Habitat Structure, Forest Composition and Landscape Dimensions as Components of Habitat Suitability for the Delmarva Fox Squirrel[1]

Raymond D. Dueser,[2] James L. Dooley, Jr.,[3] and Gary J. Taylor[4]

Abstract.—Discriminant function analysis comparing 36 occupied and 18 unoccupied sites revealed that structural variables discriminated between sample groups better than compositional variables, and the latter discriminated better than landscape variables. These results are encouraging that habitat structure will provide a reliable basis for a predictive classification model of habitat suitability. Such a model would be useful both for pre-screening the biological suitability of potential release sites and for planning, implementing and monitoring prescriptive habitat management.

The Delmarva fox squirrel *(Sciurus niger cinereus)* was placed on the federal endangered species list in 1967 (32 FR 4001; U.S. Department of Interior 1970). Remnant populations were restricted to four counties in eastern Maryland (Taylor and Flyger 1973), representing less than 10% of the historic range of the subspecies on the Delmarva Peninsula. Forest clearing and habitat fragmentation throughout the range undoubtedly contributed significantly to the present endangerment (Taylor 1973).

The U.S. Fish and Wildlife Service Recovery Plan for the restoration of the Delmarva fox squirrel to secure status emphasizes both the reintroduction of this subspecies to suitable habitats throughout the former range and prescriptive habitat management for established populations (Taylor et al. 1983). A thorough understanding of habitat requirements will be essential for both initiatives (Dueser and Terwilliger 1988).

Habitat requirements might be expressed through any of three separate but related components of habitat suitability: forest habitat structure, forest tree species composition, and surrounding landscape structure. Both habitat structure and forest composition have been shown to influence the distribution and abundance of fox squirrels in heterogeneous landscapes (Nixon and Hansen 1987).

Recent research has demonstrated the potential influence of landscape composition and structure on populations of woodland mammals occupying farmland mosaics (Wegner and Merriam 1979, Middleton and Merriam 1983, Fahrig and Merriam 1985). Furthermore, changes in the landscape of the Delmarva Peninsula almost certainly played a major role on the decline of the fox squirrel (Taylor 1973).

Given this background, the objective of this study was to compare the apparent effects of habitat structure, forest composition and landscape dimensions on the presence and absence of the Delmarva fox squirrel on 54 study sites in eastern Maryland. This analysis is the first step in the development of a predictive classification model of habitat suitability for this subspecies (cf. Houston et al. 1986).

Methods

Data Base

During a 12-mo search for remnant populations of the Delmarva fox squirrel on the Maryland Eastern Shore, Taylor (1976) located 36 "fox squirrel present" (Present) sites with extant populations and 18 "fox squirrel absent" (Absent) sites. The gray squirrel *(Sciurus carolinensis)* was present on all 54 sites. Taylor then sampled the forest habitat of each site, to compare Present forest stands with Absent stands. He established a representative 4 m x 200 m belt transect on each site, on which he recorded the number of trees by species per diameter-breast-height (DBH) size class (5-20 cm, 20.1-30 cm, 30.1-50 cm, and 50.1+ cm), percent crown cover, percent understory cover, understory density, and understory species composition. All habitat measurements were taken from June through September 1972 and 1973. These data formed the initial data base for this study.

Taylor (1976) reported the number of trees measured in each of two size classes: "small" trees (5-30 cm DBH) and "large" trees (> 30 cm DBH). We assigned each tree to one of five taxonomic groups: loblolly pine *(Pinus taeda)*, combined oak species (*Quercus* spp.), American beech *(Fagus grandifolia)*, combined hickory species (*Carya* spp.), and combined mixed

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[2]*Raymond D. Dueser is an Associate Professor in the Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903.*

[3]*James L. Dooley, Jr., is a graduate research assistant in the Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903.*

[4]*Gary J. Taylor is Associate Director of Wildlife, Department of Natural Resources, Maryland Forest, Park and Wildlife Service, Tawes State Office Building, Annapolis, MD 21401.*

hardwoods. We estimated the approximate total basal area for each size-taxonomic class by assuming an average DBH of 17.5 cm for small trees and 40.0 cm for large trees. We then estimated total basal area for all trees $\geq$ 5 cm DBH and the fraction of that total basal area represented by each taxonomic group. These basal area estimates provide a basis for comparing forest "composition" independently of forest "structure" as reflected, for example, in the raw percentage of trees counted in each taxonomic group.

