

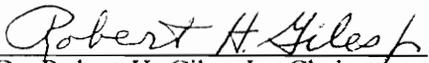
**Floral Richness Inventory of an  
Eastern U. S. Forest**

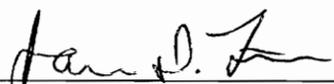
by

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**FLORAL RICHNESS INVENTORY OF AN  
EASTERN U. S. FOREST**

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(ABSTRACT)

Two watersheds on the southern end of Havens State Wildlife Management Area, Roanoke County, Virginia, were sampled for vascular plant species richness. Two-hundred and forty-eight species were identified. Three methods of sampling for species richness in eastern forests were compared: timed-search meanders, belt transects, and plots. Meanders and transects located more species in the same amount of time as plots. Plot sampling encompassed only two-thirds of the richness known from the site.

Species-area and species-effort relationships were described by exponential models (number of species =  $\ln(\text{area} + 1)$ , and number of species =  $\ln(\text{time} + 1)$ ). Models were used to predict numbers of species which might have been found had more area been sampled or had more time been spent searching. Species-area models yielded more conservative, and probably more accurate, predictions than species-time models. Predictions of species numbers were reasonable for areas as large as 60 ha, but were rather large for areas the size of Havens (2800 ha).

Sufficiency of search effort was judged using species-area and species-effort curves. However, it was difficult to tell whether the curves approached horizontal or not. Therefore, this was not a good technique to judge sampling adequacy.

Species composition observed by each of the three methods was different. Composition of species lists was 65% similar between meanders and transects, and only 51-58% similar between plots and other methods. These figures were within an expected range. A combination of two methods or repeated meanders was recommended in order to identify a higher proportion of the species present.

Seasonal and observer differences, and the effect of learning and taxonomy on richness estimates were discussed.

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# INTRODUCTION

Eastern deciduous forests are among the most species-rich ecosystems in North America. The floral composition of mixed hardwood stands, and even of oak forests, may include as many as 40 vascular plant species in a 0.1 ha quadrat (Whittaker 1965). By comparison, some high elevation spruce and fir stands have only 5 to 15 species in a similar area. Other plant communities, such as desert grasslands, rich desert communities, and forests, have 15 to 35 species in a comparable area (Whittaker 1965).

This thesis is about a floral inventory of an eastern mixed hardwood forest and about methods which can be used to complete inventories of vascular plants. A floral inventory is a catalog of an extensive study of the flora of an area. It may include locations and assessments of rare, threatened, and endangered plant populations. Inventories of plant communities are important tools in assessing, maintaining, and managing biological diversity.

Biological diversity is important for several reasons. In this introduction, I shall discuss how biodiversity may be defined, why it is important, where to look for it, and how to assess it. Diversity has proven to be a complex concept to define and measure (Hurlbert 1971, Whittaker 1972, Hill 1973). Functional, structural, spatial, temporal, and genetic aspects have been considered as important contributors to understanding biological diversity (Zedaker 1991). To clarify, biodiversity can be seen as a triad of species, habitat, and genetic diversity (Westman 1990) changing over time.

## **Genetic Diversity**

It is beyond the scope of this thesis to address the estimation of genetic diversity. However,

assessment of genetic variation within and among populations can be an important input to management decisions. For example, populations of *Trillium grandiflorum* were found to be more genetically diverse near their center of distribution than at the periphery of their range (Hoppe et al. 1992). A land manager or owner may use this information to decide to concentrate management efforts on genetically more diverse populations.

Genetic analysis can be used to interpret delineations between species (Baskauf et al. 1992). Some researchers may delineate species based on morphological and genetic analysis. Others would choose to call the putative species a subspecies, a variety, or not to assign it any differential status. Such genetic analyses and taxonomic decisions affect species diversity estimates by raising or lowering the estimated number of species present.

### **Species diversity**

Species diversity has been described by a number of indices and models (Simpson 1949, Shannon and Weaver 1949, Preston 1962, Hurlbert 1971, Whittaker 1972, Peet 1974, May 1975, Pielou 1975, Patil and Tailie 1982, Palmer 1991, and McMinn 1991), many of which use both the number of species present (species richness) and the number of individuals per species (evenness). Some researchers have assigned evenness a high value in the measurement of diversity (Shannon and Weaver 1949). In contrast, Zedaker (1991) stated that it is a value judgement to say that evenness is good; the rare will not be abundant by definition. Also, in a typical plant community, 10% of the species are common, 25% are of intermediate abundance, and 65% are rare in occurrence (Ugland and Gray *in* Magurran 1988:24). That is, rareness is a natural phenomenon and evenness may be only a human construct and value. Additionally, a community with few species and high evenness could have the same diversity, as calculated with an index, as a community with many species and low evenness (Pielou 1977). These communities are different in character, and may be in function and stability as well.

Species number (richness) is the simplest, oldest, and most fundamental measure of diversity (Peet 1974). Peet has also called richness the least ambiguous of diversity terms. Green (1979) also recommended the use of species number or a simple index based on species number and abundance

( $d = (s-1)/\log N$ ). He stated that the relationship between diversity and stability has been uncertain, and questioned what ecological phenomena diversity indices were actually measuring.

Admittedly, species counts have limitations. One limitation is that species counts are dependent on sample size. Generally, the greater the area searched or effort expended, the larger the number of species observed. Because it is virtually impossible to determine the complete composition of a community, richness is often measured as the number of species in samples of an arbitrarily chosen constant size. In order to have a richness index independent of sample size, two things must be known. First, the functional relationship between number of species per sample unit and the number of individuals per unit must be known. Peet (1974) stated that knowledge of this relationship is rare. Second, the relationship must be constant among the communities studied. This phenomenon may also be rare. Therefore, direct species counts can be compared among communities only if sample sizes are equal.

### **Habitat Diversity**

Habitat diversity is the variety of habitats present at a local, regional, or global scale. Habitat has been defined in the ecological literature as "the range of environments in which a species occurs," (Krebs 1985:256) or "any part of the earth where a species can live . . . each habitat is assumed to have suitability for that species" Krebs (1985:64-65). This species-oriented definition is appropriate to discussion of habitat diversity if one's interest is in preserving niches for all species. In fact, this definition of habitat is very similar to the niche concept -- that an organism or a species can exist within a bounded range of environmental conditions. Habitat diversity on a species scale is habitat diversity on a local scale.

Additionally, habitat can be defined to include more than populations on a local scale. Miller (1986:29,53) defined habitat as a "place where an organism lives" or an organism's "address." Here, habitat is the abiotic environment that "houses" populations or communities. Communities are defined loosely to be a collection of organisms arranged in time and space so as to have an influence upon one another and their environment (Mueller-Dombois and Ellenberg 1974). The community of organisms and the environmental factors that support it are called an ecosystem (Daubenmire 1968). Spurr and Barnes (1980) also defined "ecosystem" as a complex system of living organisms

and their abiotic environment. An ecosystem includes the relations of organisms with one another and with their abiotic environment. For example, a forest ecosystem "is a complex of trees, shrubs, herbs, bacteria, fungi, protozoa, arthropods, other invertebrates of all sizes, sorts, and descriptions, vertebrates, oxygen, carbon dioxide, water, minerals and dead organic matter that in its totality constitutes a forest. Such a complex never does and never can reach any balance or permanence. It is constantly changing both in time and in space (Spurr and Barnes 1980:366-367)."

Ecosystems may be large or small. When ecosystems are viewed at a large scale, such as an eastern oak-hickory forest, the scale under consideration is regional. However, ecosystems may also be quite small, or on a local scale. One can think of a small pond as being an ecosystem that is different from the terrestrial system around it. Or one may choose to consider a matrix of ponds and surrounding land as a wetland ecosystem. Scale is in the eye of the beholder. In this thesis, the term "habitat" will be used to refer to all aspects of the environment that affect the distribution of a species. In other words, habitat will be used in the context of a local scale. The term "ecosystem" will be used to describe the environment and biota on a community scale. Ecosystem diversity is an important contributor to global biodiversity. Within ecosystems, habitat variation contributes to species diversity.

### **The Importance of Biological Diversity**

Despite difficulties in defining biological diversity, there is a growing public will to preserve it. Since 1900, Congress has passed 28 federal acts proposing to maintain biological diversity (Office of Technology Assessment 1987). This list of legislation includes the Wilderness Act of 1964, the Wild and Scenic Rivers Act of 1968, the Endangered Species Act of 1973, the Federal Land Policy and Management Act of 1976, the National Forest Management Act of 1976, and the Public Rangelands Improvement Act of 1978. More recent examples of efforts to preserve diversity include a proposed biodiversity act in the U.S. Congress of 1992 and the World Biodiversity Congress in Rio de Janeiro, Brazil.

Species-rich areas are of special interest to the public for the following reasons. Biologically diverse areas are important resources for recreation, teaching, research, and aesthetic purposes. Aesthetic purposes may include photography, painting, and nature writing. McMinn (1991)

mentioned improvements in human health gained through direct contact with animals and the viewing of natural landscapes.

Human health may also be affected by the diversity of plant species. Plants were the first pharmaceuticals developed, and they continue to provide models in pharmaceutical research (Ehrenfeld 1988). One hundred and nineteen pure substances extracted from plants are used in medicines throughout the world. Twenty-five percent of all prescriptions dispensed in the U.S. contain active compounds extracted from higher plants (Farnsworth 1988). In addition, the preservation of plant species diversity has been advocated for the discovery of new food sources, for cross breeding to improve existing crop species, for use as natural pesticides, and for sources of fiber for construction and clothing (Plotkin 1988, McMinn 1991).

Norton (1988) talked about the amenity value of diversity. Amenity value is the perceived improvement in the quality of human life due to the existence of a species. For example, the sight of a rare wild flower or the pleasure derived from watching a bald eagle fishing are benefits of maintaining species diversity. Species diversity has option value, as well. That is, potential or expected gains in knowledge at some future time may lead to valuation of a currently unvalued species (Norton 1988). In addition, species-rich natural systems provide life support functions such as water and nutrient cycling, soil formation, flood amelioration, and provision of materials for food and shelter (McMinn 1991). Such natural systems serve as models for restoration projects.

Diversity may have beneficial effects on the productivity of ecosystems as well. For example, tropical and temperate rainforests and freshwater wetlands are examples of ecosystems that are both highly diverse and productive. However, exceptions to this generalization certainly exist. Estuarine wetlands are ecosystems in which biomass produced per unit area is very high, but species diversity is low. That is, one species dominates the system by its abundance, and few other species are present.

Diversity may or may not contribute to ecosystem stability. Stability can be defined as the ability of a system to withstand or absorb perturbation. Pielou (1975:130) argued that in mathematical models of communities, "the larger the number of species, the narrower the permissible ranges for the various parameters (interaction coefficients) if the system is to be stable." Pielou concluded that in stable systems either species interaction coefficients were within a narrow

range, or more likely, environmental stability caused the community stability that allowed for diversity.

McNaughton (1978) argued that mathematical models of communities needed to be tested with real data. He concluded that for grassland communities, more diverse ecosystems were more stable than less diverse ones. He interpreted species organization as occurring in small guilds, and concluded that interaction strength and connectance among species declined as diversity increased. Therefore, interaction coefficients in mathematical models remained within a narrow range and were not sensitive to increases in diversity.

Some people believe that biological diversity has value for its own sake. That is, its value is not dependent on roles it plays in ecosystem function or human health. Ehrenfeld (1988) discussed the value of diversity as not being dependent upon the properties of the species in question, the uses to which a species may be put, or a species role in the balance of ecosystems. For advocates of biological diversity, he says, its "value is self evident." That is, the value of biological diversity is in its current existence.

The functions and values of biodiversity will probably never be known completely and may be argued over indefinitely. But the public has demonstrated an interest in stabilizing biodiversity through the legislative process. Therefore, estimates of biodiversity are needed in order to manage for it.

### **Where to Look for Diversity**

In order to predict or explain diversity and to search the landscape efficiently, it would be useful to know about the relationship of species richness to environmental factors. Yet, there are few generalities about the relationship between richness and environment upon which biologists agree. An increase in species richness with a decrease in latitude may be one of the few (Whittaker 1965, Buzas 1972). In addition, most agree that diversity is lower on remote, small islands (MacArthur and Wilson 1967). Diversity may increase with productivity, but it declines in the most productive systems (Pimm and Gittleman 1992). Some desert systems have been noted for great diversity, yet they are known for relatively low productivity (Whittaker 1965, Pimm and Gittleman 1992).

The effect of moisture on diversity has been debated. Terbourgh (1973) concluded that in temperate North America the mesic range has greater species diversity than either wetter or drier areas. This opinion is contradicted by Whittaker (1965), Daubenmire and Daubenmire (1968), Zobel et al. (1976), Bell (1978), and Peet (1978). For example, Peet (1978) concluded that the most mesic, centrally-located Rocky Mountain forests had the lowest diversity of forest stands which varied in elevation, site moisture, and successional stage. The environmentally more severe sites had relatively high diversity, especially at the forest-grassland transition and in low elevation riparian forests. These observations may be more related to disturbance or transition than moisture, however.

Zobel et al. (1976) found greater diversity of herbaceous species on dry forest sites than on mesic sites in the Oregon Cascades, as did Daubenmire and Daubenmire (1968). The richness-dryness relationship was assumed to be related to a sparse canopy which allowed greater light penetration. Also, the presence of fewer trees meant less competition for nutrients and less potential for allelopathy. Whittaker (1965) showed that the species diversity of vascular plants in some desert areas is the richest in North America. Bell (1978) concluded that there was no correlation between moisture and richness.

Diversities of different strata (tree, shrub, herb) vary under different moisture regimes. Peet (1978) found tree species diversity highest in wet, middle or high elevation stands, and poorest at mesic middle and low elevations and xeric high elevation stands of the Colorado Rocky Mountains. As with trees, shrub diversity was highest in wet-mesic, mid-elevation stands, but unlike with trees, shrub diversity declined with elevation. There was a negative correlation between tree and shrub diversity and a positive correlation between shrub and herbaceous species cover. Herbaceous species were less diverse under heavy, light-preempting canopy.

In temperate zone forests, species diversities of vascular plant communities are affected most by richness in herbaceous species (Whittaker 1965). High diversities occur under conditions favoring herbaceous growth (open canopy, at least seasonally) such as in cove forests, open woodlands (drier ones), and in serpentine soils. Conversely, hemlock and red oak sites are low in species number. Needle litter, tannins, humus type, and allelopathy may affect herbaceous species diversity and growth adversely.

Species diversity may increase with disturbance, and it has been observed to decrease with canopy closure (Zobel et al. 1976, Peet 1978). Loucks (1970) also observed declines in diversity and productivity as the canopy closed. He observed a peak in species diversity in mesic forests 100 or 200 years following the beginning of secondary succession. He concluded that diversity is maintained by natural disturbances every 50 to 200 years. That is, the overlap of early, middle, and late successional species creates a species-rich environment. Parker and Ward (1988) also noted an increased diversity in post-disturbance forests.

Species diversity has been reported to decrease with increasing elevation (Whittaker 1956, 1960; Peet 1978). In dryer areas, diversity may peak at mid-elevation (Whittaker and Niering 1965, 1975; Daubenmire and Daubenmire 1968). Such sites may have been dry enough to inhibit a closed canopy. However, species diversity may be very high in high-elevation sites. Species diversity and the occurrence of rare plants is high in the Southern Appalachian Mountains because these areas are refugia. Several species reach their northern limit of distribution there (White et al. 1984). Other species reach their southern limit of distribution in the Southern Appalachian Mountains. In Virginia, for example, 49 plant species that are threatened, endangered, or of special concern reach their southern limits of distribution in the mountains, while 17 reach their northern limits (Porter and Wieboldt 1991).

Aspect also affects species diversity. Van Eck (1962) found species composition varied between north- and south-facing slopes. Some species were common to both, and some were not. He found more herbaceous species on northern exposures than on southern ones at three out of four sites. Aspect probably influences species distribution because it influences moisture regimes. Southern and western exposures experience higher solar incidence and evaporation rates, thus favoring the growth of some species and discouraging the growth of others.

In addition to topography and moisture regimes, availability of a seed source affects species occurrence and diversity. Proximity to a seed source was an important factor in reestablishment of vegetation at Kilauea, Hawaii, after a volcanic eruption (Smathers and Mueller-Dombois 1974). McClanahan (1986) also concluded that distance to a seed source was the best predictor of regeneration of late-successional forest species. The lack of a seed source resulted in arrested succession at some sites. The availability of dispersed seed is particularly important in disturbed

areas. Quality and quantity of seed rain, or surficial deposition, affected colonization of an Alaskan river floodplain (Walker and Chapin 1986). Since there was no evidence of a seed bank at the site, early establishment of willow and poplar was judged to be the result of high seed rain and receding water levels.

Reestablishment of vegetation at disturbed sites is also dependent on species represented in the seed bank. Regeneration of oak savannahs, prairie remnants, and wetland vegetation has been credited to longevity of seed viability in seed banks. In addition, the presence of residual plant growth serves as a source for recolonization of species which resprout and spread vegetatively.

Fertility and succession affect diversity. Peet and Christensen (1988) defined four states of forest succession: establishment, thinning, transition, and steady state (or "climax"). As forests progressed through these states, species number remained constant on fertile sites, and then increased in the steady state. On infertile sites, species numbers increased through the establishment, thinning, and transition phases, and decreased in the steady state phase. Peet and Christensen also concluded that forest herbs and shrubs exhibited an increase in richness with an increase in fertility.

Considering that few generalizations about environmental factors and their effect on species diversity can be made, it is necessary to search many different habitats in order to maximize species diversity estimates on a local scale. Habitats may be thought of as changing levels of a combination of environmental gradients such as temperature, moisture, solar radiation, mineral availability, etc. For example, Whittaker (1956) discussed differences in species occurrence and abundance in relation to a moisture gradient in his study of the vegetation of the Great Smoky Mountains. He found that species composition changed as environment changed. In addition, relative proportions of species changed continuously along the moisture gradient. Hack and Goodlett (1960) also concluded that the distribution of some tree species, as well as shrub and herbaceous cover, was closely related in their local distribution to moisture conditions. They enumerated topographic factors affecting moisture and vegetation such as slope position, landform, soil texture, aspect, elevation, and geologic structure. Mowbray and Oosting (1968) found soil texture influence on soil moisture to be a key factor in tree species growth and abundance. Travis (1982) regressed species occurrence on elevation, lithology, landform, slope position, steepness, exposure, and soil depth.

She concluded that different site factors best explained the distribution of different species. Fies (1983) predicted forest cover type with 57% to 78% accuracy using elevation, slope, slope shape, and aspect. Many other studies have related species occurrence to topographic features (Table 1).

Habitats can also be conceived as occurring in large patches or areas that are describable in terms of physiography, geology, soil type, climate, and so on. For example, Cooperrider and Thorne (1964) searched 18 different habitat types and found 1027 species in Giles County, Virginia. The habitat types included shaley slopes, limestone bluffs, rich woods (calcareous soils), sandstone ledges, mountain chaparral, sphagnum bogs and swamps, white pine forests, alluvial stream margins, and disturbed areas.

Johnson-Groh (1985) associated a rich and relictual flora associated with unusual geologic features of Ledges State Park in central Iowa. She found 437 species in 447 ha. The unusual topography and microclimate created a refugium for species from more northern and eastern climes.

The park's dissected topography contrasts sharply with the surrounding flat agricultural land, allowing an unusual assemblage of plants to exist within the various microhabitats of the park. The large number of eastern and northern species found at the Ledges State Park is unusual in central Iowa. ...

The Pennsylvanian sandstone ledges, for which the park was named, are the most prominent geological feature of the main canyon.

Several other smaller drainages empty into Pease Creek and the Des Moines River, creating a complex of steep ravines and well-drained ridges (Johnson-Groh 1985:129).

In this study, different habitats within a defined area were thoroughly searched in order to estimate species richness. If different habitat types were not obvious, different aspects and elevations were searched.

### **Sampling for Diversity (or How to Look for it)**

Identifying rare species is very important in efforts to protect endangered populations. Of the

20,000 species of vascular plants in the United States, 1,200 are threatened, 750 in danger of extinction, and approximately 100 have been extirpated (Goff et al. 1982). To sample plant communities, some type of quadrat has typically been used (Cain and Castro 1959, Mueller-Dombois and Ellenberg 1974). However, when it is important to know the complete species composition of an area, as in surveys for rare and special status plants, quadrat sampling may not be sufficient. For example, a species-area curve for a rich oak forest did not level off even after 100 quadrats had been sampled (Magurran 1988). Quadrat sampling may not identify total species composition of an area because the use of quadrats is time consuming. For example, Kirby et al. (Magurran 1988:52) observed that sampling with 18 200-m<sup>2</sup> plots yielded fewer species than six hours spent doing walk surveys.

One problem in searching an area for rare plants is to determine when enough time has been spent sampling or when enough area has been searched. There are problems with using species-area curves to determine search sufficiency. That is, species richness is dependent upon the amount of area searched. In rich areas, species-area curves may not level off before an exhaustive number of quadrats has been used (Magurran 1988).

Rather than using species-area relationships, Goff et al. (1982) used species-effort (number of species vs. time) curves to judge whether enough time had been spent searching a defined area. The area was searched in a thorough manner until no new species were discovered in 30 minutes. The number of species discovered per minute were recorded. Species-effort curves were used to judge search sufficiency. If curves leveled off, no new species had been found in 30 minutes, and the investigator felt the area had been thoroughly searched, a high level of confidence was assigned to the completeness of the species list.

One purpose of the present study was to compare methods of estimating species richness. I compared species richness and composition estimates made by using three methods: a timed-search meander (walk survey), belt transects, and plots. Time-efficient methods for detecting the highest proportion of species present in an area are important because time and funding to do such work are limited. Yet complete floras, or special searches in addition to quantitative sampling, will remain necessary to locate and protect rare, threatened, and endangered populations.

In addition, ways to judge search sufficiency were evaluated. In other words, this thesis addresses the issue of how much searching is enough. Also, species-area and species-effort relationships were modeled to estimate additional yields in richness with additional search effort. Seasonal and learning effects are discussed as well as between-observer differences.

## STUDY AREA

The study area lay almost entirely within the boundaries of Havens Wildlife Management Area. Havens is a 2800 ha area owned by the Virginia Department of Game and Inland Fisheries. The area is located on Fort Lewis Mountain between route 622 and Interstate 81, west of Salem, Virginia. The approximate latitude and longitude are 37° 20' and 80° 10', respectively. A small subarea of Havens was selected on which to demonstrate and compare different methods used to estimate species richness. The area selected was comparable in topography to many of the watersheds at the southwestern end of Havens. The watersheds on the northwest side were characterized by steep spur ridges at high elevations and narrow drainages. The watersheds on the southeast side were gently sloping near the ridgetop and narrowed into steep drainages at approximately 800 meters (Figure 1).

The study area included one 43 ha watershed on the northwest-facing slope of Fort Lewis Mountain and a 18 ha portion of the watershed on the opposite, south-east facing slope for a total of 61 ha (Figure 1). Areas comparable in width were sampled on the northwest- and southeast-facing slopes. Only the upper half of the watershed on the southeast-facing slope was sampled because the lower part of the watershed was private land. Some private land, owned by Dr. Robert H. Giles, Jr., at the base of the northwest-facing slope was included in the study.

Fort Lewis mountain is a part of the Ridge and Valley Physiographic Province. The province is characterized by a series of parallel ridges that run northeast to southwest and are separated by narrow valleys (Wood 1944). The main ridge and spur ridges at Havens are mostly northwest- and southeast-facing. The area is mainly mixed oak forest with stands of *Pinus rigida* and *Pinus pungens* on southwest slopes (Giles 1988). Elevation ranges from 430 m (1400 feet) to 985 m (3200 feet).

The average annual precipitation is 103.5 cm, with average annual snowfall of 57.4 cm. Precipitation ranges from 65.3 cm to 112.5 cm per year. The average minimum temperature is 16.8° C. and the average maximum is 28.5° C. The lowest and highest recorded temperatures, respectively, are minus 22° C and 38.3° C. The temperature has never exceeded 32.2° C for more than 9 days, but has dipped below freezing for 100 consecutive days. The growing season is 178 days (Giles unpublished).

