_S	3.0	15.0	1.0	97.3	0.7	17.9	4.1	4055.6	626.1	44.3	4.5	23.0	1.5	700.0	86.6
CSS	BHDW_P	1.0	20.9	3.3	95.7	0.9	66.6	4.3	3722.3	747.4	16.8	2.0	18.2	1.6	366.7	92.8
CSS	BHDW_S	0.9	24.8	2.6	93.0	2.6	74.6	7.4	15111.3	4426.8	18.7	7.3	26.6	2.5	300.0	76.4
CSS	OPEN	2.9	2.1	2.1	18.8	5.7	70.6	13.3	0.0	0.0	1.7	0.6	.	.	.	.
CSS	ULND_P	14.3	18.4	1.1	96.7	0.9	32.7	5.5	3439.4	622.5	20.4	2.5	17.9	0.7	554.5	51.1
CSS	ULND_S	78.5	16.7	0.9	88.2	3.9	30.8	2.3	2647.7	255.5	21.6	1.7	19.3	0.5	498.5	46.5
CSS	PINE_S	2.3	17.5	2.4	78.3	13.9	57.9	13.9	1388.9	771.8	19.1	2.0	19.8	1.6	416.7	136.4
HBN	REGEN	2.7	1.3	0.4	3.5	1.5	79.6	2.2	20833.6	12166.8	2.3	0.0	16.5	0.5	50.0	0.0
HBN	SAPLIN	43.2	8.0	0.5	89.4	1.9	55.3	3.8	12284.5	1130.3	27.1	1.7	14.9	0.3	476.5	34.9
HBN	DISTB	3.4	5.2	.	99.0	.	58.5	.	16666.9	.	56.0	.	11.5	0.5	100.0	.
HBN	OPEN	1.3	1.1	1.1	0.0	0.0	57.4	6.7	3888.9	3641.8	0.0	0.0	.	.	.	.
HBN	ULND_P	8.7	14.5	1.2	92.5	1.3	26.9	3.5	3833.4	544.3	26.7	2.2	17.4	0.7	733.3	134.0
HBN	ULND_S	27.3	16.6	0.9	92.3	1.2	27.0	3.2	4884.7	730.5	28.4	1.5	20.1	0.8	511.5	78.3
HBN	PINE_P	8.7	10.6	1.4	95.0	0.6	29.3	5.8	3722.3	1348.3	41.4	0.9	15.8	0.5	1016.7	159.0

Appendix C (cont.)

AREA	COVER_TP	OCCUR	CANMN	SE	CC	SE	HDEN	SE	TSTEM	SE	BA	SE	DBH	SE	TREES	SE
HBN	PINE_S	4.7	15.5	1.5	92.3	1.8	33.5	1.4	6222.3	1081.6	40.1	5.2	19.8	1.1	700.0	180.3
PCK	BHDW_P	1.2	15.1	2.2	96.0	1.2	42.3	16.5	10055.7	2874.5	20.2	4.0	15.0	1.3	383.3	33.3
PCK	REGEN	4.1	4.4	2.2	34.8	13.2	81.7	7.3	15139.1	3702.3	6.7	3.7	16.6	1.2	600.0	.
PCK	DISTB	3.2	10.4	2.2	93.8	2.2	54.7	9.0	26146.2	6737.1	18.7	3.3	16.6	1.2	250.0	54.8
PCK	OPEN	5.2	3.6	2.4	22.5	14.8	46.5	8.0	1416.7	877.5	6.5	4.2	18.6	2.7	250.0	50.0
PCK	ULND_P	40.0	15.6	0.9	94.2	0.8	31.9	5.3	7941.3	2203.6	25.9	1.2	17.3	0.5	475.0	36.0
PCK	ULND_S	46.2	19.2	0.6	93.0	0.9	28.8	2.9	3978.3	683.8	25.8	1.2	21.2	0.8	413.0	30.5
SLH	REGEN	7.2	4.6	2.6	31.0	15.5	82.3	12.0	67167.6	19332.4	9.0	6.0	23.5	1.8	650.0	.
SLH	DISTB	21.6	9.0	1.6	75.3	8.3	49.8	6.7	22820.8	5407.6	21.7	3.4	14.3	0.6	285.7	95.6
SLH	ULND_P	15.4	15.4	0.9	91.4	1.5	27.6	4.0	7714.4	1950.7	30.9	2.3	20.1	0.8	528.6	83.0
SLH	ULND_S	52.9	17.8	0.6	91.1	1.0	21.0	2.0	5022.8	934.1	28.8	1.1	23.6	0.7	454.5	43.1
SLH	PINE_S	2.8	21.5	.	91.0	.	27.8	.	7666.8	.	43.5	.	20.8	2.9	650.0	.
WOH	DISTB	20.4	7.2	1.1	70.4	7.7	62.2	7.1	42094.3	10727.0	19.5	2.7	14.8	1.2	166.7	33.3
WOH	OPEN	.	0.0	.	72.0	.	44.0	.	5833.4	.	10.3	.	21.0	2.6	162.5	55.4
WOH	ULND_P	28.8	12.2	0.7	94.6	0.7	29.3	4.3	6344.5	1023.7	27.0	2.1	18.3	0.5	496.7	59.3
WOH	ULND_S	49.0	13.7	0.5	92.2	0.9	27.9	3.0	6420.4	1284.7	29.6	1.5	21.4	0.6	421.2	29.2
WOH	PINE_P	1.8	12.2	0.6	79.3	9.8	29.6	3.6	4555.6	894.1	34.0	7.1	17.7	1.3	783.3	101.4