Original data were collected on land use and cover composition of the landscape surrounding a random subset of Taylor's (1976) study areas (fig. 1). Landscape variables included area of open fields, percentage of area forested, internal forest perimeter ("edge") within the sample unit, forest shape (Blouin and Connor 1985), and distance to next nearest woodland. These variables are referred to below as landscape "dimensions." They were measured by planimetry of 1:1000 black-and-white photographs (dated 1978) obtained from Eastern Shore offices of the USDA Agricultural Stabilization and Conservation Service. We initially measured each landscape variable for a 2-km^2 circular sample unit centered on the sample woodland. This unit was chosen as a first-approximation of "minimal population area" on the basis of home range size and activity (Flyger and Smith 1980). Based on the results of analyses for the 2-km^2 unit, both smaller (1-km^2) and larger (4-km^2) sample units subsequently were described in the same way.

Statistical Analyses

This comparison of habitat components is based on multivariate statistical analyses of three separate but related components of forest habitat suitability: (1) habitat structure ("What does the forest 'look like' to an observer passing through on the ground?"), (2) tree species composition ("Which tree species predominate in this forest and give it its character?"), and (3) landscape dimensions ("What are the land use and cover dimensions of the landscape mosaic in which this forest is embedded?"). Conceptually, these components represent a gradient of scales from "microscopic" habitat structure to "macroscopic" composition to "megascopic" context.

Two-group discriminant function analysis was used to compare the Present and Absent forest stands identified by Taylor (1976). Each analysis (1) computed the univariate F-ratio comparing Present and Absent sites for each habitat variable, (2) tested the centroids of Present and Absent sites for equality on the basis of a linear combination of the habitat variables (i.e., a linear discriminant function), using multivariate analysis of variance (MANOVA), (3) indicated the relative contribution of each habitat variable to any observed difference between centroids, based on the correlation between the variable and the discriminant function, (4) tested the sample variance-covariance matrices of Present and Absent sites for homogeneity using a Box's M test statistic, and (5) indicated the percentage of the variation in group membership (Present or Absent) explained by the discriminant function, based on the correlation between the membership variable and the discriminant function. (Dueser and Shugart 1978). All analyses were computed both with and without arcsin-square root transformations of percentage variables. Results of the parallel analyses were qualitatively similar in each case. For purposes of interpretability, only the results for untransformed variables are presented here. All analyses used the MANOVA and DISCRIMINANT routines of the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975).

As an unbiased test of the ability of each set of habitat variables to

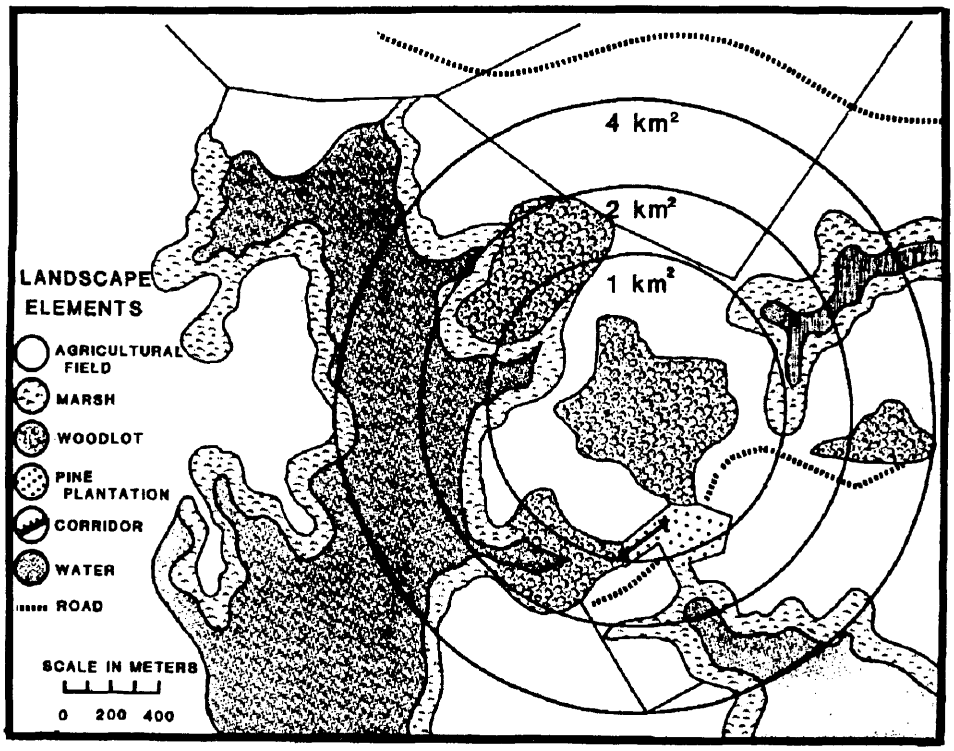

Figure 1.—Schematic diagram of 1-, 2- and 4-km^2 sample units for measuring landscape dimensions of "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland. Each sample unit was centered on one of Taylor's (1976) study areas.

classify the group membership of the study sites (i.e., Present or Absent), a jackknife procedure (Efron 1979) was used to classify each of Taylor's study areas. Each site was deleted in sequence, DISCRIMINANT was run for data from the remaining 53 sites, and a classification function was computed from these data. The deleted site was then classified on the basis of this independent classification function. The probabilistic ("predicted") classification was then compared with the actual ("observed") classification for each site.