Havens, and almost the entire Ridge and Valley Province of the Eastern United States, has been dominated in recent times by an oak-chestnut forest association. "Here, oaks and (formerly) chestnut are so abundant in most situations as to characterize the region. Various oak, oak-chestnut, and oak-chestnut-tuliptree communities occupy the climax sites. Mixed mesophytic communities, if they occur at all, are generally confined to coves and lower ravine slopes" (Braun 1950:192).

The character of oak-chestnut forest has been notably affected by the chestnut blight of this century. Chestnut no longer dominates, but appears to have been replaced by various oak associations. In this part of the Ridge and Valley Province, replacement of chestnut by chestnut oak, red oak, and scarlet oak is common (Stephenson 1970). Chestnut stems appear in the forest as root sprouts, but they rarely attain mature status.

The oak-association forest meets mixed mesophytic and hemlock-white pine-northern hardwood associations along its northern border in Pennsylvania. To the west, it is bounded by the rich, mixed mesophytic association in West Virginia. Oak forests extend south and eastward until met by the oak-pine forests of Tennessee and the Piedmont Plateau. The oak forest region is mountainous and rarely occurs on flat land. In the broad valleys of the Ridge and Valley Province, white oak is common. Mixed mesophytic associations can be found on slopes where streams have cut below the broad valleys of the Harrisburg peneplain, producing slopes of a younger erosion cycle (Braun 1950). Braun noted that in Virginia there is less indication of mixed mesophytic forest in ravines of lower slopes than is found in other states.

The understory of the oak association is typically sterile compared to the rich flora of a mixed mesophytic association.

The infertile soils derived from resistant rock of the ridges, and the shallow soil over the steeply inclined strata are not (and doubtless were not) favorable to a mixed mesophytic forest; neither were the flats of the peneplain. Oaks and chestnut probably then gained ascendancy . . . except where erosion in the present cycle has produced habitats favorable for the invasion of species of the mixed mesophytic forest (Braun 1950:508).

Where oaks dominate, typical species include: *Quercus rubra*, *Q. prinus*, *Q. alba*, *Acer rubrum*, *Betula lenta*, *Magnolia acuminata*, *Amelanchier arborea*, *Acer pennsylvanicum*, *Ilex montana*, *Hamamelis virginiana*, and species of *Rhododendron* and *Vaccinium*. Where oak does not dominate, secondary communities of *Pinus strobus* (north slopes), *P. virginiana* (shaley south slopes), and *Liriodendron tulipifera* (coves), can be found (Braun 1950).

Three geological formations are found within Havens (Amato 1974). The mountain base, including elevations from 430 to 525 m (1400 to 1700 feet), is underlain with a broad belt of the Brallier Formation.

The formation consists of a thick sequence of sparsely fossiliferous grayish-green shales and siltstones interbedded with gray and dark-brown sandstones. The lower part of the formation is mostly olive-gray to dark-gray, micaceous shale with some thin beds of siltstone and fine-grained sandstone. Sandstones become more abundant in the middle and upper parts of the formation. The Brallier erodes to a series of small, linear hills that are well expressed on aerial photographs. The formation weathers to a soil that is littered with orange to grayish-brown, silty shale chips (Amato 1974:19-20).

Soil types within the formation include: Montvallo (75%); Jefferson Leadvale (20%), Holston and Monongahela (5%), and Atkin and Philo (trace). Montvallo soils are very shallow, shaley, droughty, and of low fertility. They are usually less than 35 cm thick over hard acid shales.

Jefferson soils are well-drained, yellowish-brown soils developed from Muskingum and Wellston soils moved by water or gravity. They are found in depressions along drainages and foot

slopes. They are underlain by colluvial beds of sandstone and shale at 60-125 cm. Surface, subsurface, and parent materials contain loose stone and boulders.

Leadvale soils are formed from recent colluvial deposits of Montvallo soils. They are located in depressions in heads of drainages and at the foot of steeper slopes with Montevallo soils. They are light colored and moderately well drained. Surface soil is grayish-brown silt loam underlain by brown and yellowish-brown clay subsoil. Water is restricted from moving through the clay layer (usually less than 1.5 m thick) which lays over the parent Brallier shale (Giles unpublished).

The Chemung formation crops out in a wide belt along the upper slopes of Fort Lewis Mountain. It is estimated to be between 308 and 462 m (1000 to 1500 feet) thick. It consists of highly fossilized sandstones with interbedded shales and conglomerate outcrops (Amato 1974, Giles 1988). The formation is typified by steep to very steep slopes.

Soils within the Chemung formation include Muskingum (90%), Jefferson (8%), and Wellston (1-2%). Muskingum soils are usually less than 50 cm thick over rock. They are yellowish brown, excessively drained, sandy to stony soils on steep to very steep slopes. Wellston soils are moderately deep (about 1 m thick over bedrock). Surface soils are sandy loam to silt loam. Subsoils are thin to moderately thick clay loam. Wellston series soils are mainly non-stony and mainly occur on sloping ridges or ridgetops (Giles 1988).

The Price Formation is exposed along part of the southeastern side of Fort Lewis and Brushy mountains. The quartzose sandstones and conglomerates in the formation make it one of the best ridge-formers in the area. It is well exposed along many of the dirt roads and fire trails on the crest of Fort Lewis and Brushy mountains. The maximum thickness of the unit in the area is about 150 m, and much of the upper part has been removed by erosion. The Price and Chemung formations are the source of most of the colluvium which covers the lower slopes of Fort Lewis Mountain (Amato 1974). Most soils of the Price formation are excessively drained and shallow over bedrock. They consist of the Muskingum series (85%), Wellston (2%), and Jefferson (13%) (Giles unpublished).

## METHODS

Elevation of the study area ranged from 530 m to 975 m above sea level. I divided the study area into three elevation classes - 530 m to 699 m (low), 700 m to 825 m (middle), and above 825 m (high). On the southeast side of the mountain, no land was included in the low elevation class because the property boundary of the management area was located at around 700 m (Table 2).

**Objective 1: To compare selected methods for estimating vascular plant species richness.**

### Timed-search Meander

Three methods were used to find vascular plant species within the study area. The first method was a timed-search meander, or walk. Land within each elevation class was searched by starting at a convenient point of entry. I wandered freely through the area seeking maximum variation in topography and species. The amount of time it took to find each group of 14 species (to fill each data sheet) was recorded. When species were not recognized immediately, the time taken to identify them was not included in the timed search. When species could not be identified in the field, they were collected and identified with the help of additional references at the Massey Herbarium at Virginia Polytechnic Institute and State University. I stopped searching when I felt that further investigation would yield few or no new species observations.

Timed-search walk data were collected for three sampling periods. These data were used to assess seasonality of observed species richness and composition. Data were collected in late spring-early summer, in midsummer, and in late summer. The number of species found in each season were compared, as were species-effort curves in each season.

## **Belt Transects**

The second method used was belt transects. Transects were located at 60 m (200 ft) intervals in elevation, and they followed elevational contours (Figure 1). On the northwest side of Ft. Lewis mountain, transects extended between watershed boundaries, that is from the top of one spur ridge to another. Therefore, transect lengths were variable (Table 3), and they were estimated from a map. On the southeast facing slope, transects near the top of the ridge occurred on gentle slopes, and their lengths were measured. As spur ridges emerged (at > 90 m and below), transects extended from spur ridge to spur ridge.

Each transect was approximately two meters wide. Two meters was chosen as the effective transect width because one meter on each side of the observer could easily be examined. Each transect was divided into fourths. Aspect, elevation, slope, and canopy species were recorded at the beginning and end of each quarter segment. Aspect was recorded at the beginning and end of each transect quarter with a hand compass adjusted for declination. Two sightings, one uphill and one downhill, were taken perpendicular to the elevational contour and averaged (Zedaker and Nicholas 1990). Elevation was determined at 30 m (100 ft) intervals by using a Model M-1 surveying microaltimeter manufactured by American Paulin System in Los Angeles, California. (The same procedures were used to determine aspect and elevation for plots. Aspect was recorded from plot center.) The time to discover each group of 14 species (to fill a data sheet) was recorded and area sampled was estimated. Species-effort and species-area curves were made for all transects combined. That is, a cumulative species list was made by adding species in the order observed.

## **Plots**

The third method used was plots. Plots were located along elevational contours which alternated with belt transects. Usually five plots were placed at each elevation unless slopes were above 70 or 80% (Table 4). Both plots and belt transects were located along transects at 730 m and 790 m (Figure 1). Plots were placed 5 m above each transect to increase the likelihood of independence of the data.

Relatively small plots were used to monitor vegetation changes over aspect and elevation gradients and for frequency analyses of species ubiquity. Vegetation was sampled with plot sizes

recommended by Cain and Castro (1959) for frequency analysis. Trees were sampled with 45 10-m<sup>2</sup> plots. Two 4-m<sup>2</sup> plots for shrubs and 9 1-m<sup>2</sup> plots for herbaceous species were nested within each 10-m<sup>2</sup> plot. The rate at which species were discovered was recorded for tree, shrub, and herbaceous plots.

Mueller-Dombois and Ellenberg (1974) suggested that it was important to represent all species in vegetation studies, but that this could be done with one continuous releve or with many small quadrats. They recommended that at least 200 m<sup>2</sup> - 500 m<sup>2</sup> of canopy species and 50 m<sup>2</sup> - 200 m<sup>2</sup> of undergrowth be sampled in forested communities. In this study, 4500 m<sup>2</sup> of canopy species, 1440 m<sup>2</sup> of shrubs, and 405 m<sup>2</sup> of herbaceous vegetation were sampled. For trees, this was a sampling intensity of 0.7 %. A sampling intensity of far less than 1 % for canopy species is common in many vegetation studies of community composition. Travis (1982) used a 0.074 % sampling intensity. She reported this was 1.8 times more intensive than sampling done for regional forest inventories.

### Sampling Periods

Sampling was conducted three times between May 1991 and September 1991. The first sampling period extended from May 27, 1991 to July 17, 1991. The second sampling period began on August 12, 1991 and was completed on September 8, 1991. The third period began September 21, 1991 and was completed on September 29, 1991. During the third sampling period, only walks were conducted. Transects and plots were not used due to the lateness in the growing season and the amount of time it would have taken to complete them.

Timed-search meanders were always conducted before plots or transects were used. This was done so that the chosen walk route would not be biased by species observations made when using plots or transects. After meanders were completed, the choice to sample using plots or transects was randomized. Land in the low elevation class was searched first because several species in flower were observed there during general reconnaissance. Sampling was then conducted in high elevation areas where some early-blooming species were observed. Also, the high elevation area on the southeast side of Ft. Lewis Mountain received high solar radiation promoting an early growing season. Table 5 shows the schedule of sampling methods employed.

## Analyses

Sampling methods were compared by the numbers of species observed and by rates of species discovery. That is, the number of species observed per hour was compared among methods.

Species-area and species-effort relationships from using each method were modeled with regression to predict the numbers of species which might have been found had more time been spent searching or had more area been sampled. Models chosen were:  $\text{species} = f(\text{area (or time)})$ ;  $\text{species} = f(\ln(\text{area} + 1))$ ;  $\ln(\text{species} + 1) = f(\ln(\text{area} + 1))$ ; and  $\ln(\text{species} + 1) = f(\text{area})$ . Best models were chosen by the criteria: 1) adequate linearization of the relationship; 2) reduced variation from the regression line; and, 3) highest  $R^2$  (Connor and McCoy 1979).

Species-effort and species-area curves were visually examined to determine whether sampling had been sufficient. Curves were compared to a reference curve (Rice and Kelting 1955) to judge whether they approached horizontal. Minimum area of the community was not estimated from the curves since minimum area can be estimated from any curve whether it approaches horizontal or not (Rice and Kelting 1955, Mueller-Dombois and Ellenberg 1974). That is, minimum area for a community can be estimated (or underestimated) even if less than the "true" minimum area of that community has been sampled.

The compositions of species lists made using each method were compared for similarity using proportions. The proportion of species common to two methods was compared to the total number of species found by both methods (Kirby et al. 1986).

**Objective 2: To describe the relationship between species richness and season, observer, and learning effect.**

## Observer Differences

Differences in observed species richness and composition can occur between investigators (Goff et al. 1982). A more experienced investigator may discover more species in a given area. On August 29, 1991, I conducted a timed-search using a belt transect at 550 m on the northwest side of Ft. Lewis Mountain. On August 30, 1991, Mr. Wieboldt followed the same procedure. Along the transect, the same amount of area was searched by both observers, so total number of

species observed was compared. Composition of species lists was compared between observers by calculating the proportional similarity of the lists (Kirby et al. 1986).

### **Season and Learning Effect**

Number of species observations made using plots and transects in two sampling periods and observations from three sampling periods using meanders were compared to see if there was a detectable seasonal effect. Species-area and species-effort curves from the various periods were also compared for seasonal or learning effect. The confounding effect of learning (Kirby et al. 1986) was discussed.

### **Objective 3: To compare this study to other floral studies.**

The species list from this study was compared to partial lists compiled previously at Havens (Ritchie et al. 1984) and to a comprehensive floral inventory of Ft. Lewis Mountain by Wood (1944). Comments were made regarding the differences in species observed among studies.

## RESULTS

When data from all methods and all sampling periods were combined, 248 species from 67 families were identified on the study site (Table 6). Forty-five of these species were trees, 21 species were shrubs, and 183 species belonged to the herbaceous understory. As many as 32 vascular plant species were found in a 0.1 ha area. (Whittaker (1965) discussed the occurrence of as many as 40 vascular plant species in a 0.1 ha quadrat of eastern hardwood forests). Twenty-eight non-native species (Table 7) which occurred only along the roadside on the ridgetop were excluded from Table 6. They were excluded from the species list because they probably would not have occurred naturally on the ridgetop. They were most likely there because of the road and its weekly traffic. Common names for species or genera were taken from Scott and Wasser (1980), when available, or from Wofford (1989).

Approximately 115 hours were spent making observations in the field. In addition, approximately two days (16 hours) were required to determine the elevation at 30.5 m (100 foot) intervals in the study area. Four days (32 hours) were taken to set up transects and approximately 22.5 hours were required to set up plots. Total time in the field was approximately 190 hours. Another 160 hours (four 40-hour weeks) were spent in the Massey Herbarium at Virginia Tech identifying collected specimens. Total time spent was 350 hours or 44 8-hour days.

A previous checklist of plants observed at Havens Wildlife Management Area was compiled from observations made by Viola Ritchie, Mary Gaudette, and Barry Garrison on October 13, 1984 (Ritchie et al. 1984). That checklist included 85 species from 41 families. The authors identified 15 species that I did not find on my study area (Table 8). Some of their observations may have been made outside the boundaries of my study area. Neither the amount of time nor area they

searched was specified. However, the time spent searching that day must have been less than 11 hours, given the average day length at that latitude and time of year.

Wood (1943) also may have made some species observations within Havens. In his master's thesis, he identified 1025 species from Roanoke County. (He included introduced species in his list). He observed that "Collections have been made in as many parts of the county as possible, but since the greater part of the collecting was done in the summer of 1942, gas rationing caused some sections to be ignored" (Wood 1943:9). Some of Wood's species observations were made on Ft. Lewis Mountain. Wood described the locations of species observations by their direction and distance from the Salem post office. Observations which may have been made within Havens are listed in Table 9. Table 9 includes only those species that I did not observe in the study area.

When the 248 species I observed are added to the 15 additional species that Ritchie et al. documented and to the 64 species that Wood may have observed there, 336 species represent a minimum number of species occurring within Havens. Because the locations of Wood's observations were approximate, if one is only interested in the number of species definitely occurring within the current boundaries of the management area, Wood's observations would have to be deleted. Also, species composition may change over time. Some of the species that Wood identified on Ft. Lewis Mountain may no longer be present (taxa of doubtful persistence or waifs). Some species Wood identified may no longer be present due to loss of their habitats. This may be true especially for wetland species Wood identified in a pond area near Ft. Lewis mountain. Some of the species on his list may have been misidentifications or misapplications of species names (Porter 1994, pers. comm.). These reasons may also explain why Harvill et al. (1986, 1992) listed fewer species records from Roanoke County than Wood. For example, Harvill et al. (1986) listed 863 species known to occur in Roanoke County. Their list included exotic species that had been naturalized.

While 336 species may be considered a possible minimum number of species to be found at Havens, a few things should be kept in mind. First, Havens is a 2800 ha area. I searched 61 ha of it, and the area searched by Ritchie et al. and Wood is unknown. Together, we only searched a small fraction of the total area. In addition, species-area relationships are not linear. Methods

to predict species numbers for areas larger than the area actually searched will be discussed later in this section.

My study took place while the third edition of Harvill et al. (1992) was in press. Six species which I collected from the study site were new species observations for Roanoke County. These species were reported to Harvill et al. (1992) via Mr. Thomas Wieboldt and they are: *Carex woodii*, *Medeola virginiana*, *Monotropa uniflora*, *Muhlenbergia tenuiflora*, *Prunus virginiana*, and *Scirpus verecundus*. Additionally, 30 of the species I observed were not listed as occurring in Roanoke County by Harvill et al. (1992). However, 22 of these species are found in more than half of the counties that surround the county. Therefore, they may be likely to occur in Roanoke County as well. Also, of the 30 species not listed as occurring in the county, 11 are described by Wofford (1989) as frequently occurring in the Blue Ridge Mountains of Virginia, Tennessee, North Carolina, South Carolina, and Georgia. Eight species are described as common in occurrence, eight as occasional, and three as infrequent.

### **Comparison of Methods by Yield**

By coincidence, approximately the same amount of time was spent using meanders and transects during the first sampling period (Table 10). Plots took three and one-half hours longer time than meanders to complete. During the second sampling period, the amount of time spent on meanders and using plots was approximately equal, while transects took about four hours longer than the other methods. All methods took less time during the second period, probably because of my gains in experience.

The amount of area covered with each method was quite different. Plots sampled 0.45 ha and transects covered approximately 0.8 ha. Area was estimated with a pedometer for the meander method, but I felt that estimates were too inaccurate to use in data analyses. The pedometer often failed to register because I was moving so slowly. However, the area covered using meanders probably equaled or exceeded the area sampled using transects. Estimates of area covered using meanders, though inaccurate, were approximately 1 ha or more.

Fewer species were discovered using meanders during the first sampling period than were found using transects. One reason for this could have been my lack of experience. The meander

method requires the investigator to determine the search path. The investigator tries to maximize observed richness within the vicinity of the path. This process can be compared to optimal foraging theory, which predicts that an animal seeks to maximize energy intake per unit time (Davies 1977, Colinvaux 1986). Likewise, the botanist tries to choose a path which maximizes rate of species observations per unit time (Goff et al. 1982). This can be difficult for a novice. If the novice is "unsuccessful," fewer species are found than could have been found had he or she chosen a route which maximized the numbers of species observed. By contrast, transects provided a defined search path that was easy to follow and to replicate.

Plots were clearly the least desirable method to use during both sampling periods. Far fewer species were found using plots than by using other methods. The number of species found using plots was small because plots sampled only 55% of the area that transects did. Also, the number of species discovered using plots was probably small because a relatively small area was searched for herbaceous species. Herbaceous species, rather than woody ones, contribute the most to species richness of plants in forested ecosystems (Whittaker 1965). Because herbaceous species were sampled using subplots, a standard forestry practice for stand description, only 0.041 ha were examined for their presence. In contrast, herbaceous species were identified on the entire 0.79 ha sampled with transects and along the entire meander path.

Methods of sampling and approaches to making observations were compared using the criterion of rate of discovery (Table 10). During the first sampling period, the only significant difference in rates of new species observed per hour was between transects ( $9.7 \pm 13.1$ ) and plots ( $4.5 \pm 6.2$ ). The variance of rates was so high that no other significant differences were found using a t-test for two independent samples. That is, when beginning to search for new species, rates of discovery were very high. Near the end of a search, rates of species discovery were very low. During the second sampling period, there were no significant differences in rates of new species observations.

The fewest number of species and the lowest number per unit time were discovered using plots in the first sampling period. An average of 4.5 species per hour was observed with plots. During the first sampling period, plots located only 60-68% of the species found by using transects or meanders, respectively. Again, this was probably because less area was sampled in the same

amount of time using plots than when using other methods, and because much less area was sampled for herbaceous species using plots than other methods.

### Species-area and Species-effort Curves

The species-area relationship has been used to estimate minimum area of a community (Braun-Blanquet 1932), to determine appropriate sample size (Cain 1938), and to predict the number of species in an area larger than those sampled (Kilburn 1966). The species-effort relationship has been used to determine search sufficiency when using meanders (Goff et al. 1982). Some analyses have been done by simply plotting the number of species against area or time. Other analyses have described the relationship with equations.

Species-area data have been described using type I logarithmic (species =  $\ln(\text{area})$ ), power function ( $\ln(\text{species}) = \ln(\text{area})$ ), and log species ( $\ln(\text{species}) = \text{area}$ ) models. Connor and McCoy (1979) evaluated data from 100 studies using both untransformed data and these three transformed models which they called the exponential, power function, and logspecies models, respectively. They concluded that no one model was best at describing the data all of the time. In their analysis of 100 species-area curves, the power transformations and untransformed models provided the best fits most frequently. However, they stated, "the best-fit model for a particular species-area curve can only be determined empirically" (Connor and McCoy 1979:814).

I evaluated my data using Connor and McCoy's four models (the untransformed data and the three transformed models) in order to make predictions about species richness. Both species-area and species-effort data collected by three methods in two time periods were analyzed. Tables 11-16 show both  $R^2$  and adjusted  $R^2$  for each of the four models used to describe data collected by plot sampling, transects, and meanders, respectively, in each of two sampling periods. Adjusted  $R^2$  values were calculated with a PRESS statistic that re-ran iterations of each data sample by dropping one observation per run. Adjusted  $R^2$  values close to  $R^2$  values indicated stability of predictions made by a model.

For the data collected both with plots and transects, the untransformed data yielded fairly high  $R^2$  and high adjusted  $R^2$  values. However, it was inappropriate to model untransformed data

with parametric regression models because the data were not normally distributed. Yet even though the data were non-normal and non-linear, these models performed well at prediction.

Of the models using transformed data, the logarithmic transformation (that is, species =  $\ln(\text{time})$  and species =  $\ln(\text{area})$ ) produced higher  $R^2$  values than the power or log-species models for all data. For all models, adjusted  $R^2$  values did not fall much below  $R^2$  values, but the power and logspecies models performed rather poorly in fitting any of the data.

P-values for all models were well below 0.1 except for one model. For species-area data collected using plots in the second sampling period (Table 12), the probability of a greater  $t$  value for the intercept of the exponential model was 0.82. This means that there was a high probability that the intercept value did not differ from zero. This should not be a problem as all expected intercept values were zero. That is, at time 0, I expected to have observed no species.

There did not appear to be a difference in the selection of the best model for the data between sampling periods. That is, for species-area and species-time data from plots (Tables 11 and 12), the type I log (exponential) model provided the best fit in both sampling periods, and  $R^2$  values were very similar in both periods. The same trend was observed for data collected with transects and meanders (Tables 13-16).

The type I log transformation provided the best fit for data regardless of the method used to collect the data. That is, the model had the highest  $R^2$  values whether data were collected with plots, transects, or meanders (Tables 11-16). In addition, this model provided the best fit whether the independent variable was area or time.

For data gathered using plots (Tables 11 and 12), both time and area data were fitted well by the type I log model. For transect data (Tables 13 and 14), the models of species-time data had higher  $R^2$  values (better fit) than the models of species-area data. Thus, time was a better predictor of species numbers than area. This could be because transect area was estimated from a map, not measured, while plot area was measured and was, therefore, more precise.