Appendix D. Codes of study area names, cover types, and descriptive habitat variables for 14 fox squirrel and gray squirrel study areas in Missouri.

Study Area		Cover Type		Habitat Variables	
Name	Code	Cover Type	Code	Variable	Code
AWRA Compartment 1	AA1	Hardwood Sawtimber	HDW_ST	Percent occurrence of cover types	OCCUR
AWRA Compartment 2	AA2	Hardwood Poletimber	HDW_PT	Mean canopy height of dominant and codominant trees (m)	CANMN
Anderson WMA	AND	Pine Sawtimber	PINE_S	Canopy closure of all vegetation greater than 1.5 m in height (%)	CC
Daniel Boone Forest	BNF	Regeneration	REGEN	Horizontal density of vegetation from 0.0 to 1.5 m in height (%)	HDEN
Bunch Hollow WMA	BNH	Cedar	CEDAR	Litter ground cover (%)	LITTER
Compton Creek	CCR	Open	OPEN	Woody stems/ha	TSTEM
Cowards Hollow	COH	Crop Field	CROPS	Basal area (m^2/ha)	BA
Carman Springs North	CSN			Mean dbh	DBH
Carman Springs South	CSS			Trees/ha	TREES
Peck Ranch WMA	PCK				
Panther Spring Hollow	PSH				
Rudolf Bennitt WMA	RUB				
Whetstone Creek WMA	WHT				
White Oak Hollow	WOH				

Appendix E. Means and standard errors of the mean for descriptive habitat variables in 7 cover types on 14 fox squirrel and gray squirrel study areas in Missouri during 1985 and 1986.