Brennan et al. (1986) have proposed an alternative solution to the problem of habitat analysis. Logistic regression analysis is superior to multivariate analysis of variance when one or more of the predictor (e.g., habitat) variables is categorical (i.e., non-continuous), when the variance-covariance matrices are nonhomogeneous and/or when the data violate the assumption of multivariate normality (Press and Wilson 1978). Parallel analyses demonstrate that logistic regression analysis offers no inherent advantage over discriminant function analysis in the present case (Dooley, unpublished).

Results

Habitat Structure

Present sites had a greater percentage of trees larger than 30 cm DBH, lower percentage shrub-ground cover, and slightly lower understory vegetation density than Absent sites (table 1, $p \leq 0.05$). Present and Absent sites differ structurally on the average (MANOVA Chi-square (5) = 14.825, $p \leq 0.011$). The linear combination of structure variables accounted for 26% of the variation in group membership. The variance-covariance matrices were marginally homogeneous (Box's M = 20.056, $p \geq 0.06$). Percentage of trees greater than 30 cm DBH (r = -0.735), understory vegetation density (0.564), and percentage shrub-ground cover (0.564) are particularly important in discriminating between sites. Conceptually, Present sites have larger trees, less shrub-ground cover vegetation, and less understory than Absent sites (fig. 2). Present sites were correctly classified 79% of the time in the jackknifing procedure, and Absent sites were correctly classified 48% of the time.

Forest Tree Species Composition

All 54 study areas supported a mix of hard- and soft-mast tree species. Although Present sites had somewhat greater basal areas for American beech ($p > 0.07$) and mixed hardwoods ($p > 0.05$), there were no clear-cut univariate differences between sites in forest composition (table 2). There also was no difference in total

Table 1.—Comparison of average forest habitat structure for "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland, based on data of Taylor (1976). Tabled values are means and (standard deviations).

Habitat variables	Present (N = 36)		Absent (N = 18)		*P*
% Trees > 30 cm DBH	32.3	(12.14)	22.1	(9.26)	<0.01
% Crown cover	75.6	(17.72)	70.6	(16.08)	>0.30
% Shrub-ground cover	51.1	(26.60)	67.5	(21.85)	<0.05
Understory "density"	2.6	(1.38)	3.4	(1.04)	<0.05
% Pine composition	10.5	(10.63)	17.1	(22.23)	>0.10

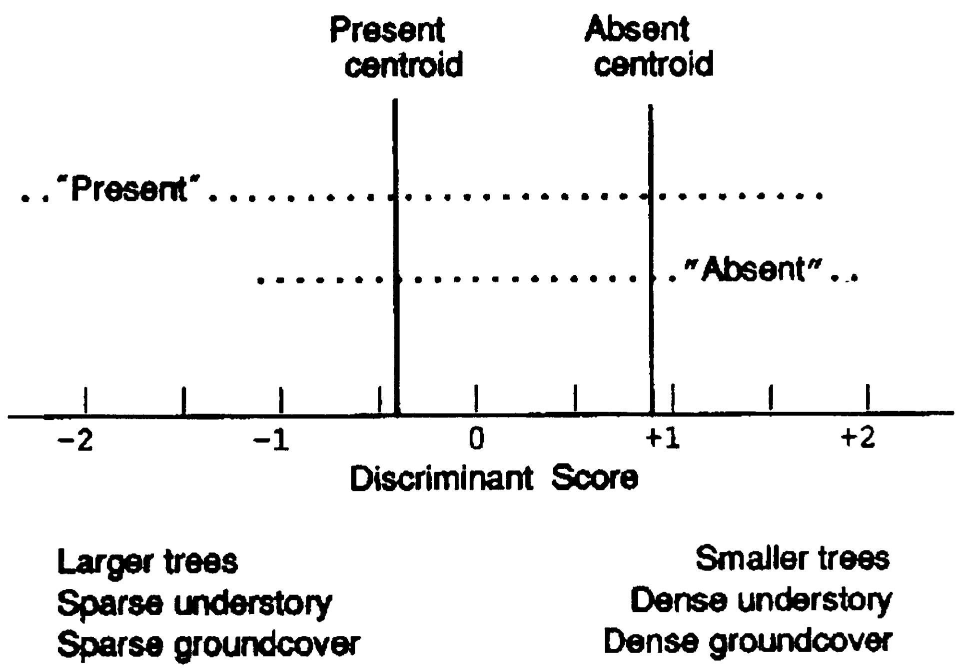

Figure 2.—Interpretation of discrimination between average "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland, based on analysis of forest habitat structure. The horizontal dashed lines indicate the range of observations for a sample group (Present or Absent).

basal area ($F(1,52) = 2.300, p > 0.13$). The two types of sites were similar in composition for both small and large trees (fig. 3). Reflecting this similarity, there was only a marginally significant multivariate difference in forest composition (MANOVA Chi-square $(5) = 10.584, p > 0.06$).