Using the type I logarithmic models, the number of species was predicted for the following situations:

- a) species numbers were predicted at final (total) observation time or area  
for each method

- b) if an area equivalent to the area sampled using transects (0.8 ha) were sampled using plots,
- c) if time were doubled,
- d) if area were doubled,
- e) if 60 ha (study site area) were sampled with plots,
- f) if 2800 ha (area of Havens) were sampled with plots (Tables 17-19).

Situation b was deleted for transect data as 0.8 ha were sampled using transects. Situations b, d, e, and f were not evaluated using meander data since no estimated area was sampled. Predicted numbers of species,  $\hat{sp}_A$  and  $\hat{sp}_T$  were calculated with both species-area and species-time equations, respectively (Table 20). Predicted area,  $\hat{a}$ , for an hypothetical time was calculated with equations derived from regressing area on time (Table 21). For example, using the data from sampling period 1 observed in plots, if time is doubled from 23.1 hours to 46.2 hours, predicted sampled area would be  $-0.025 + 0.000324(\text{time in minutes}) = -0.025 + 0.000324(46.2 \times 60) = 0.87$  ha. Then  $\hat{sp}_A$  of 135 species was calculated using  $\hat{a} = 0.87$  ha (Table 17).

For plot data (Table 17),  $\hat{sp}_A$  and  $\hat{sp}_T$  produced similar estimates of species numbers at the final observation time (scenario a). For transect data (Table 18, scenario a), species-time equations predicted species numbers (194 species) closer to observed values (199 species) than did species-area equations (181 species). Generally speaking, time equations produced larger estimates than area equations, that is  $\hat{sp}_T > \hat{sp}_A$ .

For data collected from plots,  $\hat{sp}_A$  and  $\hat{sp}_T$  were similar for the first three hypothetical situations. However, when estimates were made for areas of 60 ha or greater, the distance between the two values became large. In the latter two scenarios, species-area data predicted more likely species numbers than species-effort data. But estimated species numbers from species-area data were probably too large for areas of 60 ha and more. The estimates of species numbers from species-time data ( $\hat{sp}_T$ ) were probably too large, especially for large areas.

For both the transect and meander data, there was a large difference between predicted number of species from species-area and species-time curves. The values of  $\hat{sp}_A$  and  $\hat{sp}_T$  could be seen as a range encompassing the predicted number of species with an increase in area and time. However, both  $\hat{sp}_T$  and  $\hat{sp}_A$  were too large to be taken seriously at the 60 ha and 2800 ha scale.

Species-area data provided more conservative estimates of species numbers than did species-time data. Data from plots provided more conservative estimates of richness than data gathered by other methods. Plot data underpredicted in smaller areas. For example, Table 17 shows that if 0.79 ha had been sampled with plots, the predicted number of species was 132 or 134, while 199 species were observed in that amount of area by using transects. However, all data overpredicted species numbers for areas of 60 ha or more.

In summary, reasonable numbers of species were estimated using the type I log model with species-area data gathered by plots and transects for areas under 60 ha. For larger areas, such as 60 and 2800 ha, estimates made with species-area and species-time data from all methods probably overestimated actual species numbers (Table 17-19).

In review, the entire flora of Roanoke County may have from 863 species (Harvill et al. 1986) to 1020 (Wood 1944). It is doubtful that Havens, an area of 2800 ha, contained as many as 1/3 (400) to 2/3 (800) of the species in the county (Tables 17-19). Havens is not so diverse in habitat types as to contain such a high percentage of the county flora. Similarly, my study area may have had as many as 271 species -- the lowest predicted number of species (Table 17) -- but not many more than that due to a lack of habitat diversity within the area.

Data for the regression models already discussed violated one assumption of regression, that data are independent from one another. Since species numbers were cumulative, a new species observation depended on whether the individual being observed belonged to a species which had already been observed. Although this assumption was violated, p-values were very low and regression models made good predictions of species numbers for smaller areas.

To determine how models might behave if data were independent, species-area data from plots (sampling period 1) were selected for analysis in a blocked randomized design. (Selection was blocked to control for differences in elevation and aspect). One plot (100 m<sup>2</sup>) was selected from the data and its species numbers observed. Then two plots (200 m<sup>2</sup>) were selected and their cumulative numbers of species were tallied. I continued the analysis until the last 9 plots were selected -- an area of 900 m<sup>2</sup>.

Species-area data were modeled using the same four models as before (Table 22). Again, the untransformed model (species = area) was not used as data were not normally distributed. The

logspecies model was not considered due to high p-values and low  $R^2$  values. The power model was selected because it had higher  $R^2$  values than the exponential model. Estimates from the power model were unreasonably low for small areas and unreasonably high for large areas (Table 24).

Similar analyses were done using species-area data from transects in sampling period 1. Again, the power model had the highest  $R^2$  values (Table 25). The untransformed model was not used because of the non-normal data distribution. P-values of the logspecies model were too high to consider using that model.  $R^2$  values were rather low for the exponential model.

Modeling with the regression equation from the power model (Table 23) yielded estimated species numbers too low for areas of 60 ha and below and too high for the area of Havens (Table 26). Havens does not contain numbers of species equivalent to the flora of the entire county. The purely logarithmic relationship of the numbers in the model does not reflect the effect of the lack of habitat diversity of the area on species numbers.

In conclusion, the power model provided adequate fit for data which did not violate the assumption of independence. However, the model estimated species numbers poorly. This may be because areas used in the independent analysis were far smaller (e.g. 900 m<sup>2</sup> for plots) than in the cumulative analysis (4500 m<sup>2</sup> for plots) and were far smaller than areas for which estimates were made (4500 m<sup>2</sup> to 280,000 m<sup>2</sup>). Predictions tended to become more inaccurate as the area for which they are being made exceeded area observed. For the purposes of this study, the models developed from cumulative species numbers, cumulative areas, and cumulative times made better estimates and were preferred. Those models were developed from samples of larger areas and times.

### Search Sufficiency

When sampling a community, at least the minimum area of that community must be searched. The minimum area of a community is defined as "the smallest area in which the species composition of the community in question is adequately represented" (Mueller-Dombois and Ellenberg 1974:47). Cain (1938) suggested the minimum sample size for a community could be estimated from a species-area curve. He suggested that the area at which a 10% increase in area failed to produce a 10% increase in species numbers was sufficient. Such a point is often located on a species-area curve before it approaches horizontal.

Rice and Kelting (1955) demonstrated a difficulty with Cain's criterion, since the 10% point moves to the right as more quadrats are sampled. For example, they observed that in a single prairie community, if the total area sampled was 10 quadrats, 2.5 quadrats represented the community's minimum area. However, if sampling intensity was increased to 20 quadrats, minimum area then increased to 5 quadrats. Finally, a sample size of 100 quadrats produced an estimated minimum area of 22 quadrats. In none of these cases did the curve approach horizontal at the selected minimal area (Figure 2). Thus, estimated minimum area is dependent on sample size. Another way to say this is that minimum area can be estimated at any point along a species-area curve whether the curve is approaching horizontal or not.

In addition, a problem with scale exists when trying to apply Cain's 10% guideline and when trying to estimate minimum area of a community from a species-area curve. The shorter the y-axis in relation to the x-axis, the sooner the curve flattens and minimum area can be underestimated (Cain 1938, Rice and Kelting 1955, Goff et al. 1982, Mueller-Dombois and Ellenberg 1974). Cain suggested using a ratio of 1:3 for the y- to x-axes, but sampling until the curve flattens may lessen the problem. Mueller-Dombois and Ellenberg (1974) commented that in the relatively flat portion of the curve, the problem of ratio of the two axes is minimized. However, Kirby et al. (1986) noted that the place at which the curve flattens may be judged differently with a change in scale.

Goff et al. (1982) suggested searching until a species-effort curve leveled off. They visually inspected curves to judge subjectively when that occurred. Additionally, they were careful to search until no new species had been observed after searching for 30 minutes, hoping that would correspond to the point at which species-effort curves approached horizontal. Their objective was to observe all species within a defined area. They used a meander method because to obtain estimates of species richness, or diversity, or to ascertain the presence of rare species, they felt "elaborate quantitative analysis of vegetation rarely provides the information needed" (Goff et al. 1982:307). Mueller-Dombois and Ellenberg (1974) and Kirby et al. (1986) also suggested sampling until the species-area curve leveled off, though no methods to ascertain that point, other than visual inspection, were discussed.

In this study, I did not continue to search until no new species were found after 30 minutes of searching. However, I hoped I had at least searched until species-area or species-effort curves

leveled off. I visually inspected species-area and species-effort curves, and judged subjectively whether they had leveled off.

Inspecting species-area and species-effort curves for data from plots in both sampling periods (Figures 3, 4, and 5), it looks as though the curves are approaching horizontal. When the species-area and species-effort curves from my data are compared to a typical species-area curve (Figure 2), it looks as though curves from my data are leveling off. However, a typical curve rises and levels off many times in stair-step fashion. My curves also follow this stair-step pattern. Therefore, it is quite possible that the species-area and species-time curves from my plot data will rise again. Considering that 235 and 241 species were observed by all methods combined in the first and second sampling period, respectively, and only 121 and 112 species were found using plots alone in the first and second periods, the species-area curve would probably continue to rise with the use of more plots, but at an unknown rate.

The species-area and species-effort curves from transect data in both sampling periods appear to approach horizontal (Figures 6, 7, and 8). However, I know that in the first sampling period, 199 species were found using transects, compared to 235 species found by all methods in period 1. In period 2, 185 species were observed on transects compared to 241 species observed by 3 methods combined. That is, there were more species on the area than I found using transects. If the species-area and species-effort curves were extended to the right, they must continue to rise again. Presumably this would continue to occur at a slow rate, a trend illustrated by the right end of the curves in Figures 6-8.

Meanders were used in three sampling periods, each in the months of June, August, and September. Species-effort curves described the species-time relationships. The species-effort curve from the first period appears to level off, while the curves from the second and third sampling periods do not. This suggests that searching was sufficient in the first sampling period, but not in the second and third periods. On the first meander, 177 of 235 species were observed, 178 of 241 on the second, and 170 species observations were made using meanders during the third sampling period. There was no other number to which to compare the 170, since transects and plots were not used a third time. Again, there were more species present on the study area than were observed

using meanders in any sampling period. This indicates that the species-effort curves would continue to rise, but at an unknown rate.

Curves for the species-area and species-time data looked similar within methods and sampling periods. (For example, see Figures 3, 4, and 5). When area was regressed on time, the relationship was found to be linear with high  $R^2$  values (Tables 11-14, Figures 9 and 10). The amount of time on the x-axes was adjusted according to the time-area relationship when area was regressed on time (Table 21). This was done so that species-time curves from both sampling periods could be compared to species-area curves. Looking at species-area and species-effort data from plots for both sampling periods, the species-area and species-effort curves from period 1 look similar to one another (Figures 3 and 4), as do the species-area and species-effort curves from period 2 (Figures 3 and 5). This pattern is also observed with transect data (Figures 6, 7, and 8).

Within a method and sampling period, the differences in the shapes of the species-area or species-effort curves between sampling periods 1 and 2 suggest a seasonal or learning effect. That is, curves are steeper initially in the second period. Also, species-area and species-effort curves end higher in the first period than curves from the second sampling period. In other words, more species were found in the first period. In part, this was probably the result of a higher sampling intensity, not season. That is, more time was spent using plots in the first period than in the second (Table 10). However, nearly the same amount of time was spent using transects in each sampling period. Therefore, a different explanation for finding fewer species in the second period than the first using transects must be sought. Kirby et al. (1986) reported that there are real seasonal differences in species abundance and conspicuousness because of species phenology. Perhaps fewer species were conspicuous in the second period and abundance was lower later in the season since fewer species were found using transects. This phenomenon was more marked with transects than with plots because a far greater area (0.79 ha) was sampled for herbaceous species using transects than when using plots (0.04 ha).

The comprehensive species list (compiled from observation made using all methods) from period 1 had 235 species, and the list from period 2 had 241 species. It is true that 235 and 241 may not be significantly different, but the numbers indicate that at least as many species were

present (available for finding) in the second period as in the first. Therefore, I cannot say there was a seasonal effect in species richness, but abundance and conspicuousness may still have declined.

Any seasonal effect is also confounded by a learning effect. That is, having searched this area in June, I knew what to look for and what to expect to find in August. A learning effect would have occurred even had I searched a similar, but not identical, area (the same community type). Kirby et al. (1986) suggested that this effect cannot be eliminated, but its effect can be reduced by using predetermined routes and quadrat locations. This study used predetermined plot and transect locations, but meander routes were not predetermined. Therefore, a learning effect was minimized when using plots and transects, but not when using meanders.

As mentioned above when comparing species-area and species-effort curves between periods 1 and 2, usually the initial parts of the curve were steeper in period 2. This suggests a learning effect. The only case in which this was not observed was for species-area curves for plots between periods 1 and 2. The slope in the initial part of the a species-area curve should be less susceptible to variation than for species-time curves. That is, the area to be searched is fixed, but the time it takes to do so can vary with experience. However, one reason that species-area relationships could show experience effect, as was observed with transects, is that the researcher may recognize more species after the first sampling period. It is easier to recognize a species if the researcher knows what he or she is looking for or has developed an image of it.

To summarize, the initial portions of the species-area and species-effort curves rose more steeply during the second sampling period (and third, for meanders) than for the first. This indicates that I was learning. Secondly, judgments as to whether curves had leveled off or not were somewhat subjective. But all curves appeared to approach horizontal except for the species-effort curves from meander data in the second and third sampling periods. The 30-minute guideline of Goff et al. (1986) -- to search until no new species were found after 30 minutes -- could have been employed with meanders to increase confidence in search sufficiency. Thirdly, the highest proportion of species was found using transects, but meanders performed equally well in the second period with greater botanical experience of the investigator (Tables 10 and 27). This indicates that transects may be quite useful for beginners, but meanders work well for those with even a small amount of botanical knowledge. Plots are not useful for obtaining complete floras, and must be

used in conjunction with another method if a complete species list, accurate richness or diversity estimates, or rare species are being sought.

When numbers of species observations for plots and transects are added together, they are nearly equivalent to species numbers observed when lists from plots and meanders are combined. I found that a combination of plots and meanders estimated approximately 70% of total species observed (248) on the study area when data from all seasons and methods were combined. A combination of plots and transects estimated 80% of total richness. Thus, plots could be used satisfactorily with either sampling method, depending on the experience of the investigator. However, the combined use of transects and meanders located a higher percentage of total species numbers observed during the study than did a combination of plots and any other method. That is, a combination of transects and meanders yielded 97% of the total species observed at the study site. Belt transects, such as I used, were not measured and did not provide accurate areal estimates. If accuracy in area sampled is important, a point intercept transect, or perhaps a plotless method, would work well.

### Observer Differences

A way to check observer competency is to compare that person's search effort to that of an expert. Tom Wieboldt, Associate Curator of the Massey Herbarium at Virginia Tech, assisted me by making a species list along a transect one day after I had made such a list. Weather conditions were favorable both days - clear and warm - and Tom and I made our observations in the morning.

Tom observed 24 more taxa than I. He identified 94 taxa, and I observed only 70. Of the 24 additional taxa Tom identified, he identified 17 of those taxa to species, 5 to genus, and there were 2 taxa he could not positively identify. Half of the 24 taxa he observed were taxa with which I was unfamiliar at the time, and half were oversights on my part. (At this time, after a recent field season, I still might have difficulty identifying 10 of those taxa in the field).

I recorded 4 taxa that Tom overlooked. Also, the species I identified as *Medeola virginiana* may have been *Isotria verticillata* instead. Also, I misidentified *Andropogon* sp. as *Panicum* sp. Had I identified these species correctly, Tom would have observed 22 more taxa than I, rather than 24 taxa more than I. Species that we both observed are listed opposite one another in Table 28.

Spaces in the table occur across from a species observation that one of us made but the other did not, except in the cases of *Medeola*, *Isotria*, and *Andropogon*, as mentioned above.

The similarity of our lists was compared by taking the proportion we both had observed over the total number of identified taxa (Kirby et al. 1986). Our lists were 70% similar. Kirby et al. (1986) compared lists between observers, season, and methods in a study with replication. Using observers of similar experience (that is, assumed equal competence), no differences in species richness of their lists were found. Even so, lists between observers were only 53-76% similar in species composition when sampling at the same site in the same season using the same method (walks, n = 18). Even the same observer using the same method (walks) in the same season at the same site (though route may have varied), produced lists only 60-80% similar to one another with repeat observations (n = 12). Therefore, the 70% similarity between Mr. Wieboldt's and my list (Table 28) is within an expected range.

### **Similarity of Species Composition**

Using the proportion of species in common to the total number of species, species composition of lists made from using different methods were compared (Table 29). Species lists from transects and timed-search meanders were most similar. During the first sampling period, 146 species were common to both meanders and transects, 48 were seen only on transects, and 32 were seen only on meanders. During the second sampling period, 47 species were seen only on meanders and 35 species were unique to transects.

Plots were more dissimilar to lists from meanders and transects than lists from meanders and transects were to one another. This is probably because far fewer species were discovered using plots than by other methods. That contributed to a low numerator (a low number of species in common to another method) and to a relatively low similarity. Fewer species were discovered using plots than other methods because less area was sampled with plots and far less area was searched for herbaceous species using plots. Kirby et al. (1986) found that 13-15 hours were required to produce a species list equivalent in length to one obtained from a three hour walk. Also, during the first sampling period, only eight species were uniquely discovered on plots. Of those eight species, four were rare or difficult to identify. The other four should have been observed using

meanders or transects. The fact that they were not was probably an oversight. During the second sampling period, only one species was unique to plots. It was a common species, *Aster undulatus*, but it was rarely seen during the study. This was also likely an oversight.

It is not surprising that lists from meanders and transects were only 65% similar, considering that species lists made by the same observer using the same method at the same site in the same season may only be 60-80% similar (Kirby et al. 1986). Meanders and transects were both adequate methods in terms of species richness and composition observed. I observed 75% of total species composition (248 species) using meanders alone and 85% of total species using transects (Table 27). However, when the two methods were combined, 97% of the total species composition and numbers were observed. This suggests some benefit to combining search strategies in a floral inventory.

# DISCUSSION

## The Species-area Relationship

Is there a theoretical basis for the species-area relationship? Williams (1964) proposed that as the amount of area sampled is increased, new habitats with their associated species are encountered, and thus species number increases with area. This point of view is referred to as the habitat diversity hypothesis (Connor and McCoy 1979). Most large-scale floras are assumed to be diverse for this reason.

Preston (1960, 1962) and MacArthur and Wilson (1967) proposed the "area-per se hypothesis." That is, species numbers are a function of immigration and extinction rates. Extinction rates are inversely proportional to population size, and population size is directly proportional to area. Thus, larger areas have bigger populations, lower extinction rates, and more species. In addition, immigration rates depend on the distance from a source and may vary in proportion to it.

Connor and McCoy (1979) proposed that species number is a sampling phenomenon. That is, larger areas are subject to more samples, and thus more species are found. In discussing these three hypotheses, Connor and McCoy (1979:793) remarked,

each mechanism is probably important in determining the correlation between species number and area in one or another species assemblage. but practically it is difficult to assess their proportional contribution in any particular study . . . all three explanations (and perhaps more) should be kept in mind. ... The reasons underlying local diversity patterns can be elucidated only by sound biological examination and experimentation, not by the

invocation of currently accepted dogma.

This study was not designed to discover the underlying nature of the species-area relationship. Therefore, no definitive conclusions about the underlying mechanisms of the species-area relationship at my study site can be reached from my observations. However, the three hypotheses can be discussed in relationship to this study. The habitat-diversity hypothesis seems a common-sense statement based on observations which have been made in many large-scale studies involving many community types (Wood 1944, Cooperrider and Thorne 1964, Goff et al. 1982, White et al. 1984, Johnson-Groh 1985). On my study area, different habitat types apparently existed as a result of different aspects. For example, different species assemblages were present on west-facing and east-facing slopes. West-facing slopes were dominated by *Quercus prinus*, *Pinus rigida*, *Pinus pungens*, *Kalmia latifolia*, and ericaceous herbs. North and east-facing slopes had a hardwood canopy (*Quercus prinus*, *Quercus rubra*, *Quercus alba*) with a much more open understory (not shrubby) including *Acer pensylvanicum* and a greater variety of herbs. Though no community typing was done in this study, the dominance of different tree species could be seen from the valley below; that is, pine associations were observed on west-facing slopes, and hardwoods on north and east-facing slopes.

Even though the study took place within one forest type, oak-association, habitats within the forest of different aspects, moisture regimes, soils, and exposures to disturbance (roads) contributed to new species observations. For example, I observed new species in areas near the ridge road as well as in the small alluvial area near the confluence of Mason's Creek with Mary's Creek (northwest side, low elevation). The argument could be made that at least different micro-habitats, if not different community types, were present and contributed to greater species richness than if they had been absent.

The "area-per se" hypothesis would be difficult to test in an area such as my study site. It would seem that an "island" of some type would be required. That is, populations were not isolated from a source population at my study area. Also, extinctions might be unlikely due to proximity of seed sources and propagules just outside the area. Certainly immigration and extinction are factors operating in the area. Observations of such phenomena would require a long-term study.

Such a study would be better suited to an island type environment, such as accidental wetland sites on reclaimed coal mines. For example, prior to the implementation of a coal mine surface reclamation act in 1984, bulldozers occasionally left depressions in the ground when mine sites were regraded. Water collected in the depressions. Unplanned wetlands resulted where none had existed before, presumably from a combination of suitable hydrology and propagules transported by wind and waterfowl. Such "islands" in the landscape could be studied, plant populations monitored over time, species immigrations tracked, and correlations between extinction rates and area (of different sized wetlands) made.

Sampling intensity no doubt affected estimated species richness during this study. For example, when 0.45 ha were searched using plots, 112-121 species were found in the first and second sampling periods, respectively. When 0.79 ha were searched using transects, 185-199 (Table 10) species were observed. The relationship between sampling intensity and richness has led researchers to suggest that only studies that sample comparable areas can properly be compared. Sampling in proportion to area does not seem to mitigate this problem unless the true "minimum area" of a community is established by sampling much larger areas than are usually sampled (Rice and Kelting 1955, Mueller-Dombois and Ellenberg 1974). In such cases, minimum areas and their associated richnesses could be compared among studies. It also seems that boundaries of an area should be natural (encompassing a community type) or areas should be large if boundaries are not natural. For example, my entire study area could have been smaller than the minimum area of Havens and smaller than the minimum area of an eastern hardwood community.

Increases in species numbers and abundances have been noted along borders between two vegetation types when compared to species numbers and abundances within homogenous communities (Gysel and Lyon 1980). Leopold (1933) suggested that a greater number of edge types is correlated to a greater number of species. He observed that population densities for species with low travel radius were proportional to the sum of the habitat type peripheries.

The shape of an area, that is, the nature of its boundary, may affect species richness. Imagine two areas, one circular and the other irregular in shape. The latter would have a greater amount of edge and therefore a greater expected species richness. Patton (1975) related the amount of "edge" to species numbers and abundances in the following way:

$$DI = TP/2 \sqrt{\pi * A}$$

where TP = total perimeter and  $A$  = area. A circle would have a  $DI = 1.0$ . Any value greater than 1 indicates a shape with greater edge complexity than a circle.

A similar concept is used in limnology (Wetzel 1983). Shoreline development,  $D$ , is the ratio of the length of shoreline ( $L$ ) to the circumference of a circle of area equal to that of the lake

$$D = L/2 \sqrt{\pi * A} .$$

Circular lakes approach minimum shoreline development, a value of  $D = 1.0$ . Shoreline development is important because it reflects the potential for the development of littoral communities in proportion to lake volume.

Presumably, in most species-area studies, edge is not sampled. That is, the investigator tries to estimate the richness or diversity within one community type. Little, if any, sampling is done in the transition zone between communities when one of the objectives is to characterize the species-area relationship of one community type. Edge may still affect richness within the community as a result of "edge effect" and species migrations. That is, species present because of a transition zone between two communities enter a certain distance inside the edge of the community under study. Species numbers could be higher near complex edges than simple ones, and higher if there is a great deal of sampling done at the periphery of the area than if little sampling occurs there.