AREA	COVER_TP	OCCUR	CANMN	SE	CC	SE	HDEN	SE	LITTER	SE
AA1	CEDAR	4.4	4.8	0.5	47.7	12.5	57.8	6.0	33.9	6.2
AA1	OPEN	5.5	6.3	1.7	46.3	20.9	46.8	12.1	9.3	7.7
AA1	HDW_PT	14.0	9.6	0.8	95.3	0.3	33.0	4.7	48.1	3.3
AA1	HDW_ST	61.5	13.5	0.6	93.6	1.1	32.8	2.7	47.0	3.4
AA1	PINE_S	3.2	12.3	1.1	81.7	5.2	28.3	4.5	44.8	5.8
AA1	REGEN	4.8	0.0	[illegible]	2.3	2.3	56.7	5.2	24.6	7.5
AA2	CEDAR	24.4	3.0	1.0	58.5	22.2	66.3	6.2	25.4	7.9
AA2	OPEN	4.8	0.0	0.0	0.0	0.0	52.5	9.6	1.6	0.0
AA2	HDW_PT	17.4	13.5	0.6	96.2	1.2	26.4	2.7	53.4	7.7
AA2	HDW_ST	53.3	15.0	1.7	96.8	0.5	32.7	4.6	55.3	5.3
AND	OPEN	1.2	9.0	.	0.0	.	31.8	.	16.4	.
AND	HDW_PT	4.0	9.2	1.4	81.5	7.3	28.5	5.4	26.6	9.3
AND	HDW_ST	74.4	13.9	1.1	92.1	1.4	24.7	2.7	39.0	3.1
AND	REGEN	20.4	7.3	3.0	23.8	13.6	85.6	5.4	15.2	5.2
BNF	HDW_PT	21.2	13.2	1.3	97.5	0.3	35.2	6.6	67.6	6.9
BNF	HDW_ST	60.4	14.6	0.7	94.5	0.9	25.2	2.4	65.6	3.0
BNF	REGEN	18.4	2.4	0.4	74.8	18.1	98.2	0.5	54.9	7.4
BNH	CROPS	24.0	0.0	0.0	0.0	0.0	54.2	17.9	11.2	7.3
BNH	HDW_PT	33.5	13.9	2.5	93.1	1.6	54.7	4.9	34.0	5.4
BNH	HDW_ST	42.5	17.6	1.0	95.0	1.0	53.9	7.2	37.9	1.7
CCR	HDW_PT	29.6	14.0	1.0	96.4	1.1	18.9	3.6	86.0	2.6
CCR	HDW_ST	57.2	19.0	1.1	97.6	0.2	21.7	4.5	69.9	6.2
CCR	REGEN	13.2	3.9	0.4	93.0	4.3	83.5	5.3	47.0	7.7
COH	HDW_PT	10.4	15.5	1.6	95.0	1.5	34.5	10.6	50.3	15.9
COH	HDW_ST	80.6	16.8	0.6	92.7	1.2	22.1	2.9	70.6	3.8
COH	REGEN	9.0	2.3	0.2	46.3	25.8	95.4	2.2	35.5	1.4
CSN	HDW_ST	90.4	14.7	0.6	96.1	0.8	20.2	1.9	76.4	5.5
CSN	PINE_S	9.6	15.0	1.0	97.3	0.7	17.9	4.1	86.3	4.3
CSS	OPEN	1.6	0.0	.	2.0	.	90.3	.	0.0	.
CSS	HDW_PT	22.4	14.3	1.0	96.5	1.5	18.3	2.6	76.2	6.4
CSS	HDW_ST	76.0	14.5	1.0	96.6	0.6	21.7	1.9	77.1	2.5
PCK	OPEN	2.8	0.0	.	0.0	.	72.2	.	1.6	.
PCK	HDW_PT	42.4	16.2	0.7	94.4	0.9	32.4	7.7	62.5	6.2
PCK	HDW_ST	41.6	19.8	0.6	92.8	1.2	29.9	3.8	67.2	3.1
PCK	REGEN	10.8	3.1	0.5	52.8	17.3	76.5	4.8	39.7	8.8
PSH	HDW_PT	24.0	16.1	0.6	81.2	14.2	22.9	3.1	65.8	4.1
PSH	HDW_ST	71.6	18.9	0.4	95.6	0.6	24.3	3.3	72.6	3.8
PSH	REGEN	4.4	2.8	0.3	18.7	15.2	99.4	0.1	33.3	3.0
RUB	OPEN	34.4	0.3	0.3	0.0	0.0	53.6	3.7	1.2	0.9
RUB	HDW_PT	38.0	14.8	0.6	92.4	1.5	47.9	3.7	37.7	4.5
RUB	HDW_ST	21.6	17.0	1.9	96.7	0.7	46.2	9.3	27.3	6.3
RUB	REGEN	6.0	2.9	0.2	65.3	20.5	97.4	0.1	18.7	1.6
WHT	CROPS	1.2	.	.	.	.	.	.	.	.
WHT	OPEN	17.2	0.5	0.5	0.0	0.0	51.2	7.1	1.2	0.8
WHT	HDW_PT	39.6	14.6	0.7	81.5	4.2	42.9	2.9	35.0	4.3
WHT	HDW_ST	28.8	14.2	1.2	87.5	2.7	33.7	6.4	41.8	9.3
WHT	REGEN	13.2	1.8	0.1	0.3	0.3	71.1	7.4	2.7	2.7
WOH	OPEN	2.0	11.9	1.4	69.5	14.5	52.6	10.7	18.0	1.7
WOH	HDW_PT	36.8	12.5	1.1	94.3	1.1	15.2	5.3	74.5	4.0
WOH	HDW_ST	61.2	13.9	0.8	90.9	1.3	26.9	4.4	56.2	8.1

Appendix E (cont.)