A more common phenomenon may occur when sampling within a community. Gysel and Lyon (1980) suggested that edges may occur where two successional states or conditions meet within a community. Therefore, even when sampling is done in the interior of a community, windfalls, fires, or past forestry activities can create an edge and an increase in species numbers. Additionally, two "conditions" could meet, such as a spring within a forest, the edges of rock outcrops, waterfalls, seasonal streams, etc. In such cases, sampling across these transitions by using a transect would increase species richness estimates. Estimates will be higher than if these "induced" edges are not present.

In addition, structural diversity of a community can affect richness. That is, an observer might expect a tropical rainforest to be more rich in species because it has many more layers of species than a grassland (Giles, personal communication). Magurran (1988) cited several studies

that indicate a correlation between woodland structural diversity and bird species richness. A similar correlation was found between structural diversity of fields and woodlands and insect diversity. Given Arrhenius's equation (Connor and McCoy 1979:794):

$$S = k * A^z$$

$z$  might increase with increased volume (structural diversity) or increased complexity of edge (Giles, personal communication).

### Modeling of the Species-area Relationship

Preston (1960, 1962) derived a log-normal relative abundance distribution which with similar assumptions leads to the power function form of the species-area relationship. Preston (1962) also showed that the log-series distribution apparently present in many studies was more likely a sampling distribution derived from an underlying truncated log-normal distribution. Preston's work has subsequently led to the near-uniform acceptance of the power function as the best model of the species-area relationship. ... If the log-normal relative abundance distribution predominates in nature, then the power function may have theoretical justification. However, since both the log-normal distribution and the power function are so robust in their ability to approximate the distribution of abundances and species numbers may reflect nothing more than the central limit theorem (May 1975). These properties are a strong practical justification for the use of the power function, yet cloud its biological interpretation (Connor and McCoy 1979:796-797).

In Connor and McCoy's review of 100 species-area curves, they found that 35 curves were best fitted by an untransformed model, 43 were best fitted by the power function, 27 by the exponential model, and 14 by the logspecies model. The best fit of untransformed curves may have been due to apparent linearity of the relationship between species number and area which resulted from sampling a narrow range of areas. In any event, the power function was the best fit on 36%

of the examples. Even if a power model fits the data best, an underlying log-normal distribution cannot be assumed. Even if the power model always provided the best fit to the data, which it did not in my study, its biological interpretation would remain cloudy. That is, the best fit of the power model to species-area data may be a result of the central limit theorem and the fit of the model to the data does not imply an underlying log-normal distribution of the species-abundance relationship.

In a more refined view of the species-area relationship, Williams (1964) used both exponential and power models on different portions of the species-area curve. He said that when dealing with very small areas and perhaps as few as a few hundred individuals, species-area curves rise rapidly in a curvilinear relationship best described by:

$$S = \alpha \ln(1 + N/\alpha) \text{ or } 2.3 \alpha \log(1 + N/\alpha).$$

For larger samples than those dealing with only a few hundred individuals or a very small area within the same association, a straight line relationship between  $S$  and  $\log N$  is observed. This implies that "a constant multiplication of the area produces a constant addition to the number of species" (Williams 1964:98). He described this portion of the relationship (curve) by:

$$S = \alpha \ln(N/\alpha) \text{ or } 2.3 \alpha \log(N/\alpha).$$

The rate of species accumulation will accelerate again if and when an increase in sample size reaches "the limit of the single environment or association (which may be after a few square yards or some hundreds of square miles according to the diversification of the physical environment" (Williams 1964:99). This straight line is described by Williams with the formula:

$$\log S = k \log(N/x).$$

Finally, Williams (1964) discussed an ultimate straight-line rise in the species-area relationship which would occur if we added continental floras together to produce a world flora. This would occur since the floras of two continents are more different from one another than the floras of two halves of one continent. Diversity of origin, evolution, and isolation presumably make this so.

My study site surely included more than a few hundred individuals. Therefore, I observed the first two (exponential) portions of the species-area relationship that Williams (1964) described. I also believe that the limits of a single environment were reached at my site (including the log-log portion of the curve). That is, the rate of accumulation of species numbers accelerated in stairstep

fashion repeatedly (for example, Figure 6). Perhaps this occurred because the limit of "the single environment" (Williams 1964:99) was reached. Single environments may encompass only a few square yards. They were perhaps represented on the study area by area of different aspects, habitats near the road, and the alluvial area by Mason's Creek.

Conner and McCoy (1979) also discussed whether there is biological significance of the parameters of species-area models; that is, whether the slope and intercept are biologically meaningful. They concluded that the regular occurrence of slope values between 0.2 and 0.4 (Preston's canonical values; Preston 1962) in the power model may be a coincidence of any regression with a high  $r$  and a small range of dependent variable (species number) compared to the independent variable (area). Commonly, only studies with high  $r$  values are published and available for review.

Connor and McCoy (1979) also interpreted intercept values as having no meaning, other than that a 0 intercept indicates no species occurring in 0 area (for the untransformed and exponential models). For power ( $\ln(\text{species} + 1) = \ln(\text{area} + 1)$ ) and logspecies ( $\ln(\text{species} + 1) = \text{area}$ ) models, they interpreted an intercept greater than 0 to mean that some number of species exists in 1 unit of area (because  $\ln(1) = 0$ ).

### **Limits of Prediction**

Kilburn (1966) indicated that his equations relating area to numbers of species overpredicted species numbers in areas larger than those sampled. Unfortunately, he illustrated his point by comparing his studies of 900-m<sup>2</sup> quadrats, each within a prairie or pine community type, with county floras. Equations developed for his quadrats grossly overpredicted the number of species that might be found in an area as large as a county. This is not a surprising conclusion. None of the species area curves from Kilburn's data approached horizontal. All curves were still rising in an exponential J-shape. Extrapolation from such a curve would lead to predicting very high numbers of species, perhaps even an infinite number, for large areas (Figure 14).

My study also indicated the impracticality of extrapolating results from small areas (60 ha) to large ones (7000 ha; Tables 17-19). However, for predicting areas not much larger than those sampled, prediction equations can be used. Equations may be useful for areas twice as large as

those sampled. Also, good predictions of species numbers in 60 ha were made using plot data from 0.45 ha. In such cases, the assumption must be made that the additional area does not include community types not represented in the sampled area.

### **Taxonomy and Species Richness**

An issue that needs further consideration and discussion is the impact of taxonomic decisions on richness estimates. Taxonomic and systematic studies on various species, genera, and families are constantly being completed in the field of botany. New species, subspecies, and hybrids may be proposed in these studies, or a taxon may be moved from one genus or family to another in the light of new evidence. Taxonomic decisions are partly based on interpretation of putative evolutionary relationships. There will always be a lack of information in that sphere, so the debates will possibly never be resolved.

The field investigator should keep abreast of taxonomic revisions reported in the literature, and he or she can also use a reputable key in the field to help determine taxa. The investigator must use his or her best judgement as to which taxon a collected specimen represents. Hybrids and subspecies may be present in a study area, and the investigator should do his or her best to identify and report these as a matter of botanical interest.

Taxonomic decisions are also based on the concept of a species. What constitutes a plant species? Species have traditionally been delineated by commonly shared morphological characteristics consistently expressed among individuals. In other words, "phenetic discontinuities" separate species (Levin 1979:383).

In this day and age, commonly shared characteristics may extend to chloroplast DNA, when feasible, which is considered a fairly conservative character. However, such a species concept begs a few deeper questions, such as: "How or why are characteristics consistently shared among individuals?" "How much similarity is required to 'constitute' or 'delineate' a species?" That is, what is the nature of a plant species?

Levin (1979:381) discussed three features that "allegedly make a species a unique evolutionary unit," and he argued against accepting any of them at face value. The first feature is the apparently undisputed reality of a species. Mayr, as quoted in Levin, says "that species are real objective units,

because the delimitation of each species is definite, and not open to argument except in border-line cases" (Levin 1979:381). Levin refutes this view. He holds that the "reality" of a species is simply *not* defensible since debate on species delimitations have occurred and probably will continue within many plant genera.

Secondly, species supposedly have interbreeding populations, that is, unrestricted gene flow among populations. But Levin (1979) discussed several examples of restricted propagule dispersal in plants, proposing that long-term dispersal of viable propagules is the exception, not the rule. Matlack (1992) also reported slow migration rates of species as being closely linked to seed dispersal mode. This suggested low dispersal ability of some species.

Thirdly, species are supposed to be incapable of interbreeding. Yet numerous examples of hybridization among species exist in the plant kingdom. In addition, plants may alter their chromosome number through reproduction resulting in polyploid entities, which often have been given species status. Levin (1979:383) also suggested that reproductive genetic barriers may not correspond at all to the "phenetic discontinuities upon which utilitarian taxonomies are based."

This brings us to the point of utilitarianism. The tradition of delimitation of species by phenotypic, identifiable traits will continue because of its utility. Species delimitations give us some way to estimate and conceive of diversity. However, it is always wise to remember that our delimitation is "artificial" if it does not reflect underlying evolutionary mechanisms. To quote Levin's abstract (Levin 1979:381):

The species concept is a central tenet of biological diversity. Attempts to describe diversity have led to empirical concepts of species based on assumptions found wanting in plants. Plant species lack reality, cohesion, independence, and simple evolutionary or ecological roles. The concept of species for plant taxonomists and evolutionists can only serve as a tool for characterizing diversity in a mentally satisfying way. Diversity is idiosyncratic. It is impossible to reconcile idiosyncrasy with preconceived ideas of diversity. The search for hidden likenesses is unlikely to yield a unifying species concept. The

concept that is most operational and utilitarian for plants is a mental abstraction which orders clusters of diversity in multidimensional character space.

Although the concept of species may be artificial, it is useful. There is enough agreement on the "boundaries" or "identity" of a large number of taxa. For those taxa in which delimitations are debated, one can be guided by choosing a reputable key, reputable studies, and using one's own observations to make a judgment.

Williams (1964) commented that misidentification of species can cause the overestimation of species numbers. However, failure to distinguish among species, due to lack of knowledge or recognition, can lead to an underestimate of species numbers.

The main error in the recorded number of species is one of underestimation due to insufficient knowledge. This error is small in small areas and in well-studied countries, but may be very large in some tropical area where no extended study has ever been made. There are two possible sources of overestimation: first mis-identification, and secondly the inclusion in some floras of exotic forms which have been brought in only in recent times by agriculture and commerce. It is, however, unlikely that either of these will outweigh the effect of lack of knowledge (Williams 1964:95).

In conclusion, misidentifications and inclusion of exotic species can cause overestimates of species richness. Lack of sufficient knowledge (or sampling) of an area can lead to underestimates of richness. Disagreements over what constitutes a species may increase or decrease richness estimates of an area to some degree.

## CONCLUSIONS AND RECOMMENDATIONS

Timed-search meanders and transects worked better than plots for estimating species richness of the study area. The first two methods yielded higher richness estimates in similar amounts of time than did plot sampling. That is, meanders and transects covered more area in similar amounts of time than when I used plot sampling. However, if accurate estimates of area are required, plots, measured transects, point-intercept transects, or plotless methods must be used. Measured transects could possibly take as long to set up as plots.

Species compositions of lists made from meanders were different than those from transects. A combination of methods, if feasible, would identify a higher proportion of species present than would one method alone. However, a higher proportion of species than could be found by one method alone could be found by using repeated meanders (Kirby et al. 1986). That is, the same area should be re-sampled at least once by the same observer on subsequent days using different routes within the same sampling season. Repeated meanders should be used again in a second and third sampling season. Species detection depends on the paths chosen and plant distribution (Kirby et al. 1986). Kirby et al. (1986) also concluded that the number of species detected by a walk at any one season ranged from 56% to 76% of the total number of species found by all walks made at that season. That is, if all walks represented total species richness, any one walk would detect only 56% to 76% of all species there. Greater detection may result from a greater number of walks through the same area.

If one method must be chosen, the experienced investigator should use meanders. This method requires the least amount of set-up time. It can be quite successful in locating a high percentage of species, particularly if Goff's 30-minute guideline is used (Goff et al. 1982).

For investigators with a lack of botanical experience, I recommend the use of transects. Even systematically-placed transects can locate high numbers of species and provide sufficient guidelines for a search. Non-randomly placed transects, which would be preferable when crossing through many microhabitats, would require some experience to locate.

Sampling should be conducted in a minimum of two sampling seasons, though three are preferred (May, July, and September). Real seasonal differences in species abundance and conspicuousness occur because of different flowering times of different species (Kirby et al. 1986). Kirby et al. (1986) suggests that if a researcher wants to know one site in depth, send the same observer over two seasons. If examining many sites, a team of competent observers needs to be sent so as many sites as possible may be observed in the same season. Finally, a learning effect can be positive when the same observer repeats observations within an area or within similar communities. One learns where to look for species in less time.

If species-area or species-effort data are modeled, appropriate models cannot be determined a priori. Models can be used to predict species richness in areas larger than those searched. I found predictions made with species-area data more conservative and probably more likely than predictions made with species-effort data, especially when extrapolating to large areas. Care must be taken when predicting not to extrapolate data taken from one community type to areas containing several communities (underprediction results). Researchers should also not estimate for large areas from data taken from small areas in which the species-area curve is still rising to much larger areas (overprediction results). Under- and overprediction of richness may also occur from misidentifications.

I found that decisions as to whether species-area and species-effort curves had leveled off were somewhat subjective. However, the use of Goff's 30-minute guideline might have alleviated this problem (Goff et al. 1982), and I should have used it. The leveling-off of the species-effort curve would have allowed me to say that enough time had been spent searching.

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Table 1. Abiotic and biotic factors affecting plant species distribution.

Factors	Related Literature
Aspect	Carvell and Tryon 1959; Del Moral 1972; Stephenson 1974, 1976; Zobel et al. 1976; Peet 1978; McEvoy et al. 1980; Travis 1982; Fies 1983; Johnson-Groh and Farrar 1985; Farrar and Johnson-Groh 1988
Availability of micro-sites for germination	Collins 1988
Competition	Mowbray and Oosting 1968; Pielou 1975, 1979; Zobel et al. 1976; Green 1979; Collins 1988
Cover type	Collins 1988
Disturbance frequency	Collins 1988
Elevation	Whittaker 1956, 1960; Hack and Goodlett 1960; Del Moral 1972; Adams and Rhoades 1976; Stephenson 1976; Peet 1978; Travis 1982; Fies 1983; Phillippi and Boebinger 1986
Exposure	Hack and Goodlett 1960
Geology	Hack and Goodlett 1960; Del Moral 1972; Stephenson 1976; Bell 1978; Travis 1982
Landform	Hack and Goodlett 1960; Travis 1982; Fies 1983; Farrar and Johnson-Groh 1988
Litter depth	Collins 1988
Microclimate	McEvoy et al. 1980; Jones and Churchill 1987
Moisture	Whittaker 1956, 1960; Carvell and Tryon 1959; Hack and Goodlett 1960; Stephenson 1976; Zobel et al. 1976; Peet 1978; Blackman and Ware 1982; Kasmer et al. 1984; Jones and Gresham 1985
Plant moisture stress	Zobel et al. 1976
Precipitation	Martin 1988
Predation	Collins 1988
Proneness to drought	Daubenmire 1968
Slope inclination	Stephenson 1976; McEvoy et al. 1980; Travis 1982; Fies 1983; Kasmer et al. 1984; Johnson-Groh and Farrar 1985

Table 1, cont'd.

Factors	Related Literature
Slope position	Carvell and Tryon 1959; Hack and Goodlett 1960; Stephenson 1976; McEvoy et al. 1980; Travis 1982; Johnson-Groh and Farrar 1985
Snow pack	Zobel et al. 1976
Soil depth	McEvoy et al. 1980; Travis 1982; Collins 1988
Soil mineralization	Stephenson 1976; Kasmer et al. 1984
Soil nutrients	Zobel et al. 1976; Kasmer et al. 1984; Collins 1988
Soil pH	Stephenson 1976; Kasmer et al. 1984
Soil texture	Hack and Goodlett 1960; Mowbray and Oosting 1968; Stephenson 1976; McEvoy et al. 1980
Solar insolation	McEvoy et al. 1980; Fountain 1986
Successional stage	Bell 1978; Peet 1978; Kasmer et al. 1984; Collins 1988
Temperature	Zobel et al. 1976
Vegetative propagation	Collins 1988

Table 2. Aspect and elevation of the five subareas of the study area at Fort Lewis Mountain, Roanoke County, Virginia.

Area	Aspect*	Elevation (m)
NW-low	NW	530-699
NW-mid	NW	700-825
NW-high	NW	825-975
SE-high	SE	825-975
SE-mid	SE	700-825

\* Aspect denotes the side of the main ridge the subarea is located on. Within the middle elevation subareas, spur ridge slopes at 90 degree angles to the main ridge create NE and SW exposures.

Table 3. Elevations and lengths of belt transects used at Ft. Lewis Mountain, Roanoke County, Virginia, 1991.

Elevation (m)	Aspect <sup>1</sup>	Length (m)
530	NW	10
550	NW	194
610	NW	557
670	NW	483
730	NW	460
790	NW	339
855	NW	266
915	NW	242
975	NW	242
975	SE	242
915	SE	266
855	SE	169
790	SE	269
730	SE	219

Total transect length = 3958 m

Total transect area = 3958 m x 2 m = 0.79 ha

<sup>1</sup>Aspect denotes side of main ridge.

Table 4. Elevations and numbers of plots at each elevation, Ft. Lewis Mountain, Roanoke County, Virginia, 1991.

Elevation (m)	Aspect <sup>1</sup>	Number of plots
530	NW	2
580	NW	5
640	NW	5
730	NW	4
790	NW	4
885	NW	5
945	NW	5
945	SE	5
885	SE	5
790	SE	5
730	SE	0

Total area sampled with plots = 45 x 100 m<sup>2</sup> = 0.45 ha

<sup>1</sup>Aspect denotes the direction faced by the side of the mountain.

Table 5. Sampling schedule, Ft. Lewis Mountain, Roanoke County, Virginia, 1991.

Date	Type and location of sampling
Sampling Period 1	
5/27/91	walk, low elevation, northwest side
5/28/91	walk, low elevation, northwest side; transect, 550 m northwest side
5/29/91	transects, 550 m and 610 m, northwest side
5/31/91	transect, 530 m, northwest side
6/2/91	plots, 640 m, northwest side
6/3/91	plots, 580 m, northwest side
6/4/91	plots, 580 m, northwest side
6/7/91	walk, high elevation, southeast side
6/8/91	plots, 530 m, northwest side
6/11/91	walk, high elevation, southeast side
6/13/91	plots, 945 m, southeast side
6/15/91	walk, high elevation, northwest side
6/17/91	walk, high elevation, northwest side
6/18/91	transect, 670 m, northwest side
6/19/91	plots, 945 m, southeast side
6/21/91	walk (by Tom Wieboldt), high elevation, northwest side
6/24/91	plots, 885 m, southeast side
6/26/91	plots, 945 m, northwest side
6/27/91	plots, 885 m, northwest side
6/28/91	transects, 855 m and 915 m, southeast side
6/29/91	transects, 855 m, 915 m, 975 m northwest side and 975 m southeast side
7/1/91	walk, middle elevation, southeast side
7/2/91	plots, 790 m, southeast side
7/3/91	transects, 730 m and 790 m, southeast side
7/11/91	walk, middle elevation, northwest side
7/14/91	transects, 730 m and 790 m, northwest side
7/16/91	plots, 790 m, northwest side
7/17/91	plots, 730 m, northwest side
Sampling Period 2	
8/12/91	walk, low elevation, northwest side
8/13/91	walk, low elevation, northwest side
8/14/91	transects, 550 m and 610 m, northwest side
8/15/91	transect, 670 m, northwest side; plots, 580 m and 640 m, northwest side
8/16/91	580 m and 530 m, northwest side
8/19/91	walk, high elevation, southeast side
8/20/91	walk, high elevation, northwest side
8/21/91	transects, 855 m, 915 m and 975 m, southeast side
8/22/91	transects, 855 m, 915 m, 975 m northwest side
8/23/91	plots, 885 m and 945 m, southeast side

Table 5, cont'd.

8/24/91 8/29 and 8/30/91	plots, 885 m and 945 m, northwest side observer differences, transect, 550 m, northwest side
<b>Date</b>	<b>Type and location of sampling</b>
9/1/91 9/2/91	walk, middle elevation, northwest side plots, 790 m, southeast side; transect, 790 m, southeast side
9/5/91 9/7/91 9/8/91	plots, 790 m, southeast side transects, 730 m and 790 m, northwest side plots, 730 m and 790 m, northwest side

Sampling period 3

9/21/91 9/22/91 9/26/91 9/28/91 9/29/91	walk, low elevation, northwest side walk, high elevation, southeast side walk, high elevation, northwest side walk, middle elevation, southeast side walk, middle elevation, northwest side
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Table 6. Species list from study area within Havens, Ft. Lewis Mountain, summer 1991.

Species	Common Name	Family
<i>Acer pensylvanicum</i>	striped maple <sup>1</sup>	Aceraceae
<i>Acer rubrum</i>	red maple <sup>1</sup>	Aceraceae
<i>Acer saccharum</i>	sugar maple <sup>1</sup>	Aceraceae
<i>Actaea pachypoda</i>	baneberry <sup>1</sup>	Ranunculaceae
<i>Adiantum pedatum</i>	American maidenhair fern <sup>1</sup>	Sinopteridaceae
<i>Agrostis perennans</i>	bentgrass <sup>1</sup>	Poaceae
<i>Ailanthus altissima</i>	tree-of-heaven ailanthus <sup>1</sup>	Simaroubaceae
<i>Allium cernuum</i>	nodding onion, onion <sup>1</sup>	Liliaceae
<i>Alnus serrulata</i>	hazel alder <sup>1</sup>	Betulaceae
<i>Amelanchier arborea</i>	downy serviceberry <sup>1</sup>	Rosaceae
<i>Amianthium muscaetoxicum</i>	flypoison	Liliaceae
<i>Amphicarpaea bracteata</i>	hog peanut	Fabaceae
<i>Andropogon</i> sp.	bluestem <sup>1</sup>	Poaceae
<i>Anemone quinquefolia</i>	wood anemone <sup>1</sup>	Ranunculaceae
<i>Antennaria plantaginifolia</i>	plantainleaf pussytoes <sup>1</sup>	Asteraceae
<i>Aplectrum hyemale</i>	putty root	Orchidaceae
<i>Apocynum</i> sp.	dogbane <sup>1</sup>	Apocynaceae
<i>Aralia nudicaulis</i>	wild sarsparilla <sup>1</sup>	Araliaceae
<i>Arisaema triphyllum</i>	jack-in-the-pulpit <sup>1</sup>	Araceae
<i>Aristolochia macrophylla</i>	Dutchman's pipe	Aristolochiaceae
<i>Aruncus dioicus</i>	goat's beard	Rosaceae
<i>Asclepias exaltata</i>	poke milkweed	Asclepiadaceae
<i>Asclepias quadrifolia</i>	whorled milkweed	Asclepiadaceae
<i>Asplenium platyneuron</i>	ebony spleenwort	Aspleniaceae
<i>Aster cordifolius</i>	aster <sup>1</sup>	Asteraceae
<i>Aster divaricatus</i>	aster <sup>1</sup>	Asteraceae
<i>Aster infirmus</i>	aster <sup>1</sup>	Asteraceae
<i>Aster macrophyllus</i>	bigleaf aster <sup>1</sup>	Asteraceae
<i>Aster patens</i>	aster <sup>1</sup>	Asteraceae
<i>Aster schreberi</i>	aster <sup>1</sup>	Asteraceae
<i>Aster undulatus</i>	aster <sup>1</sup>	Asteraceae
<i>Athyrium filix-femina</i>	common ladyfern <sup>1</sup>	Woodsiaceae
<i>Aureolaria flava</i>		Scrophulariaceae
<i>Aureolaria laevigata</i>		Scrophulariaceae
<i>Baptisia tinctoria</i>	yellow wild indigo <sup>1</sup>	Fabaceae
<i>Betula lenta</i>	sweet birch <sup>1</sup>	Betulaceae
<i>Bidens</i> sp.	beggarticks <sup>1</sup>	Asteraceae
<i>Botrychium virginianum</i>	rattlesnake fern	Ophioglossaceae
<i>Brachyelytrum erectum</i>		Poaceae
<i>Bromus ciliatus</i>	fringed brome <sup>1</sup>	Poaceae
<i>Calamagrostis porteri</i>	reedgrass <sup>1</sup>	Poaceae
<i>Campanula divaricata</i>	bellflower <sup>1</sup>	Campanulaceae
<i>Carex appalachica</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex cephalophora</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex communis</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex digitalis</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex laxiflora</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex oligocarpa</i>	fewfruit sedge <sup>1</sup>	Cyperaceae
<i>Carex pensylvanica</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex platyphylla</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex rosea</i>	sedge <sup>1</sup>	Cyperaceae

Table 6, cont'd.

<i>Carex swanii</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex virescens</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carex woodii</i>	sedge <sup>1</sup>	Cyperaceae
<i>Carya cordiformis</i>	bitternut hickory <sup>1</sup>	Juglandaceae
<i>Carya glabra</i>	pignut hickory <sup>1</sup>	Juglandaceae
<i>Carya ovalis</i>	red hickory <sup>1</sup>	Juglandaceae
<i>Carya ovata</i>	shagbark hickory <sup>1</sup>	Juglandaceae
<i>Carya tomentosa</i>	mockernut hickory <sup>1</sup>	Juglandaceae
<i>Castanea dentata</i>	American chestnut <sup>1</sup>	Fagaceae
<i>Chenopodium album</i>	lambquarters goosefoot <sup>1</sup>	Chenopodiaceae
<i>Chimaphila maculata</i>	pipsissewa <sup>1</sup>	Ericaceae
<i>Chrysogonum virginianum</i>	green-and-gold	Asteraceae
<i>Cimicifuga racemosa</i>	cohosh bugbane <sup>1</sup>	Ranunculaceae
<i>Collinsonia canadensis</i>	stoneroot	Lamiaceae
<i>Comptonia peregrina</i>	alien sweetfern <sup>1</sup>	Myricaceae
<i>Conopholis americana</i>	American squawroot <sup>1</sup>	Orobanchaceae
<i>Convallaria montana</i>	lily-of-the-valley	Liliaceae
<i>Coreopsis major</i>	coreopsis; tickseed <sup>1</sup>	Asteraceae
<i>Coreopsis verticillata</i>	coreopsis; tickseed <sup>1</sup>	Asteraceae
<i>Cornus florida</i>	flowering dogwood <sup>1</sup>	Cornaceae
<i>Corylus americana</i>	American filbert <sup>1</sup>	Betulaceae
<i>Corylus cornuta</i>	beaked filbert <sup>1</sup>	Betulaceae
<i>Crataegus</i> sp.	hawthorn <sup>1</sup>	Rosaceae
<i>Cunila origanoides</i>		Lamiaceae
<i>Cypripedium acaule</i>	pink lady's slipper	Orchidaceae
<i>Danthonia spicata</i>	poverty danthonia <sup>1</sup>	Poaceae
<i>Dennstaedtia punctilobula</i>	hayscented fern	Dennstaedtiaceae
<i>Desmodium nudiflorum</i>	barestem tickclover <sup>1</sup>	Fabaceae
<i>Diervilla lonicera</i>	common bush-honeysuckle <sup>1</sup>	Caprifoliaceae
<i>Dioscorea villosa</i>	wild yam	Dioscoreaceae
<i>Dryopteris marginalis</i>	marginal woodfern	Dryopteridaceae
<i>Epigaea repens</i>	trailing-arbutus <sup>1</sup>	Ericaceae
<i>Erechtites hieracifolia</i>	American burnweed <sup>1</sup>	Asteraceae
<i>Eupatorium purpureum</i>	joe-pye-weed	Asteraceae
<i>Eupatorium rugosum</i>	eupatorium <sup>1</sup>	Asteraceae
<i>Eupatorium sessilifolium</i>	eupatorium <sup>1</sup>	Asteraceae
<i>Fagopyrum esculentum</i>	common buckwheat <sup>1</sup>	Polygonaceae
<i>Fagus grandifolia</i>	American beech <sup>1</sup>	Fagaceae
<i>Festuca obtusa</i>	fescue <sup>1</sup>	Poaceae
<i>Fraxinus americana</i>	white ash <sup>1</sup>	Oleaceae
<i>Galax aphylla</i>	coltsfoot galax <sup>1</sup>	Diapensiaceae
<i>Galium circaeazans</i>	bedstraw <sup>1</sup>	Rubiaceae
<i>Galium latifolium</i>	bedstraw <sup>1</sup>	Rubiaceae
<i>Galium triflorum</i>	sweet-scented bedstraw <sup>1</sup>	Rubiaceae
<i>Gaultheria procumbens</i>	checkerberry wintergreen <sup>1</sup>	Ericaceae
<i>Gaylussacia baccata</i>	black huckleberry <sup>1</sup>	Ericaceae
<i>Geranium maculatum</i>	wild geranium	Geraniaceae
<i>Geum</i> sp.	avens <sup>1</sup>	Rosaceae
<i>Goodyera pubescens</i>	downy rattlesnake-plantain <sup>1</sup>	Orchidaceae
<i>Hamamelis virginiana</i>	common witchhazel <sup>1</sup>	Hamamelidaceae
<i>Helianthus divaricatus</i>	sunflower <sup>1</sup>	Asteraceae
<i>Heuchera americana</i>	alumroot <sup>1</sup>	Saxifragaceae
<i>Heuchera pubescens</i>	alumroot <sup>1</sup>	Saxifragaceae

Table 6, cont'd.

<i>Hexastylis</i> sp.	heartleaf; wild ginger	Aristolochiaceae
<i>Hieracium paniculatum</i>	hawkweed <sup>1</sup>	Asteraceae
<i>Hieracium venosum</i>	hawkweed <sup>1</sup>	Asteraceae
<i>Houstonia caerulea</i>	common bluets <sup>1</sup>	Rubiaceae
<i>Houstonia longifolia</i>		Rubiaceae
<i>Hydrangea arborescens</i>	smooth hydrangea <sup>1</sup>	Saxifragaceae
<i>Hypoxis hirsuta</i>	common goldstargrass <sup>1</sup>	Liliaceae
<i>Ilystrix patula</i>	common bottlebrushgrass <sup>1</sup>	Poaceae
<i>Ilex montana</i>	mountain holly <sup>1</sup>	Aquifoliaceae
<i>Iris verna</i>	dwarf iris	Iridaceae
<i>Isotria verticillata</i>	whorled pogonia	Orchidaceae
<i>Juglans</i> sp.	walnut or butternut	Juglandaceae
<i>Kalmia latifolia</i>	mountain-laurel kalmia <sup>1</sup>	Ericaceae
<i>Laportea canadensis</i>	wood nettle	Urticaceae
<i>Lathyrus venosus</i>	veiny peavine <sup>1</sup>	Fabaceae
<i>Lespedeza hirta</i>		Fabaceae
<i>Lespedeza intermedia</i>	wand lespedeza <sup>1</sup>	Fabaceae
<i>Ligusticum canadense</i>	American lovage	Apiaceae
<i>Lilium michauxii</i>	Michaux's lily	Liliaceae
<i>Lilium superbum</i>	turk's-cap lily	Liliaceae
<i>Lindera benzoin</i>	common spicebush <sup>1</sup>	Lauraceae
<i>Linum striatum</i>	flax <sup>1</sup>	Linaceae
<i>Liriodendron tulipifera</i>	North American tuliptree <sup>1</sup>	Magnoliaceae
<i>Lycopodium digitatum</i>	running pine	Lycopodiaceae
<i>Lycopodium obscurum</i>	ground pine	Lycopodiaceae
<i>Lycopodium tristachyum</i>	ground cedar	Lycopodiaceae
<i>Lysimachia quadrifolia</i>	fourleaf loosestrife <sup>1</sup>	Primulaceae
<i>Magnolia acuminata</i>	cucumber-tree magnolia <sup>1</sup>	Magnoliaceae
<i>Medeola virginiana</i>	Indian cucumber root	Liliaceae
<i>Melanthium hybridum</i>	bunch-flower	Liliaceae
<i>Melilotus</i> sp.	sweetclover <sup>1</sup>	Fabaceae
<i>Menziesia pilosa</i>	menziesia <sup>1</sup>	Ericaceae
<i>Mitchella repens</i>	partridgeberry <sup>1</sup>	Rubiaceae
<i>Monarda clinopodia</i>	bee balm <sup>1</sup>	Lamiaceae
<i>Monotropa hypopithys</i>	pinemap	Ericaceae
<i>Monotropa uniflora</i>	common Indian-pipe <sup>1</sup>	Ericaceae
<i>Muhlenbergia tenuiflora</i>	muhly <sup>1</sup>	Poaceae
<i>Nyssa sylvatica</i>	blackgum tupelo <sup>1</sup>	Nyssaceae
<i>Oenothera fruticosa</i>	eveningprimrose <sup>1</sup>	Onagraceae
<i>Osmunda cinnamomea</i>	cinnamon fern <sup>1</sup>	Osmundaceae
<i>Ostrya virginiana</i>	American hophornbeam <sup>1</sup>	Betulaceae
<i>Oxydendrum arboreum</i>	sourwood <sup>1</sup>	Ericaceae
<i>Panicum capillare</i>	witchgrass panicum <sup>1</sup>	Poaceae
<i>Panicum clandestinum</i>	deertongue panicum <sup>1</sup>	Poaceae
<i>Panicum commutatum</i>	panic grass	Poaceae
<i>Panicum depauperatum</i>	panic grass	Poaceae
<i>Panicum dichotomum</i>	panic grass	Poaceae
<i>Panicum latifolium</i>	wideleaf panicum <sup>1</sup>	Poaceae
<i>Paronychia canadensis</i>		Caryophyllaceae
<i>Parthenocissus quinquefolia</i>	Virginia creeper <sup>1</sup>	Vitaceae
<i>Penstemon laevigatus</i>	penstemon <sup>1</sup>	Scrophulariaceae
<i>Phlox ovata</i>	phlox <sup>1</sup>	Polemoniaceae
<i>Phryma leptostachya</i>	lopseed	Phrymaceae
<i>Phytolacca americana</i>	common pokeberry <sup>1</sup>	Phytolaccaceae

Table 6, cont'd.

<i>Pieris floribunda</i>	fetter bush	Ericaceae
<i>Pinus pungens</i>	tablemountain pine <sup>1</sup>	Pinaceae
<i>Pinus rigida</i>	pitch pine <sup>1</sup>	Pinaceae
<i>Pinus strobus</i>	white pine <sup>1</sup>	Pinaceae
<i>Pinus virginiana</i>	Virginia pine	Pinaceae
<i>Polygonatum biflorum</i>	Solomon's seal	Liliaceae
<i>Polygonatum pubescens</i>	Solomon's seal	Liliaceae
<i>Polygonum convolvulus</i>	dullseed cornbind <sup>1</sup>	Polygonaceae
<i>Polygonum scandens</i>	hedge cornbind <sup>1</sup>	Polygonaceae
<i>Polypodium virginianum</i>	common polypody	Polypodiaceae
<i>Polystichum acrostichoides</i>	Christmas hollyfern <sup>1</sup>	Dryopteridaceae
<i>Populus grandidentata</i>	bigtooth aspen <sup>1</sup>	Salicaceae
<i>Porteranthus trifoliatu</i> s	Indian physic	Rosaceae
<i>Potentilla canadensis</i>	cinquefoil <sup>1</sup>	Rosaceae
<i>Potentilla simplex</i>	cinquefoil <sup>1</sup>	Rosaceae
<i>Prenanthes altissima</i>	rattlesnakeroot <sup>1</sup>	Asteraceae
<i>Prenanthes trifoliata</i>	threeleaf rattlesnakeroot	Asteraceae
<i>Prunus serotina</i>	black cherry <sup>1</sup>	Rosaceae
<i>Prunus virginiana</i>	common chokecherry <sup>1</sup>	Rosaceae
<i>Pteridium aquilinum</i>	common bracken fern <sup>1</sup>	Dennstaedtiaceae
<i>Pycnanthemum incanum</i>	mountainmint <sup>1</sup>	Lamiaceae
<i>Pyrola americana</i>	shinleaf, pyrola <sup>1</sup>	Ericaceae
<i>Pyrularia pubera</i>	Allegheny oilnut <sup>1</sup>	Santalaceae
<i>Quercus alba</i>	white oak <sup>1</sup>	Fagaceae
<i>Quercus coccinea</i>	scarlet oak <sup>1</sup>	Fagaceae
<i>Quercus ilicifolia</i>	scrub oak <sup>1</sup>	Fagaceae
<i>Quercus marilandica</i>	blackjack oak <sup>1</sup>	Fagaceae
<i>Quercus prinus</i>	chestnut oak <sup>1</sup>	Fagaceae
<i>Quercus rubra</i>	northern red oak <sup>1</sup>	Fagaceae
<i>Quercus velutina</i>	black oak <sup>1</sup>	Fagaceae
<i>Rhododendron calendulaceum</i>	flame azalea	Ericaceae
<i>Rhododendron maximum</i>	rosebay rhododendron <sup>1</sup>	Ericaceae
<i>Rhododendron periclymenoides</i>	pinxter flower	Ericaceae
<i>Rhododendron prinophyllum</i>	election pink	Ericaceae
<i>Rhus typhina</i>	staghorn sumac <sup>1</sup>	Anacardiaceae
<i>Ribes rotundifolium</i>	gooseberry <sup>1</sup>	Saxifragaceae
<i>Robinia pseudoacacia</i>	black locust <sup>1</sup>	Fabaceae
<i>Rosa carolina</i>	Carolina rose <sup>1</sup>	Rosaceae
<i>Rubus allegheniensis</i>	Allegheny blackberry <sup>1</sup>	Rosaceae
<i>Rubus flagellaris</i>	northern dewberry <sup>1</sup>	Rosaceae
<i>Rubus occidentalis</i>	blackcap raspberry <sup>1</sup>	Rosaceae
<i>Rubus odoratus</i>		Rosaceae
<i>Sanicula marilandica</i>	snakeroot	Apiaceae
<i>Sassafras albidum</i>	white sassafras <sup>1</sup>	Lauraceae
<i>Scirpus verecundus</i>	bulrush <sup>1</sup>	Cyperaceae
<i>Scutellaria saxatilis</i>	skullcap <sup>1</sup>	Lamiaceae
<i>Scutellaria serrata</i>	skullcap <sup>1</sup>	Lamiaceae
<i>Senecio</i> sp.	groundsel <sup>1</sup>	Asteraceae
<i>Silene stellata</i>	silene; <sup>1</sup> catchfly <sup>1</sup>	Caryophyllaceae
<i>Silene virginica</i>	catchfly; <sup>1</sup> fire pink	Caryophyllaceae
<i>Smilacina racemosa</i>	feather solomonplume <sup>1</sup>	Liliaceae
<i>Smilax glauca</i>	cat greenbrier <sup>1</sup>	Smilacaceae
<i>Smilax rotundifolia</i>	common greenbrier <sup>1</sup>	Smilacaceae
<i>Solidago arguta</i>	goldenrod <sup>1</sup>	Asteraceae

Table 6, cont'd.

<i>Solidago curtisii</i>	goldenrod <sup>1</sup>	Asteraceae
<i>Solidago flexicaulis</i>	goldenrod <sup>1</sup>	Asteraceae
<i>Solidago roanensis</i>	goldenrod <sup>1</sup>	Asteraceae
<i>Sphenopholis nitida</i>	wedgegrass <sup>1</sup>	Poaceae
<i>Stellaria pubera</i>	starwort; <sup>1</sup> giant chickweed	Caryophyllaceae
<i>Tephrosia virginiana</i>	Virginia goatsrue <sup>1</sup>	Fabaceae
<i>Thalictrum revolutum</i>	meadowrue <sup>1</sup>	Ranunculaceae
<i>Thaspium barbinode</i>	meadow parsnip	Apiaceae
<i>Thaspium trifoliatum</i>	meadow parsnip	Apiaceae
<i>Thelypteris noveboracensis</i>	New York fern	Thelypteridaceae
<i>Tilia americana</i>	American linden <sup>1</sup>	Tiliaceae
<i>Tilia heterophylla</i>	white basswood <sup>1</sup>	Tiliaceae
<i>Toxicodendron radicans</i>	common poison-ivy <sup>1</sup>	Anacardiaceae
<i>Trientalis borealis</i>	American starflower <sup>1</sup>	Primulaceae
<i>Trifolium repens</i>	white clover <sup>1</sup>	Fabaceae
<i>Tsuga canadensis</i>	Canada hemlock <sup>1</sup>	Pinaceae
<i>Tsuga caroliniana</i>	Carolina hemlock	Pinaceae
<i>Uvularia perfoliata</i>	bellwort	Liliaceae
<i>Uvularia pudica</i>	bellwort	Liliaceae
<i>Vaccinium angustifolium</i>	lowbush blueberry	Ericaceae
<i>Vaccinium erythrocarpum</i>	bearberry	Ericaceae
<i>Vaccinium pallidum</i>	low blueberry	Ericaceae
<i>Vaccinium stamineum</i>	deerberry <sup>1</sup>	Ericaceae
<i>Viburnum acerifolium</i>	mapleleaf viburnum <sup>1</sup>	Caprifoliaceae
<i>Viburnum prunifolium</i>	blackhaw viburnum <sup>1</sup>	Caprifoliaceae
<i>Vicia caroliniana</i>	Carolina vetch	Fabaceae
<i>Vicia</i> sp.	vetch <sup>1</sup>	Fabaceae
<i>Viola hastata</i>	Halberd-leaved violet	Violaceae
<i>Viola palmata</i>		Violaceae
<i>Viola pedata</i>	Birdfoot violet	Violaceae
<i>Viola pubescens</i>		Violaceae
<i>Viola triloba</i>		Violaceae
<i>Vitis aestivalis</i>	summer grape <sup>1</sup>	Vitaceae
<i>Vitis vulpina</i>	frost grape <sup>1</sup>	Vitaceae
<i>Zizia aurea</i>	golden alexander	Apiaceae
<i>Zizia trifoliata</i>	golden alexander	Apiaceae

<sup>1</sup> from Scott and Wasser (1980).

Table 7. List of species observed only along the ridge road on Havens Wildlife Management Area, 1991.

Species	Common Name	Family
<i>Agastache scrophulariaefolia</i>		Lamiaceae
<i>Ambrosia artemisifolia</i>	common ragweed <sup>1</sup>	Asteraceae
<i>Aster dumosus</i>	bush aster <sup>1</sup>	Asteraceae
<i>Aster laevis</i>		Asteraceae
<i>Bromus pubescens</i>		Poaceae
<i>Chrysanthemum leucanthemum</i>	ox-eye daisy	Asteraceae
<i>Coreopsis pubescens</i>	tickseed sunflower	Asteraceae
<i>Dactylis glomerata</i>	orchardgrass <sup>1</sup>	Poaceae
<i>Diarrhena americana</i>		Poaceae
<i>Erigeron annuus</i>	daisy fleabane	Asteraceae
<i>Erigeron strigosus</i>	daisy fleabane	Asteraceae
<i>Galinsoga quadriradiata</i>	Peruvian daisy	Asteraceae
<i>Hedeoma pulegioides</i>	pennyroyal	Lamiaceae
<i>Helianthus strumosus</i>	sunflower	Asteraceae
<i>Juncus tenuis</i>	poverty rush <sup>1</sup>	Juncaceae
<i>Muhlenbergia frondosa</i>		Poaceae
<i>Muhlenbergia schreberi</i>	nimblewill muhly <sup>1</sup>	Poaceae
<i>Oxalis dillenii</i>		Oxalidaceae
<i>Oxalis stricta</i>	common yellow oxalis <sup>1</sup>	Oxalidaceae
<i>Pilea pumila</i>	Canada clearweed <sup>1</sup>	Urticaceae
<i>Plantago rugelii</i>	blackseed plantain <sup>1</sup>	Plantaginaceae
<i>Polygonum aviculare</i>	prostrate knotweed <sup>1</sup>	Polygonaceae
<i>Polygonum caespitosum</i>	smartweed	Polygonaceae
<i>Polygonum persicaria</i>	spotted ladythumb <sup>1</sup>	Polygonaceae
<i>Rumex</i> sp.	dock	Polygonaceae
<i>Solidago rugosa</i>	wrinkled goldenrod <sup>1</sup>	Asteraceae
<i>Verbena urticifolia</i>		Verbenaceae
<i>Veronica officinalis</i>	common speedwell <sup>1</sup>	Scrophulariaceae

<sup>1</sup> from Scott and Wasser (1980).

Table 8. Species observations from Ritchie et al. (1984) that were not observed by the author on the study site at Havens Wildlife Management Area, 1991.

Species	Common Name	Family
<i>Achillea millefolium</i>	common yarrow <sup>1</sup>	Asteraceae
<i>Anaphalis margaritacea</i>	common pearlyeverlasting <sup>1</sup>	Asteraceae
<i>Arctium minus</i>	burdock	Asteraceae
<i>Castanea pumila</i>	Allegheny chinkapin <sup>1</sup>	Fagaceae
<i>Celtis occidentalis</i>	common hackberry <sup>1</sup>	Ulmaceae
<i>Chrysopsis</i> sp.	goldenaster <sup>1</sup>	Asteraceae
<i>Cichorium intybus</i>	common chicory <sup>1</sup>	Asteraceae
<i>Coronilla varia</i>	common crownvetch <sup>1</sup>	Fabaceae
<i>Lepidium virginicum</i>	peppergrass <sup>1</sup>	Brassicaceae
<i>Lespedeza cuneata</i>	sericea lespedeza <sup>1</sup>	Fabaceae
<i>Rumex acetosella</i>	sheep sorrel	Polygonaceae
<i>Streptopus roseus</i>	twisted stalk <sup>1</sup>	Liliaceae
<i>Tiarella cordifolia</i>	Allegheny foamflower <sup>1</sup>	Saxifragaceae
<i>Tussilago farfara</i>	coltsfoot	Asteraceae
<i>Vaccinium corymbosum</i>	highbush blueberry <sup>1</sup>	Ericaceae
<i>Verbascum thapsus</i>	flanned mullein <sup>1</sup>	Scrophulariaceae

<sup>1</sup> from Scott and Wasser (1980).

Table 9. List of species observed by Wood (1944) probably occurring within Havens Wildlife Management Area, Roanoke County, Virginia. 1991.