AREA	COVER_TP	TSTEM	SE	BA	SE	DBH	SE	TREES	SE
AA1	CEDAR	10111.2	894.1	12.2	4.6	16.6	1.5	266.7	92.8
AA1	OPEN	11833.5	5457.8	8.0	1.1	21.7	2.7	200.0	50.0
AA1	HDW_PT	6500.1	917.9	37.0	1.9	15.1	0.5	900.0	189.3
AA1	HDW_ST	7678.7	853.3	25.1	1.9	22.9	1.1	346.4	40.8
AA1	PINE_S	8222.3	2642.9	55.7	3.3	19.9	0.6	1000.0	50.0
AA1	REGEN	8222.3	3646.9	3.8	2.0	.	.	.	.
AA2	CEDAR	4500.1	548.6	12.0	4.1	17.3	0.8	433.3	33.3
AA2	OPEN	4000.1	4000.1	0.0	0.0	.	.	.	.
AA2	HDW_PT	4366.7	762.7	37.3	3.3	21.4	1.1	760.0	76.5
AA2	HDW_ST	8309.6	2162.2	34.3	2.2	22.4	0.8	535.7	36.1
AND	OPEN	1666.7	.	0.0	.	14.0	.	50.0	.
AND	HDW_PT	6000.1	1043.1	8.6	1.7	14.9	0.6	350.0	119.0
AND	HDW_ST	5416.7	664.3	17.7	1.1	25.4	1.3	264.3	31.2
AND	REGEN	16791.9	4296.6	8.0	1.5	19.5	4.3	100.0	0.0
BNF	HDW_PT	3458.4	758.8	23.8	2.8	17.9	0.9	575.0	66.1
BNF	HDW_ST	4551.3	494.1	25.5	1.7	23.6	0.8	400.0	37.6
BNF	REGEN	64792.6	9843.7	18.6	5.3	15.0	.	50.0	.
BNH	CROPS	1433.4	1433.4	0.2	0.2	.	.	.	.
BNH	HDW_PT	9646.0	1835.9	32.2	1.5	16.8	0.5	762.5	121.7
BNH	HDW_ST	11166.8	2790.7	25.8	3.4	25.2	1.7	493.8	53.8
CCR	HDW_PT	2381.0	450.9	27.0	2.2	17.2	0.6	757.1	109.9
CCR	HDW_ST	4257.6	759.6	25.4	1.7	21.4	1.1	404.5	34.0
CCR	REGEN	35611.6	3640.0	19.7	2.9	16.9	2.8	150.0	76.4
COH	HDW_PT	13778.0	4770.1	24.8	1.4	18.3	0.9	900.0	152.8
COH	HDW_ST	6774.6	830.0	26.9	1.7	19.5	0.4	1076.5	127.8
COH	REGEN	76389.9	9673.7	4.6	2.0	15.5	1.4	100.0	0.0
CSN	HDW_ST	4210.6	395.1	35.7	1.9	21.1	0.5	684.2	47.6
CSN	PINE_S	4055.6	626.1	44.3	4.5	23.0	1.5	700.0	86.6
CSS	OPEN	0.0	.	0.0	.	.	.	.	.
CSS	HDW_PT	4208.4	1143.4	27.5	4.5	19.4	1.5	525.0	77.7
CSS	HDW_ST	3460.8	360.3	27.9	2.1	19.6	0.7	668.8	66.1
PCK	OPEN	333.3	.	0.0	.	.	.	.	.
PCK	HDW_PT	7333.4	3051.0	25.3	1.0	16.5	0.5	568.8	47.2
PCK	HDW_ST	3819.5	777.6	27.2	1.6	20.7	0.9	445.8	39.1
PCK	REGEN	17633.6	2466.1	6.2	3.9	11.5	0.5	100.0	.
PSH	HDW_PT	5250.1	1320.6	30.5	1.7	17.2	0.6	850.0	91.3
PSH	HDW_ST	3738.1	504.5	29.7	1.7	19.6	0.7	557.1	39.2
PSH	REGEN	39722.8	5342.4	5.7	5.2	.	.	.	.
RUB	OPEN	95.2	95.2	0.3	0.3	.	.	.	.
RUB	HDW_PT	8037.1	1449.2	24.9	2.3	17.8	0.5	788.9	98.2
RUB	HDW_ST	7944.6	873.1	23.7	6.8	23.3	1.1	462.5	178.4
RUB	REGEN	52334.1	9311.1	13.4	4.9	12.5	0.5	100.0	.
WHT	CROPS	.	.	.	.	.	.	.	.
WHT	OPEN	17875.2	10353.0	0.0	0.0	.	.	.	.
WHT	HDW_PT	6687.6	1107.1	20.9	2.3	21.2	0.9	393.8	48.6
WHT	HDW_ST	6444.5	2453.9	26.0	1.8	23.7	1.1	408.3	50.7
WHT	REGEN	18444.7	6818.1	0.0	0.0	.	.	.	.
WOH	OPEN	38083.9	1416.7	17.7	4.0	18.1	1.7	250.0	50.0
WOH	HDW_PT	4285.8	1141.9	26.0	2.5	21.3	0.9	392.9	55.0
WOH	HDW_ST	8410.4	2018.5	29.2	2.3	21.6	0.9	403.8	44.4