Species	Common Name	Family
<i>Alettris farinosa</i>	colicroot	Liliaceae
<i>Anemone virginiana</i>	thimbleweed	Ranunculaceae
<i>Angelica venenosa</i>	angelica	Apiaceae
<i>Arabis canadensis</i>	sicklepod	Brassicaceae
<i>Arabis laevigata</i>		Brassicaceae
<i>Aralia spinosa</i>	Hercules club	Araliaceae
<i>Aronia melanocarpa</i>	black chokeberry	Rosaceae
<i>Asclepias longifolia</i>		Asclepiadaceae
<i>Aureolaria pedicularia</i>		Scrophulariaceae
<i>Betula alleghaniensis</i>	yellow birch	Betulaceae
<i>Carex laevivaginata</i>		Cyperaceae
<i>Carex vulpinoidea</i>		Cyperaceae
<i>Carya pallida</i>	sand hickory	Juglandaceae
<i>Centella asiatica</i>		
<i>Cercis canadensis</i>	redbud	Fabaceae
<i>Chamaelirium luteum</i>	blazing star	Liliaceae
<i>Circaea lutetiana</i> spp. canadensis	enchanter's nightshade	Onagraceae
<i>Cleistes divaricata</i>	spreading pogonia	Orchidaceae
<i>Danthonia sericea</i>	danthonia	Poaceae
<i>Desmodium glutinosum</i>	tick trefoil	Fabaceae
<i>Desmodium rotundifolium</i>	tick trefoil	Fabaceae
<i>Epilobium coloratum</i>		Onagraceae
<i>Eragrostis frankii</i>	love grass	Poaceae
<i>Erythronium americanum</i>	trout lily	Liliaceae
<i>Eupatorium fistulosum</i>	joe-pye-weed	Asteraceae
<i>Festuca myuros</i>	fescue	Poaceae
<i>Glyceria striata</i>	manna grass	Poaceae
<i>Helianthus laevigatus</i>	sunflower	Asteraceae
<i>Hypericum gentianoides</i>		Clusiaceae
<i>Iris cristata</i>	dwarf crested iris	Iridaceae
<i>Juncus acuminatus</i>	rush	Juncaceae
<i>Krigia virginica</i>	dwarf dandelion	Asteraceae
<i>Lespedeza nuttallii</i>	bush clover	Fabaceae
<i>Liatris graminifolia</i>	blazing star	Asteraceae
<i>Linum virginianum</i>	flax	Linaceae
<i>Liparis lilifolia</i>	lily-leaved twayblade	Orchidaceae
<i>Lyonia ligustrina</i>	maleberry	Ericaceae
<i>Melanthium virginicum</i>	bunch-flower	Liliaceae
<i>Muhlenbergia mexicana</i>		Poaceae
<i>Oenothera laciniata</i>	evening primrose	Onagraceae
<i>Osmunda regalis</i>	royal fern	Osmundaceae
<i>Pedicularis canadensis</i>	lousewort	Scrophulariaceae
<i>Penstemon canescens</i>	beard tongue	Scrophulariaceae
<i>Phlox subulata</i>	moss pink	Polemoniaceae
<i>Polygala polygama</i>	milkwort	Polygalaceae
<i>Polygonum tenue</i>	smartweed	Polygonaceae
<i>Pycnanthemum flexuosum</i>	mountain mint	Lamiaceae

Table 9, cont'd.

Species	Common Name	Family
<i>Ranunculus recurvatus</i>	hooked buttercup	Ranunculaceae
<i>Rhododendron catawbiense</i>	mountain rosebay	Ericaceae
<i>Rhus copallina</i>	winged sumac	Anacardiaceae
<i>Robinia hispida</i>	bristly locust	Fabaceae
<i>Scleria triglomerata</i>	nutrush	Cyperaceae
<i>Scrophularia lanceolata</i>	figwort	Scrophulariaceae
<i>Scutellaria elliptica</i>	skullcap	Lamiaceae
<i>Seriocarpus asteroides</i>		Asteraceae
<i>Seriocarpus linifolius</i>		Asteraceae
<i>Solidago bicolor</i>	goldenrod	Asteraceae
<i>Stenanthium gramineum</i>	featherbells	Liliaceae
<i>Stylosanthes biflora</i>	pencil flower	Fabaceae
<i>Triodanis perfoliata</i>	Venus' looking glass	Campanulaceae
<i>Viola hirsutula</i>	violet	Violaceae
<i>Viola rostrata</i>	long spurred violet	Violaceae
<i>Viola sagittata</i>	violet	Violaceae

Table 10. Time, area, number of species, and rates of species discovery for each sampling method in the Havens Wildlife Management Area, Roanoke County, Virginia, 1991.

Method	Time (hrs)	Area (ha)	Number of Species	New Species Observed/hour
Sampling Period 1				
Meanders	19.6		177	6.4 ± 3.9
Transects	19.7	0.79	199	9.7 ± 13.1
Plots	23.1	0.45	121	4.5 ± 6.2
Sampling Period 2				
Meanders	15		178	12.2 ± 11.1
Transects	19.2	0.79	185	9.7 ± 17.8
Plots	15.4	0.45	112	6.4 ± 10.6

Table 11.  $R^2$  and adjusted  $R^2$  ( $R^2_{\lambda}$ ) for four models using species-area and species-time data from plots, sampling period 1.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
Species X Area	$R^2 = 0.93$ $R^2_{\lambda} = 0.92$	$R^2 = 0.94$ $R^2_{\lambda} = 0.94$	$R^2 = 0.71$ $R^2_{\lambda} = 0.70$	$R^2 = 0.43$ $R^2_{\lambda} = 0.42$
		$p > t^s_i = 0.03$ $p > t^s_m = 0.0001$ $p > F^7 = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$
Species X Time	$R^2 = 0.96$ $R^2_{\lambda} = 0.95$	$R^2 = 0.94$ $R^2_{\lambda} = 0.94$	$R^2 = 0.71$ $R^2_{\lambda} = 0.70$	$R^2 = 0.48$ $R^2_{\lambda} = 0.47$
		$p > t_i = 0.05$ $p > t_m = 0.0001$ $p > F = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$
Area X Time	$R^2 = 0.98$ $R^2_{\lambda} = 0.98$			

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 12.  $R^2$  and adjusted  $R^2$  ( $R^2_{\lambda}$ ) for four models using species-area and species-time data from plots, sampling period 2.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
Species	$R^2 = 0.89$	$R^2 = 0.96$	$R^2 = 0.67$	$R^2 = 0.38$
X Area	$R^2_{\lambda} = 0.88$	$R^2_{\lambda} = 0.95$	$R^2_{\lambda} = 0.66$	$R^2_{\lambda} = 0.37$
		$p > t^5_i = 0.82$	$p > t_i = 0.0001$	$p > t_i = 0.0001$
		$p > t^6_m = 0.0001$	$p > t_m = 0.0001$	$p > t_m = 0.0001$
		$p > F^7 = 0.0001$	$p > F = 0.0001$	$p > F = 0.0001$
Species	$R^2 = 0.92$	$R^2 = 0.96$	$R^2 = 0.62$	$R^2 = 0.41$
X Time	$R^2_{\lambda} = 0.90$	$R^2_{\lambda} = 0.96$	$R^2_{\lambda} = 0.42$	$R^2_{\lambda} = 0.40$
		$p > t_i = 0.0034$	$p > t_i = 0.0001$	$p > t_i = 0.0001$
		$p > t_m = 0.0001$	$p > t_m = 0.0001$	$p > t_m = 0.0001$
		$p > F = 0.0001$	$p > F = 0.0001$	$p > F = 0.0001$
Area	$R^2 = 0.98$			
X Time	$R^2_{\lambda} = 0.98$			

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 13.  $R^2$  and adjusted  $R^2$  ( $R^2_{\lambda}$ ) for four models using species-area and species-time data from transects, sampling period 1.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
Species	$R^2 = 0.96$	$R^2 = 0.82$	$R^2 = 0.81$	$R^2 = 0.54$
X Area	$R^2_{\lambda} = 0.95$	$R^2_{\lambda} = 0.82$	$R^2_{\lambda} = 0.81$	$R^2_{\lambda} = 0.53$
		$p > t^5_i = 0.0001$ $p > t^6_m = 0.0001$ $p > F^7 = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$
Species	$R^2 = 0.96$	$R^2 = 0.92$	$R^2 = 0.83$	$R^2 = 0.65$
X Time	$R^2_{\lambda} = 0.96$	$R^2_{\lambda} = 0.92$	$R^2_{\lambda} = 0.83$	$R^2_{\lambda} = 0.65$
		$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$	$p > t_i = 0.0001$ $p > t_m = 0.0001$ $p > F = 0.0001$
Area	$R^2 = 1.0$			
X Time	$R^2_{\lambda} = 1.0$			

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 14.  $R^2$  and adjusted  $R^2$  ( $R^2_{\lambda}$ ) for four models using species-area and species-time data from transects, sampling period 2.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
Species	$R^2 = 0.90$	$R^2 = 0.88$	$R^2 = 0.58$	$R^2 = 0.38$
X Area	$R^2_{\lambda} = 0.88$	$R^2_{\lambda} = 0.88$	$R^2_{\lambda} = 0.58$	$R^2_{\lambda} = 0.37$
		$p > t^5_i = 0.007$	$p > t_i = 0.0001$	$p > t_i = 0.0001$
		$p > t^6_m = 0.0001$	$p > t_m = 0.0001$	$p > t_m = 0.0001$
		$p > F^7 = 0.0001$	$p > F = 0.0001$	$p > F = 0.0001$
Species	$R^2 = 0.93$	$R^2 = 0.97$	$R^2 = 0.71$	$R^2 = 0.52$
X Time	$R^2_{\lambda} = 0.93$	$R^2_{\lambda} = 0.97$	$R^2_{\lambda} = 0.71$	$R^2_{\lambda} = 0.52$
		$p > t_i = 0.0001$	$p > t_i = 0.0001$	$p > t_i = 0.0001$
		$p > t_m = 0.0001$	$p > t_m = 0.0001$	$p > t_m = 0.0001$
		$p > F = 0.0001$	$p > F = 0.0001$	$p > F = 0.0001$
Area	$R^2 = 0.99$			
X Time	$R^2_{\lambda} = 0.99$			

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 15.  $R^2$  and adjusted  $R^2$  ( $R^2_{\lambda}$ ) for four models using species-time data from meanders, sampling period 1.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
Species	$R^2 = 0.95$	$R^2 = 0.97$	$R^2 = 0.79$	$R^2 = 0.52$
X Time	$R^2_{\lambda} = 0.95$	$R^2_{\lambda} = 0.97$	$R^2_{\lambda} = 0.78$	$R^2_{\lambda} = 0.51$
		$p > t_i^5 = 0.0001$	$p > t_i = 0.0001$	$p > t_i = 0.0001$
		$p > t_m^6 = 0.0001$	$p > t_m = 0.0001$	$p > t_m = 0.0001$
		$p > F^7 = 0.0001$	$p > F = 0.0001$	$p > F = 0.0001$

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 16.  $R^2$  and adjusted  $R^2$  ( $R^2_{\lambda}$ ) for four models using species-time data from meanders, sampling period 2.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
Species	$R^2 = 0.85$	$R^2 = 0.96$	$R^2 = 0.60$	$R^2 = 0.43$
X Time	$R^2_{\lambda} = 0.83$	$R^2_{\lambda} = 0.96$	$R^2_{\lambda} = 0.59$	$R^2_{\lambda} = 0.41$
		$p > t_i^5 = 0.0001$	$p > t_i = 0.0001$	$p > t_i = 0.0001$
		$p > t_m^6 = 0.0001$	$p > t_m = 0.0001$	$p > t_m = 0.0001$
		$p > F^7 = 0.0001$	$p > F = 0.0001$	$p > F = 0.0001$

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 17. Observed and estimated species numbers from plot data for six different situations.

Period 1					
	sp	$\hat{sp}_A$	$\hat{sp}_T$	Area(100m <sup>2</sup> units)	Time(hrs)
a	121	115	113	45	23.1
b		132	134	79	$\hat{t} = 42$
c		135	138	$\hat{a} = 87$	46.2
d		136	139	90	$\hat{t} = 47.7$
e		271	297	6000	$\hat{t} = 3094$
f		394	443	280,000	$\hat{t} = 144,331$

Period 2					
	sp	$\hat{sp}_A$	$\hat{sp}_T$	Area(100m <sup>2</sup> units)	Time(hrs)
a	112	105	106	45	15.4
b		120	123	79	$\hat{t} = 27.3$
c		124	129	$\hat{a} = 93$	31.8
d		123	128	90	$\hat{t} = 31$
e		238	275	6000	$\hat{t} = 2034$
f		344	410	280,000	$\hat{t} = 94,916$

- a) observed and predicted numbers of species from all plots at final observation time or area
- b) if area sampled by plots equalled area sampled by transects (0.79 ha)
- c) if time were doubled
- d) if area were doubled
- e) if 60 ha were sampled
- f) if 2800 ha were sampled

sp = number of species

$\hat{sp}_A$  = number of species predicted from species-area relationship

$\hat{sp}_T$  = number of species predicted from species-time relationship

$\hat{a}$  = area predicted from area-time relationship

$\hat{t}$  = time predicted from area-time relationship

Table 18. Observed and estimated species numbers from transect data for five different situations.

Period 1					
	sp	$\hat{sp}_A$	$\hat{sp}_T$	Area(100m <sup>2</sup> units)	Time(hrs)
a	199	181	194	79	19.7
c		217	242	$\hat{a} = 156$	39.4
d		218	243	158	$\hat{t} = 40$
e		413	518	6000	$\hat{t} = 1519$
f		618	808	280,000	$\hat{t} = 70,886$

Period 2					
	sp	$\hat{sp}_A$	$\hat{sp}_T$	Area(100m <sup>2</sup> units)	Time(hrs)
a	185	174	181	79	19.2
c		197	218	$\hat{a} = 153$	38.4
d		198	220	158	$\hat{t} = 39.7$
e		328	426	6000	$\hat{t} = 1486$
f		464	645	280,000	$\hat{t} = 69,308$

- a) observed and predicted numbers of species from all plots at final observation times and areas  
 c) if time were doubled  
 d) if area were doubled  
 e) if 60 ha were sampled  
 f) if 2800 ha were sampled

sp = number of species

$\hat{sp}_A$  = number of species predicted from species-area relationship

$\hat{sp}_T$  = number of species predicted from species-time relationship

$\hat{a}$  = area predicted from area-time relationship

$\hat{t}$  = time predicted from area-time relationship

Table 19. Observed and estimated species numbers from meander data for four different situations.

Period 1			
	sp	$\hat{sp}_T$	Time(hrs)
a	177	167	19.6
c		214	39.2
e		457	1500
f		714	70,000

Period 2			
	sp	$\hat{sp}_T$	Time(hrs)
a	178	168	15
c		204	30
e		408	1500
f		609	70,000

- a) observed and predicted numbers of species from meanders at final observation time
- c) if time were doubled
- e) if time spent = approximate time to search 60 ha (see Table 18, option e)
- f) if time spent = approximate time to search 2800 ha (see Table 18, option f)

sp = number of species

$\hat{sp}_T$  = number of species predicted from species-time relationship

Table 20. Species-area and species-time relationships from data collected by three methods in two sampling periods at Havens Wildlife Management Area, Roanoke County, Virginia, 1991.

Sampling Period 1		
Method	Independent variable	Equation
Plots	area	species = $-8.27 + 32.1 \cdot \ln(\text{area} + 1)$
Plots	time	species = $-7.63 + 37.9 \cdot \ln(\text{time} + 1)$
Transects	area	species = $-52.7 + 53.5 \cdot \ln(\text{area} + 1)$
Transects	time	species = $-35.4 + 75.5 \cdot \ln(\text{time} + 1)$
Meanders	time	species = $-31.5 + 66.8 \cdot \ln(\text{time} + 1)$
Sampling Period 2		
Method	Independent variable	Equation
Plots	area	species = $27.4 \cdot \ln(\text{area} + 1)$
Plots	time	species = $7.3 + 35.1 \cdot \ln(\text{time} + 1)$
Transects	area	species = $17.9 + 35.6 \cdot \ln(\text{area} + 1)$
Transects	time	species = $9.9 + 57 \cdot \ln(\text{time} + 1)$
Meanders	time	species = $26.7 + 52.2 \cdot \ln(\text{time} + 1)$

Table 21. Area-time relationships from data collected by plots and transects during both sampling periods at Havens Wildlife Management Area, Roanoke County, Virginia, 1991.

Method	Sampling Period	Equation
Plots	1	area = $-2.54 + 1.94 \cdot \text{time}$
Plots	2	area = $-1.56 + 2.95 \cdot \text{time}$
Transects	1	area = $3.95 \cdot \text{time}$
Transects	2	area = $-2.35 + 4.04 \cdot \text{time}$

Area is in 100 m<sup>2</sup> units, and time is in hours.

Table 22.  $R^2$  and adjusted  $R^2$  ( $R^2_A$ ) for four models using species-area data from plots independently selected, sampling period 1.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
	$R^2 = 0.85$ $R^2_A = 0.83$	$R^2 = 0.77$ $R^2_A = 0.74$	$R^2 = 0.93$ $R^2_A = 0.93$	$R^2 = 0.54$ $R^2_A = 0.48$
$p > t_i^5$	0.08	0.47	0.25	0.005
$p > t_m^6$	0.0001	0.0009	0.0001	0.02
prob > F <sup>7</sup>	0.0001	0.0009	0.0001	0.02

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob > F = probability of a greater F value for the model

Table 23. Species-area relationships from independent areas (plots and transects) collected in the first sampling period at Havens Wildlife Management Area, Roanoke County, Virginia, 1991.

Method	Independent variable	Equation
Plots	area	$\ln(\text{species} + 1) = 0.37 + 0.89 * \ln(\text{area} + 1)$
Transects	area	$\ln(\text{species} + 1) = 1 + 0.48 * \ln(\text{area} + 1)$

Table 24. Observed and estimated species numbers from independent species-area data gathered using plots in sampling period 1.

	sp	$\hat{sp}_A$	Area(100m <sup>2</sup> units)	Time(hrs)
a	121	43	45	23.1
b		71	79	$\hat{t} = 42$
d		79	90	$\hat{t} = 47.7$
e		3340	6000	$\hat{t} = 3094$
f		100,000	280,000	$\hat{t} = 144,331$

- a) observed and predicted numbers of species from all plots at final observation time or area
- b) if area sampled by plots equaled area sampled by transects (0.79 ha)
- d) if area were doubled
- e) if 60 ha were sampled
- f) if 2800 ha were sampled

sp = number of species

$\hat{sp}_A$  = number of species predicted from species-area relationship

$\hat{a}$  = area predicted from area-time relationship

$\hat{t}$  = time predicted from area-time relationship

Table 25.  $R^2$  and adjusted  $R^2$  ( $R^2_A$ ) for four models using species-area data from transects independently selected, sampling period 1.

	Untransformed <sup>1</sup>	Exponential <sup>2</sup>	Power <sup>3</sup>	Logspecies <sup>4</sup>
	$R^2 = 0.01$ $R^2_A = -0.06$	$R^2 = 0.39$ $R^2_A = 0.34$	$R^2 = 0.69$ $R^2_A = 0.66$	$R^2 = 0.14$ $R^2_A = 0.08$
$p > t_i^5$	0.0004	0.25	0.09	0.0001
$p > t_m^6$	0.68	0.01	0.0001	0.16
prob > $F^7$	0.68	0.01	0.0001	0.16

<sup>1</sup>Untransformed model: species = area

<sup>2</sup>Exponential model: species =  $\ln(\text{area} + 1)$

<sup>3</sup>Power model:  $\ln(\text{species} + 1) = \ln(\text{area} + 1)$

<sup>4</sup>Logspecies model:  $\ln(\text{species} + 1) = \text{area}$

<sup>5</sup> $p > t_i$  = probability of a greater t for the intercept value

<sup>6</sup> $p > t_m$  = probability of a greater t for the slope value

<sup>7</sup>prob >  $F$  = probability of a greater F value for the model

Table 26. Observed and estimated species numbers from independent species-area data gathered using transects in sampling period 1.

	sp	$\hat{sp}_A$	Area(100m <sup>2</sup> units)	Time(hrs)
a	199	22	79	19.7
d		30	158	$\hat{t} = 40$
e		177	6000	$\hat{t} = 1519$
f		1100	280,000	$\hat{t} = 70,886$

- a) observed and predicted numbers of species from all plots at final observation time or area
- d) if area were doubled
- e) if 60 ha were sampled
- f) if 2800 ha were sampled

sp = number of species

$\hat{sp}_A$  = number of species predicted from species-area relationship

$\hat{a}$  = area predicted from area-time relationship

$\hat{t}$  = time predicted from area-time relationship

Table 27. Percentage of total species observed using each method.

Methods	Sampling Period 1	Sampling Period 2
Transects	85 %	77 %
Meanders	75 %	74 %
Plots	51 %	46 %

Table 28. List of species observed at my study site by the author and by Mr. Thomas Wieboldt on August 29, 1991 and August 30, 1991, respectively.

Author's List	Mr. Wieboldt's list
<i>Acer pensylvanicum</i>	<i>Acer pensylvanicum</i>
<i>Acer rubrum</i>	<i>Acer rubrum</i>
<i>Amelanchier arborea</i> <sup>1</sup>	<i>Amelanchier arborea</i>
	<i>Andropogon</i> sp.
	<i>Andropogon</i> other <sup>1</sup>
	<i>Angelica venanosa</i>
	<i>Antennaria plantaginifolia</i>
<i>Aster</i> sp.	<i>Aster infirmus</i>
	<i>Aster undulatus</i>
	<i>Aristolochia serpentaria</i>
	<i>Aurcolaria</i> sp.
<i>Betula lenta</i>	<i>Betula lenta</i>
<i>Carex</i> sp.	<i>Carex</i> sp.
	<i>Carya ovata</i>
<i>Carya</i> sp.	<i>Carya tomentosa</i>
<i>Castanea dentata</i>	<i>Castanea dentata</i> <sup>1</sup>
<i>Chimaphila maculata</i>	<i>Chimaphila maculata</i>
<i>Coreopsis major</i>	<i>Coreopsis major</i>
<i>Cornus florida</i>	<i>Cornus florida</i>
<i>Desmodium nudiflorum</i>	<i>Desmodium nudiflorum</i>
<i>Dioscorea villosa</i>	<i>Dioscorea villosa</i>
<i>Epigaea repens</i>	<i>Epigaea repens</i>
<i>Eupatorium rugosum</i> <sup>1</sup>	<i>Eupatorium rugosum</i>
<i>Fraxinus americana</i>	
<i>Galax aphylla</i>	<i>Galax aphylla</i>
	<i>Galium circaezans</i>
	<i>Gaylussacia baccata</i>
<i>Gaultheria procumbens</i>	<i>Gaultheria procumbens</i>
<i>Geranium maculatum</i>	<i>Geranium maculatum</i>
<i>Goodyera pubescens</i>	<i>Goodyera pubescens</i>
<i>Hamamelis virginiana</i>	<i>Hamamelis virginiana</i>
	<i>Helianthus divaricatus</i>
	<i>Heuchera</i> sp.
<i>Houstonia longifolia</i>	<i>Houstonia longifolia</i>
	<i>Hydrangea</i> <sup>1</sup>
<i>Hypoxis hirsuta</i>	<i>Hypoxis hirsuta</i>
	<i>Isotria verticillata</i>
<i>Ilex montana</i>	<i>Ilex montana</i>
<i>Kalmia latifolia</i>	<i>Kalmia latifolia</i>
<i>Lespedeza</i> sp.	<i>Lespedeza intermedia</i>
<i>Lilium</i> sp. <sup>1</sup>	<i>Lilium</i> sp.
<i>Liriodendron tulipifera</i>	<i>Liriodendron tulipifera</i>
<i>Lysimachia quadrifolia</i>	<i>Lysimachia quadrifolia</i>
<i>Magnolia acuminata</i>	
<i>Medeola virginiana</i>	
	<i>Mitchella repens</i>
	<i>Monotropa uniflora</i>
	<i>Monotropa hypopithys</i>
<i>Nyssa sylvatica</i>	<i>Nyssa sylvatica</i>
	<i>Ostrya virginiana</i>

Table 28, cont'd.

Oxydendrum arboreum	Oxydendrum arboreum
Panicum sp.	Panicum commutatum Panicum dichotomum Panicum latifolium <sup>1</sup>
Panicum sp. <sup>2</sup>	
Parthenocissus quinquefolia	Parthenocissus quinquefolia
Pinus rigida	
Pinus strobus	Pinus strobus
Polygonatum biflorum	Polygonatum biflorum
Porteranthus trifolius	Porteranthus trifolius
Potentilla sp.	Potentilla sp.
Pterideum aquilinum	Pterideum aquilinum
Pyrola pubera	Pyrola rotundifolia Pyrola pubera
Quercus alba	Quercus alba
Quercus coccinea <sup>1</sup>	Quercus coccinea
Quercus prinus	Quercus prinus
Quercus rubra	Quercus rubra Quercus velutina
Rhododendron maximum	Rhododendron maximum
Rhododendron nudiflorum <sup>1</sup>	Rhododendron nudiflorum
Rhus radicans	Rhus radicans
Robinia pseudoacacia	Robinia pseudoacacia
Rubus sp.	Rubus sp.
Sassafras albidum	Sassafras albidum
Smilacina racemosa	Smilacina racemosa
Smilax glauca	Smilax glauca
Smilax rotundifolia	Smilax rotundifolia Solidago arguta <sup>1</sup> Solidago bicolor Solidago curtisii
Solidago curtisii	Thalictrum dioicum
Thalictrum sp.	
Thaspium or Zizia sp.	
Trientalis borealis	Trientalis borealis
Tsuga canadensis	Tsuga canadensis
Tsuga carolina	Tsuga carolina
Uvularia pudica	Uvularia pudica Vaccinium angustifolium <sup>1</sup>
Vaccinium pallidum	Vaccinium pallidum
Vaccinium stamineum	Vaccinium stamineum
Viburnum acerifolium	Viburnum acerifolium Vicia caroliniana
Viola hastata <sup>1</sup>	Viola hastata
Viola sp.	Viola sp.
Vitis sp.	Vitis sp.

<sup>1</sup> There was some question as to the positive identification of these species.

<sup>2</sup> This specimen was probably *Andropogon sp.* as identified by Mr. Wieboldt.

Table 29. Similarity of species composition among methods.

Methods	Sampling Period 1	Sampling Period 2
Meanders vs. Transects	0.65	0.65
Meanders vs. Plots	0.51	0.53
Transects vs. Plots	0.53	0.58

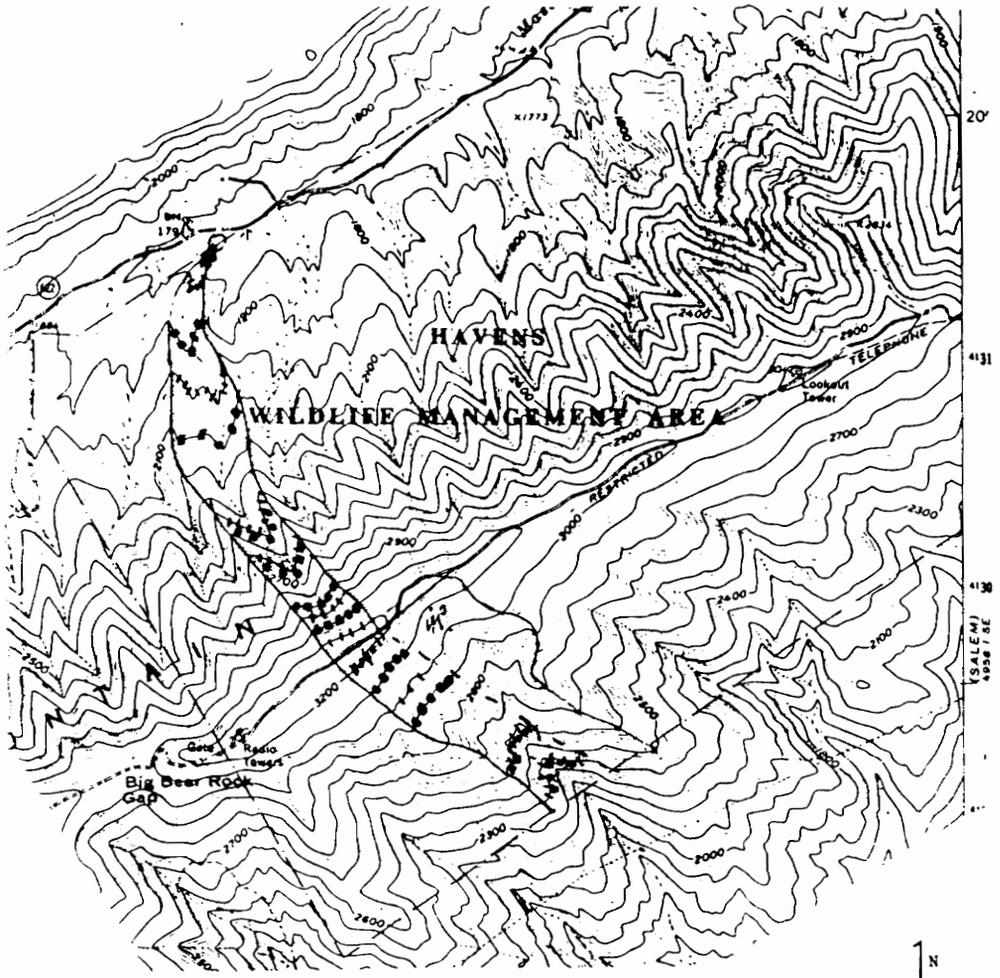


Figure 1. Study area.

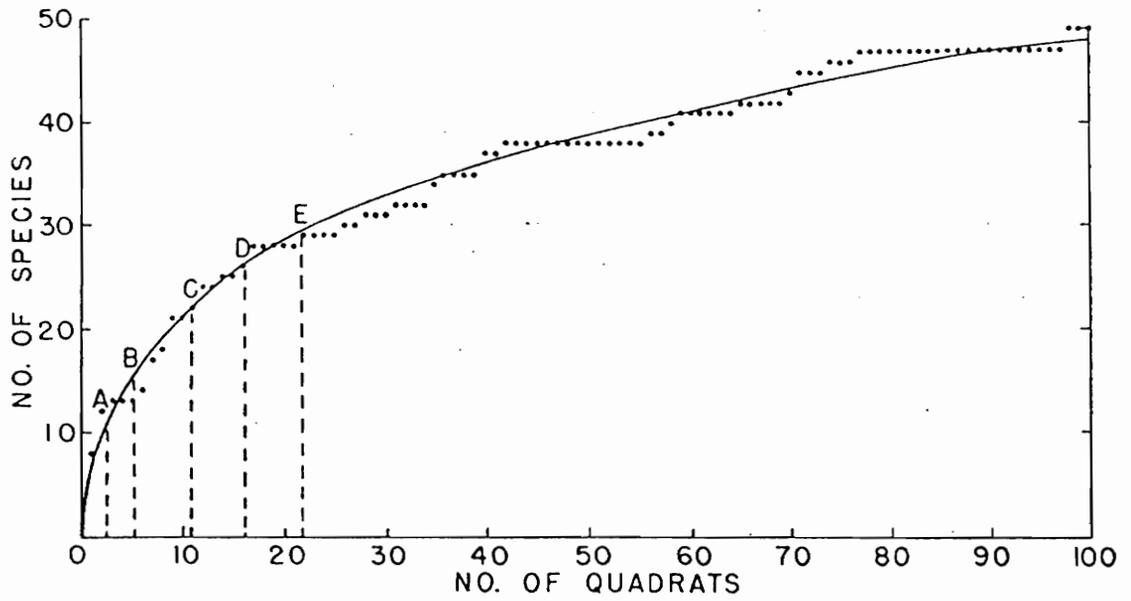


Figure 2. Species-area curve for McClain County Prairie. Reproduced from Rice and Kelting (1955:8).

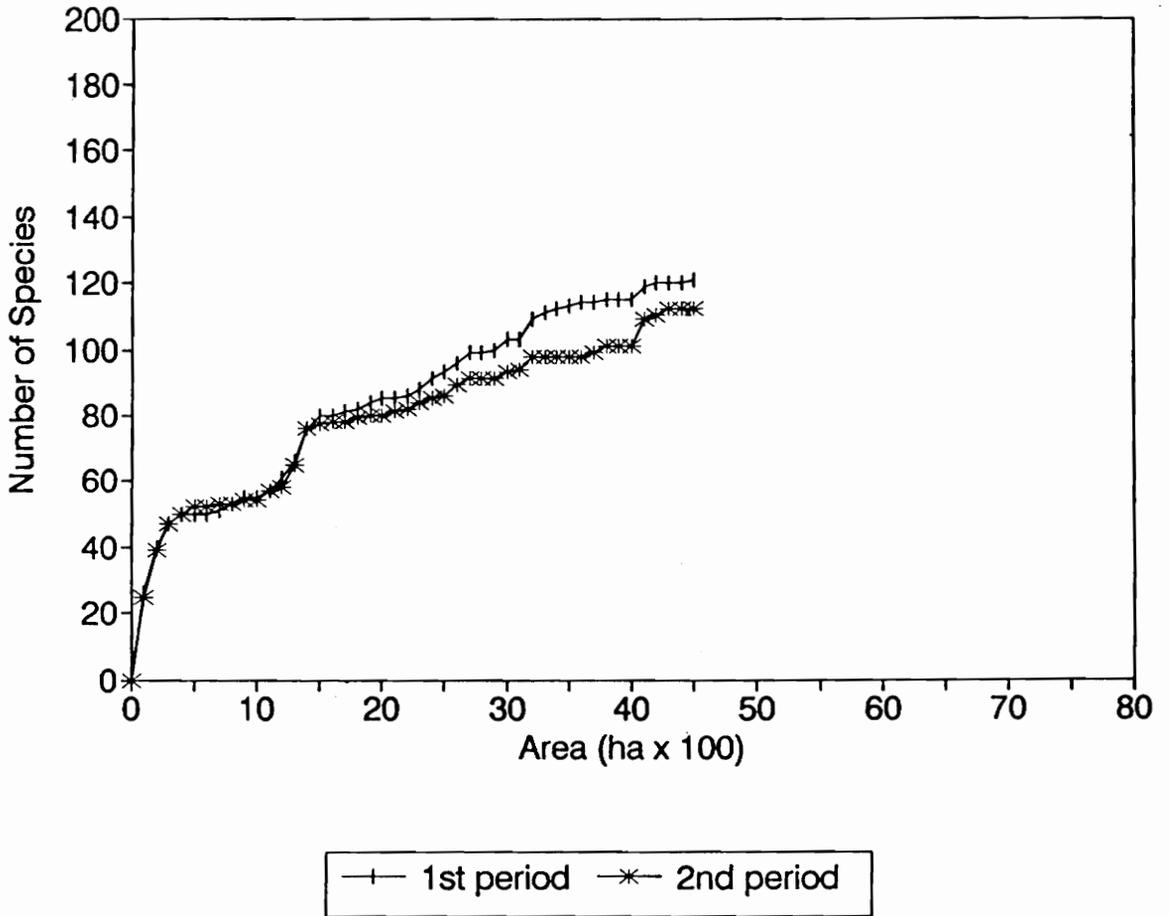


Figure 3. Plant species-area curves for data collected with plots from the Havens State Wildlife Management Area, 1991.

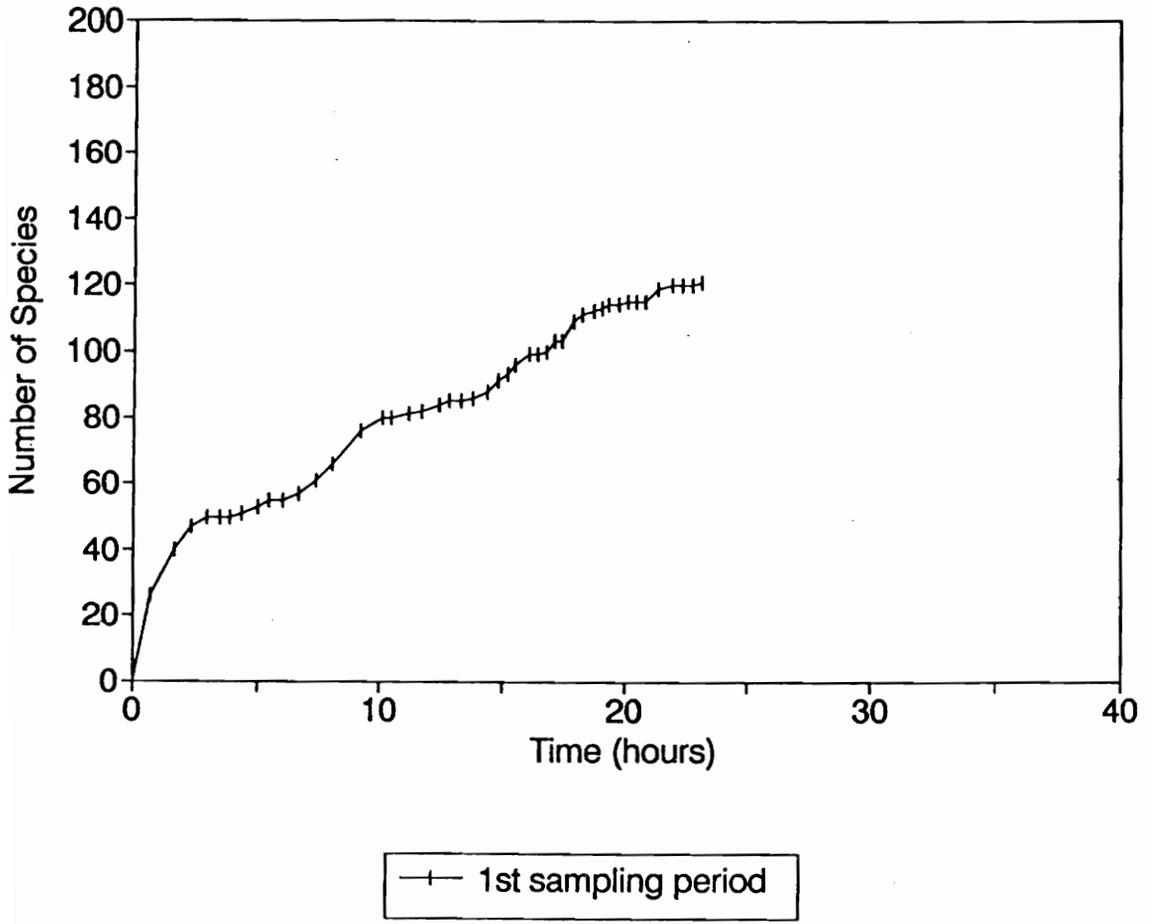


Figure 4. Species-effort curve for data collected with plots in the first sampling period from the Havens State Wildlife Management Area, 1991.

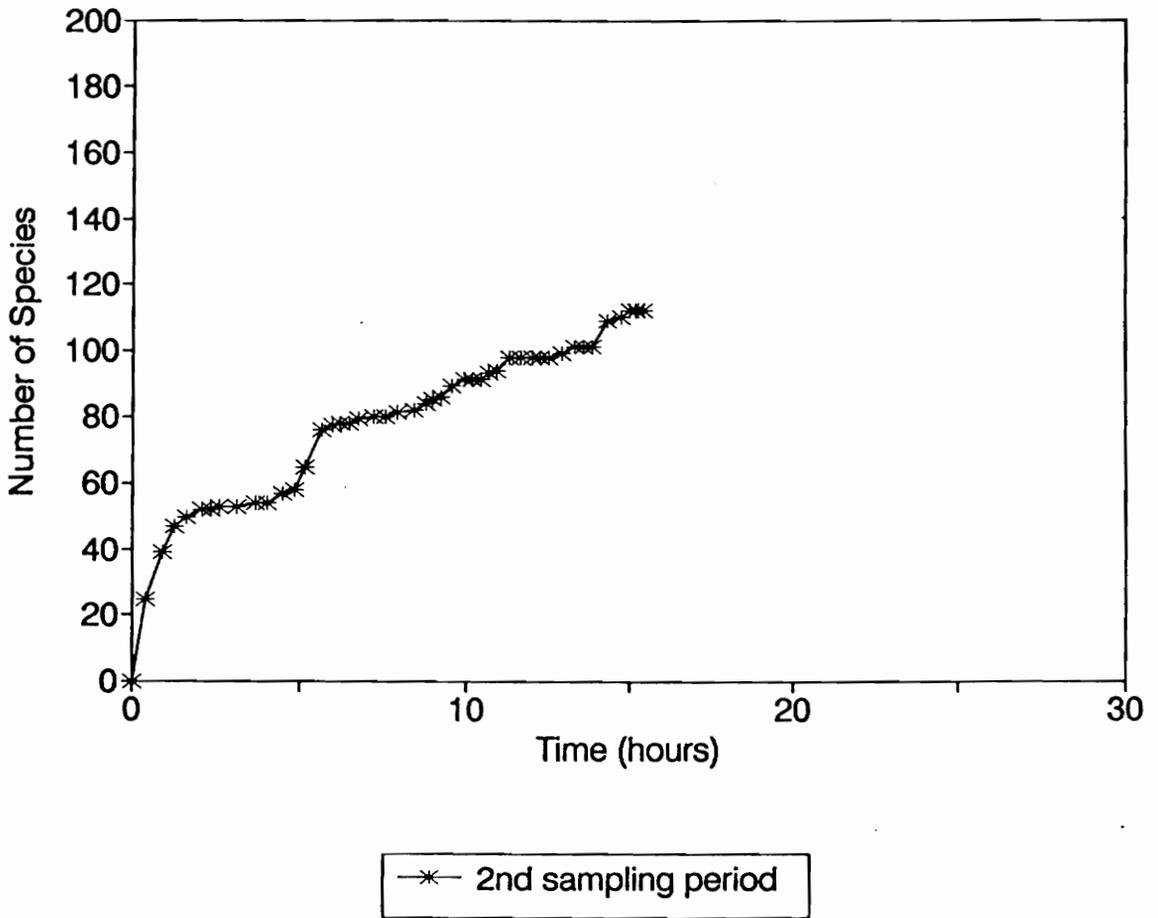


Figure 5. Species-effort curve for data collected with plots in the second sampling period from the Havens State Wildlife Management Area, 1991.

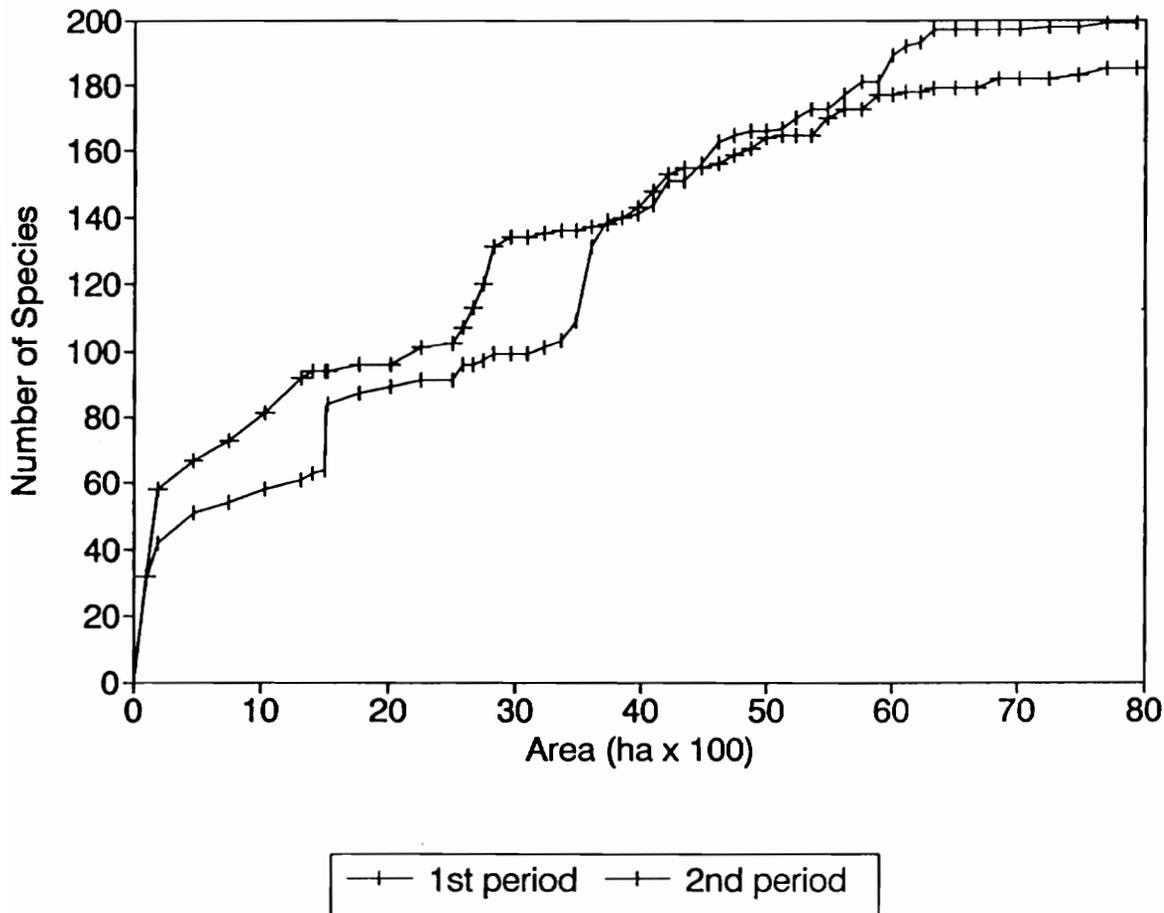


Figure 6. Plant species-area curves for data collected with transects from the Havens State Wildlife Management Area, 1991.

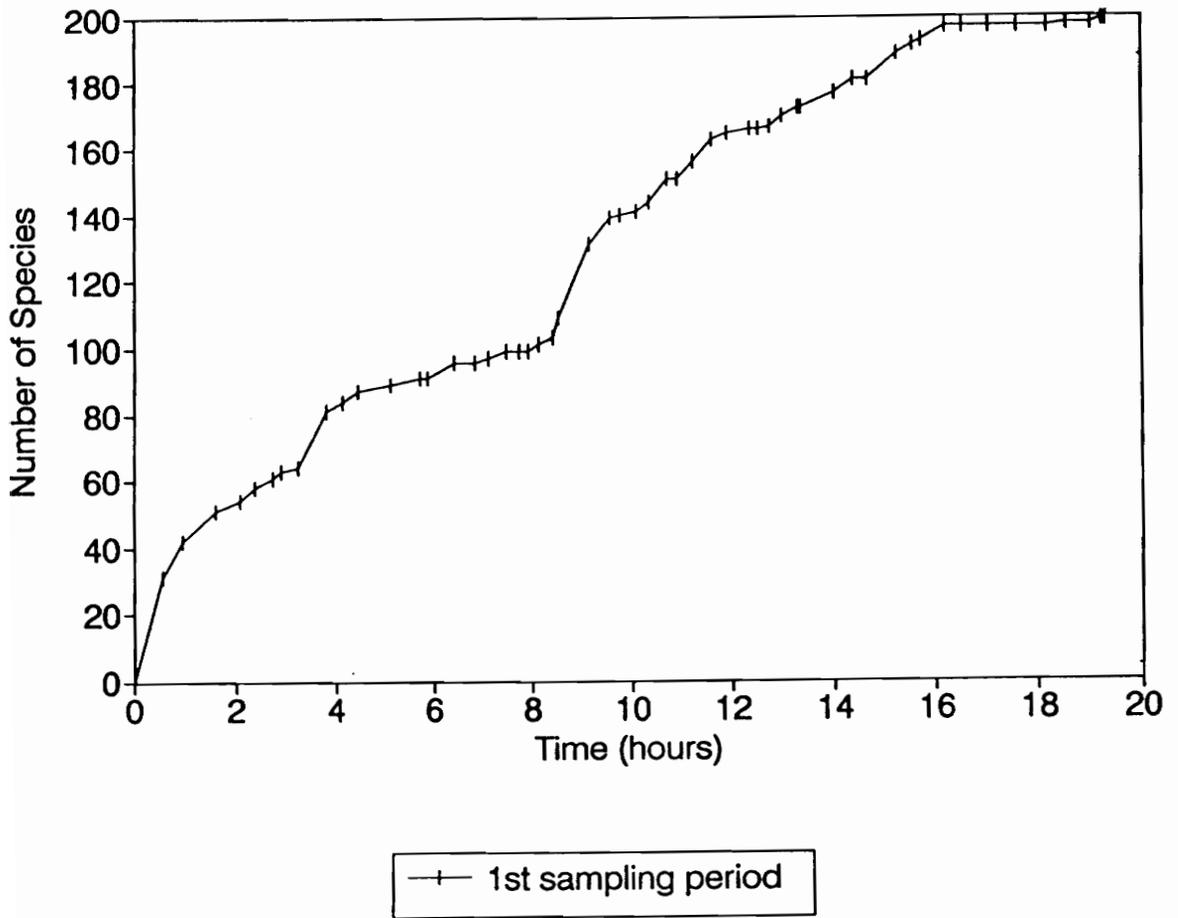


Figure 7. Species-effort curve for data collected with transects in the first sampling period from the Havens State Wildlife Management Area, 1991.

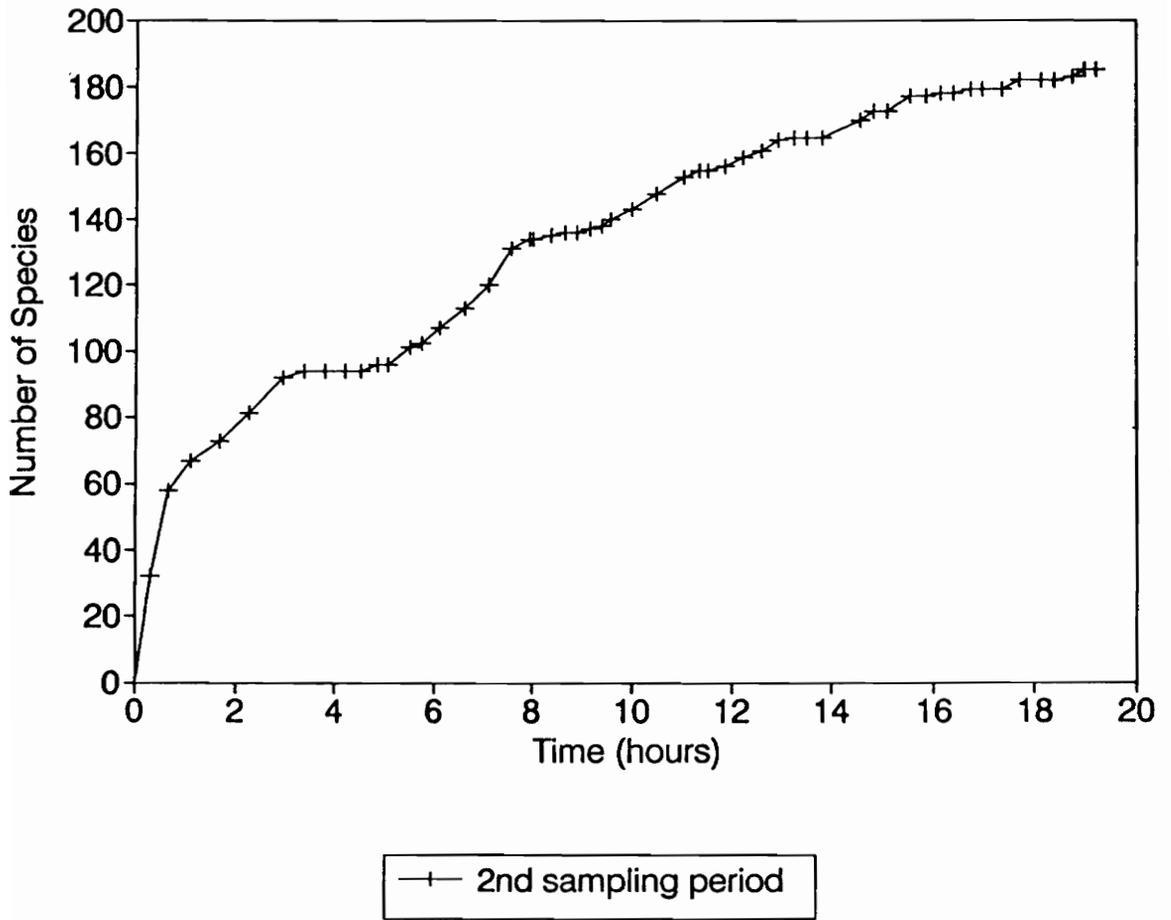


Figure 8. Species-effort curve for data collected with transects in the second sampling period from the Havens State Wildlife Management Area, 1991.

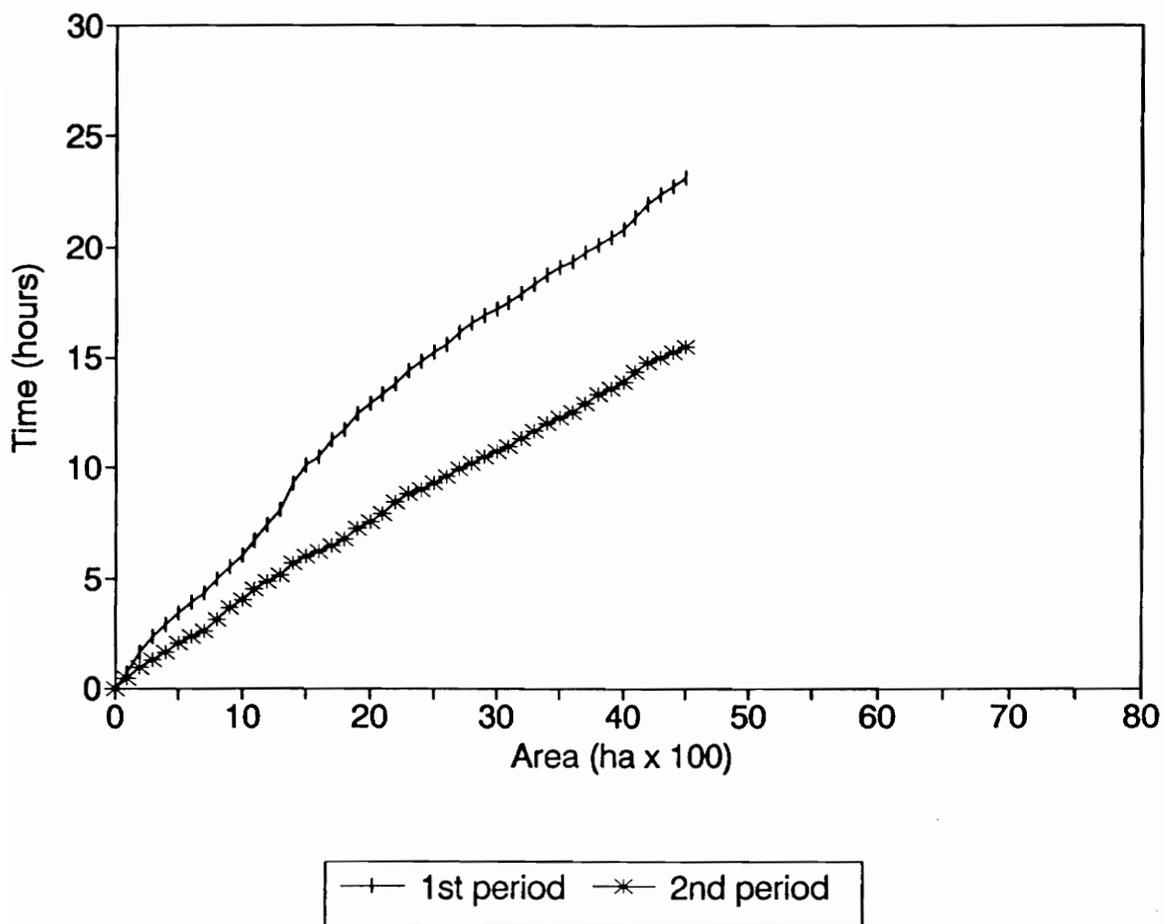


Figure 9. Time-area relationship for vascular plant data collected with plots from the Havens State Wildlife Management Area, 1991.

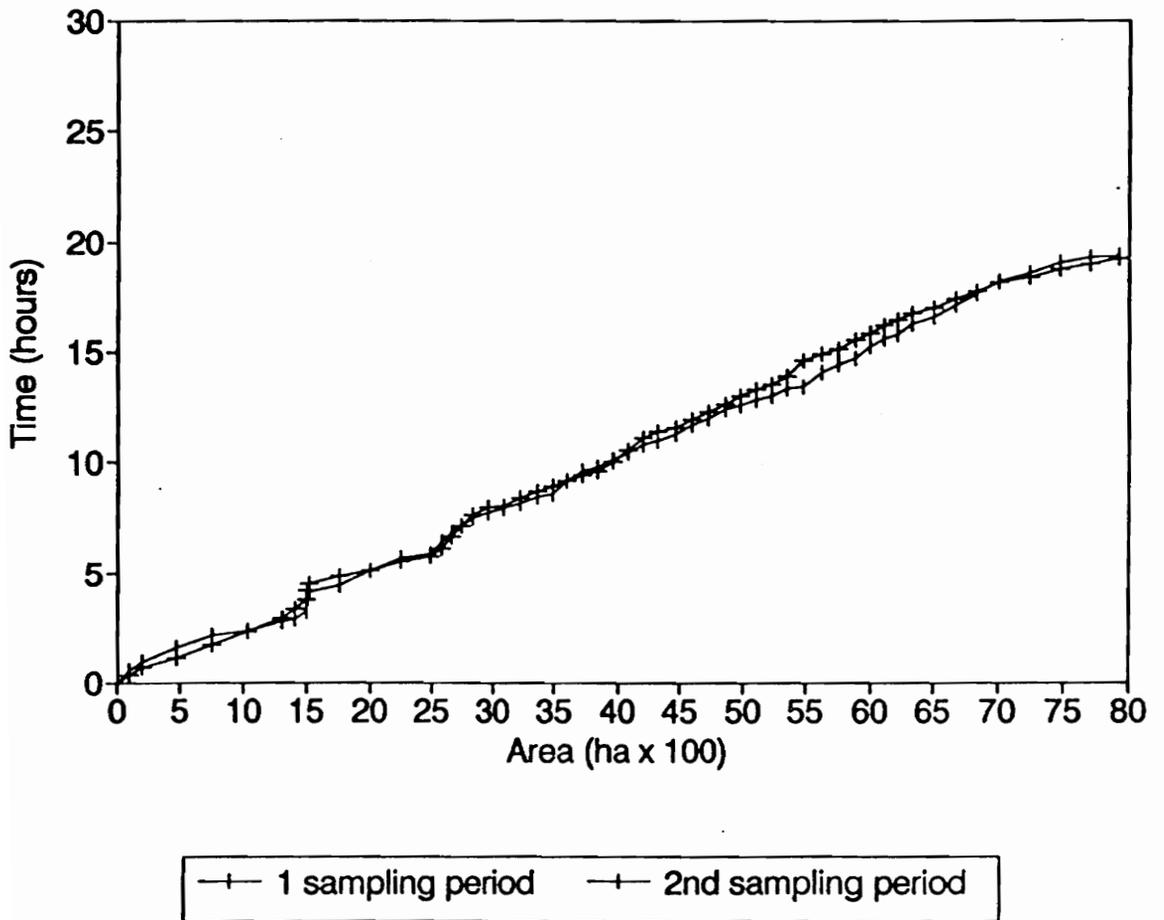


Figure 10. Time-area relationship for vascular plant data collected with transects from the Havens State Wildlife Management Area, 1991.

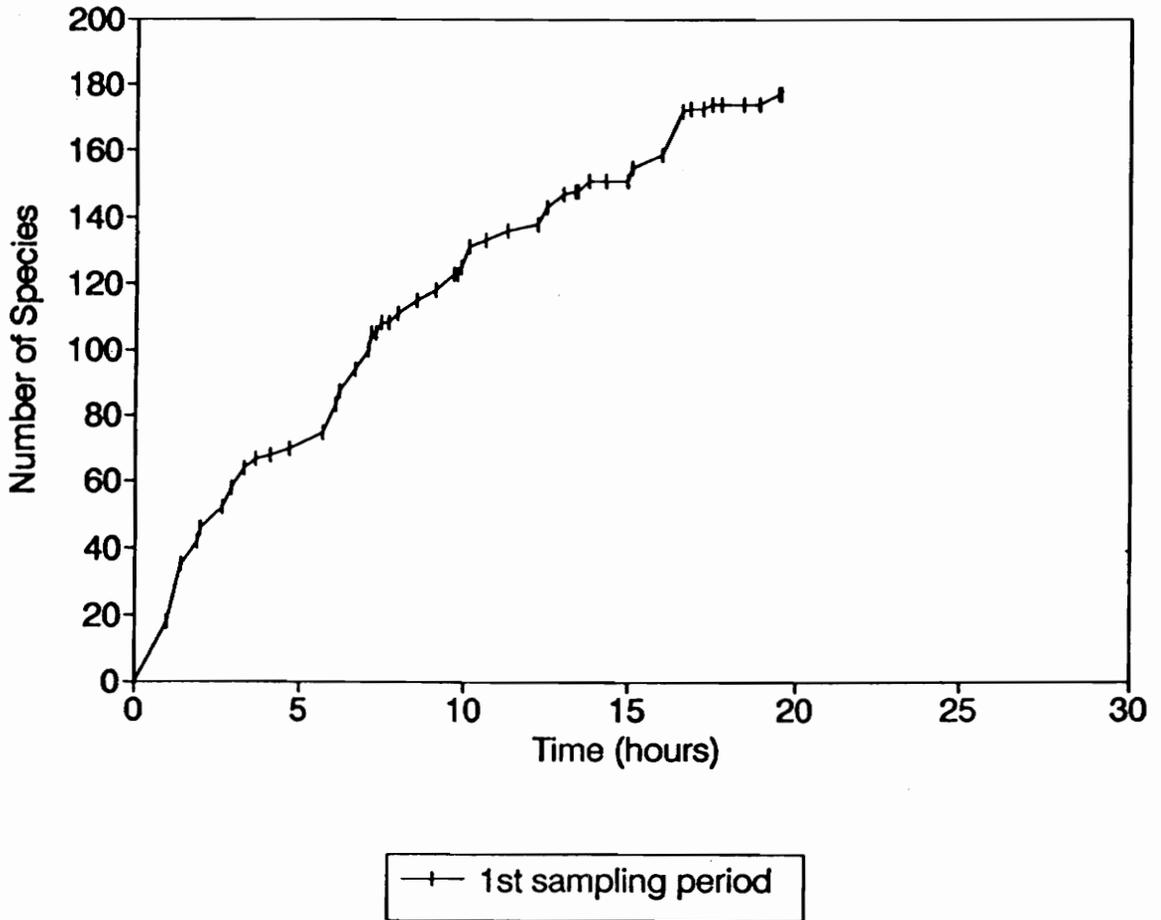
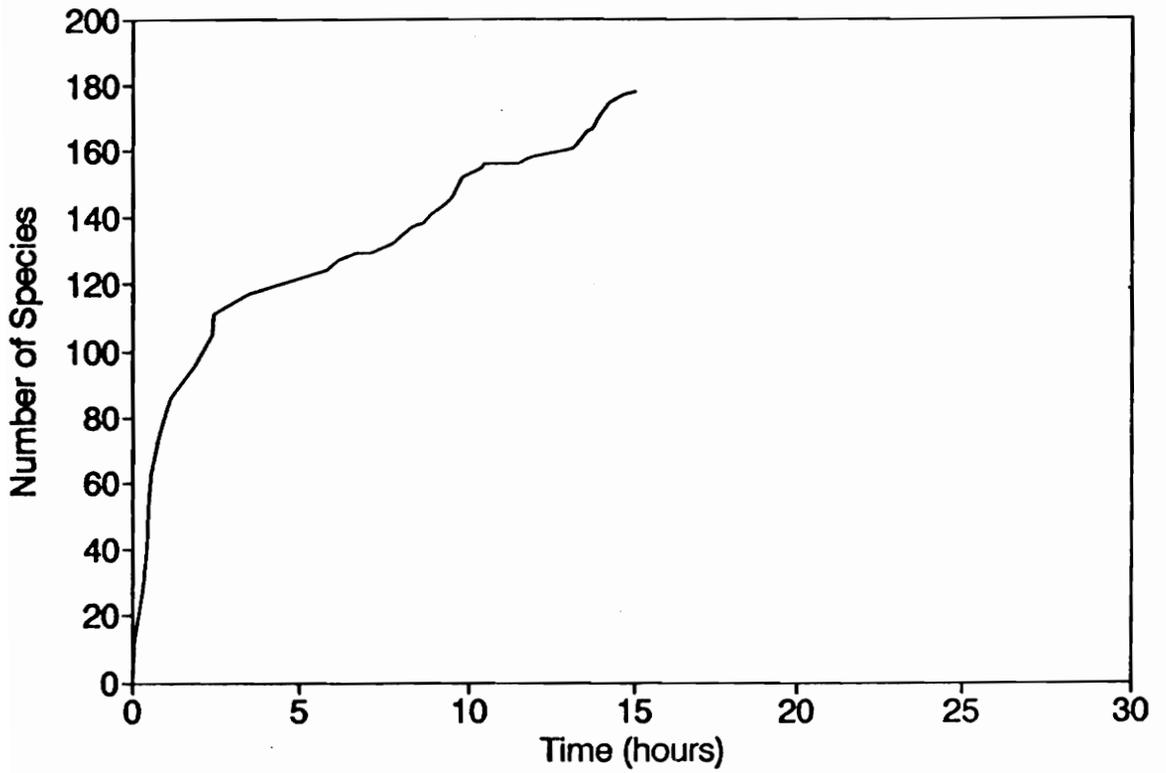


Figure 11. Species-effort curve for data collected with meanders in the first sampling period from the Havens Wildlife Management Area, 1991.



— 2nd sampling period

Figure 12. Species-effort curve for data collected with meanders in the second sampling period from Havens State Wildlife Management Area, 1991.

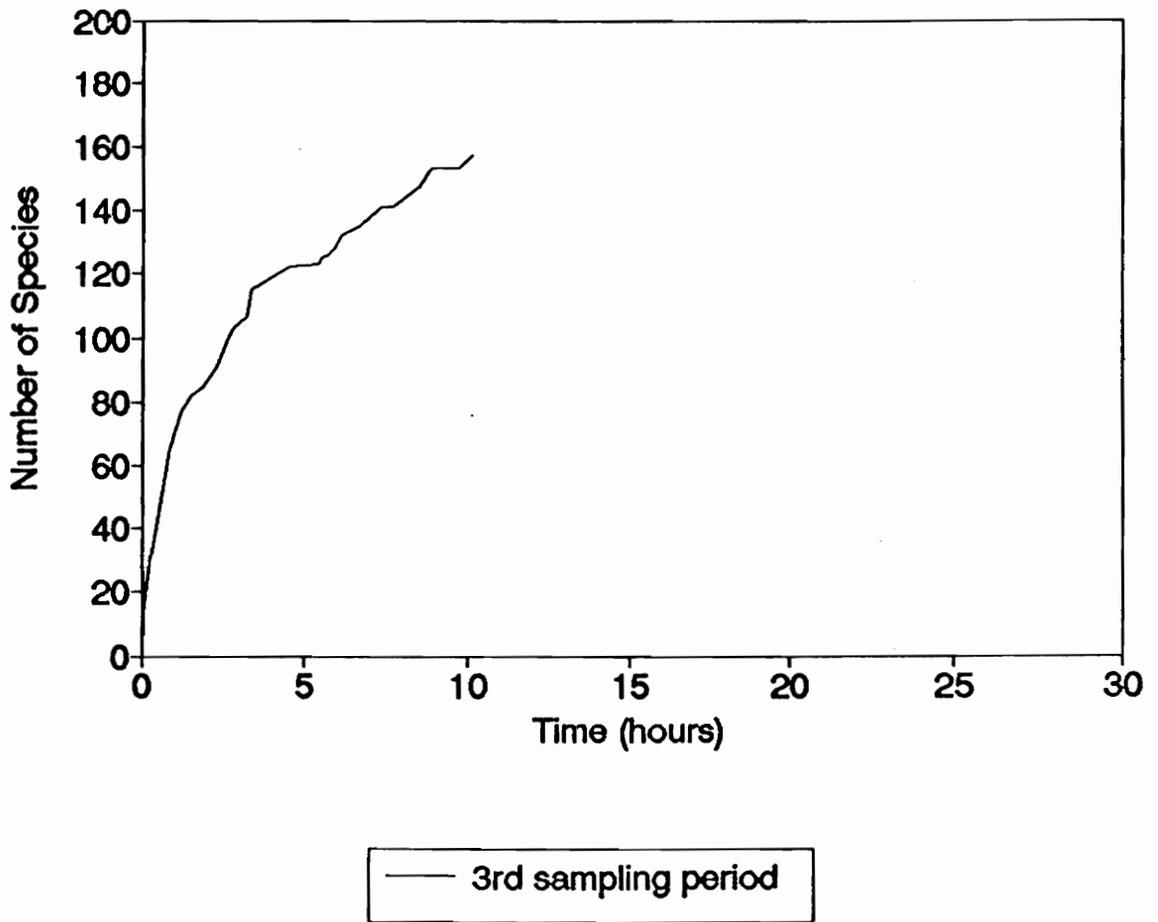


Figure 13. Species-effort curve for data collected with meanders in the third sampling period from the Havens State Wildlife Management Area, 1991.

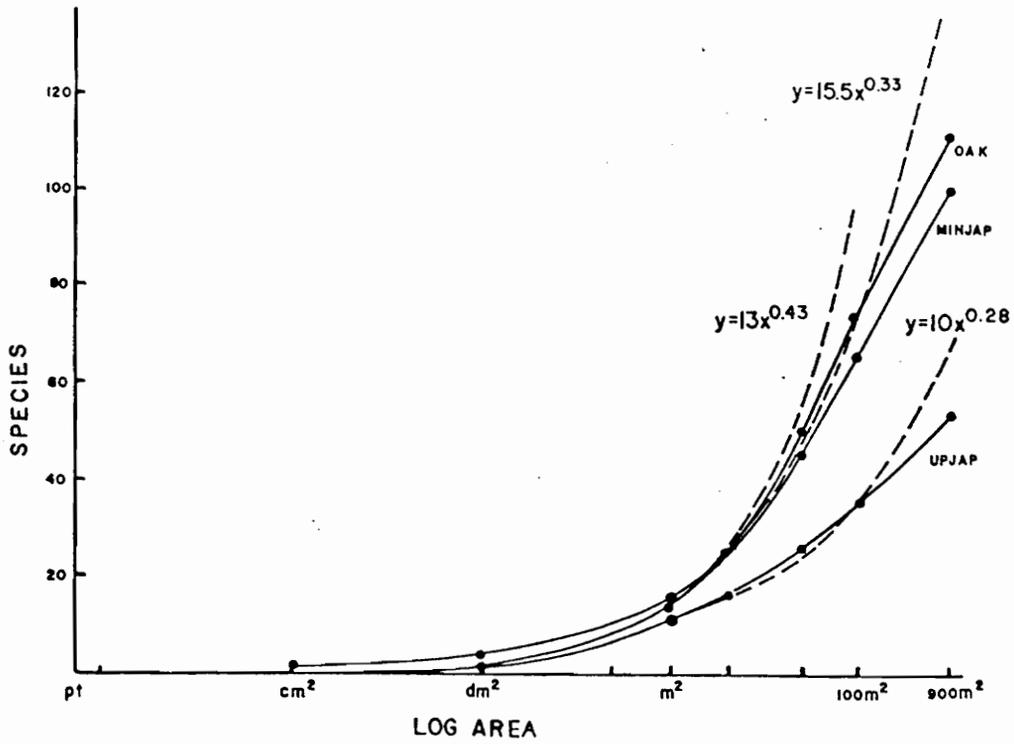


Figure 14. Comparison of species-log area equations (dashed lines) with actual plot data for three 900-m<sup>2</sup> sample plots. Reproduced from Kilburn (1966:838).

## VITA

The author was born on June 6, 1958, in Hampton, Iowa. She grew up on a farm 2 miles from Iowa Falls, Iowa. She graduated in 1981 with a degree in German and International Studies from Iowa State University. After traveling and serving abroad for the Church of the Brethren in Northern Ireland, she returned to Iowa and worked in a group home and at a library. In 1987, she returned to Iowa State University for studies in wildlife biology and botany. She has worked as a research assistant on a midwestern wetlands restoration project, as an intern for a non-profit land trust, as an intern with the Bureau of Land Management, as a research assistant for the National Park Service, as a teaching and research assistant for the Department of Fisheries and Wildlife at Virginia Tech, and as a botanist for the College of Forestry at Virginia Tech.

A handwritten signature in cursive script that reads "Nancy Mason". The signature is written in black ink and is positioned to the right of the main text block.