The linear combination of composition variables accounted for 19% of the variation in group membership. The variance-covariance matrices were conspicuously non-homogeneous (Box's $M = 61.549, p < 0.001$). Present sites were correctly classified 79% of the time, and Absent sites were correctly classified 48% of the time.

Although the correct classification rates were the same as for structural variables, the two sets of variables misclassified different sites.

Landscape Dimensions

Five landscape variables were measured for the 2-km^2 circular sample unit centered on the target woodland of 38 of the Taylor's (1976) study areas. Present sites were somewhat closer to the next nearest forest tract than Absent sites (table 3, $p < 0.03$). Despite this modest difference, there was no significant multivariate difference in landscape dimensions between sites (MANOVA Chi-square $(5) = 8.574, p > 0.127$).

Present and Absent woodlands also were similar in area, averaging 9.4 and 10.0 ha, respectively, as photographed in 1978. The linear combination of landscape variables accounted for 23% of the variation in group membership. The variance-covariance matrices were homogeneous (Box's $M = 19.926, p > 0.39$). As with forest composition, there was no consistent difference in landscape dimensions between Present and Absent sites. Present sites were correctly classified 78% of the time, and Absent sites were correctly classified 40% of the time.

To evaluate the possibility that the negative result in the test for equality of group centroids came about because we were measuring landscape variables on an "incorrect" spatial scale, we repeated the landscape analysis for both smaller (1-km^2) and larger (4-km^2) circular sample units, still centered on the woodland of interest. Again, there were no consistent group differences on either scale ($p > 0.40$, table 4).

Either the landscapes surrounding the sample Present and Absent woodlands do not differ consistently, or they differ on a scale of measurement or in a way not revealed by the present analyses.

Table 2.—Comparison of average tree species composition for "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland, based on estimated basal area (cm^2 per 800-m^2 sample transect) per taxonomic group. Data from Taylor (1976). Tabled values are means and (standard deviations).

Taxonomic group	Present (N = 36)		Absent (N = 18)		P
Loblolly pine	5359	(1099.84)	7339	(2278.43)	>0.35
Oak species	9547	(1061.24)	9628	(1378.18)	>0.95
American beech	3293	(679.62)	1400	(546.56)	>0.07
Hickory	1583	(611.77)	1050	(263.26)	>0.50
Mixed hardwoods	9498	(1032.96)	6514	(690.13)	>0.05

Table 3.—Comparison of average landscape dimensions for "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland. Variables measured for 2-km^2 circular sample unit centered on study woodland. Tabled values are means and (standard deviations).

Landscape variables	Present (N = 27)		Absent (N = 11)		P
Area open fields (ha)	99.3	(6.4)	96.3	(11.9)	>0.81
% Forested area	56.4	(3.6)	50.1	(6.0)	>0.35
Internal perim. (km)	5.3	(2.0)	6.2	(1.9)	>0.21
Forest "shape"	136.4	(54.5)	153.0	(44.9)	>0.38
Dist. next woodlot (km)	0.4	(0.1)	0.8	(0.2)	<0.03

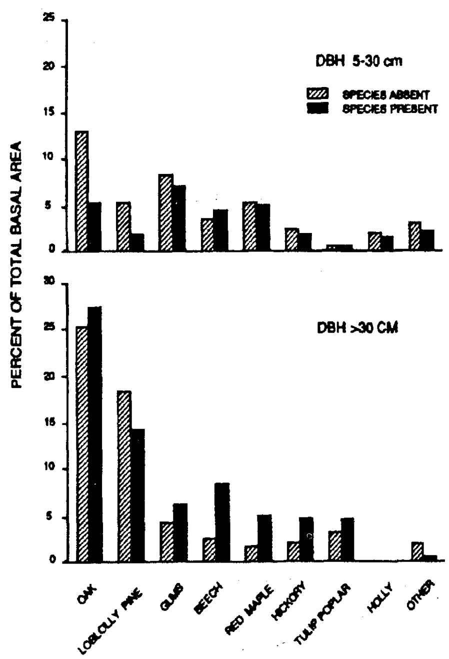

Figure 3.—Average forest tree species composition of "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland. "Other" category includes a variety of small trees such as cherry (*Prunus* spp.) and flowering dogwood (*Cornus florida*).

Discussion

Present Habitat

The present habitat of the Delmarva fox squirrel consists primarily of relatively small stands of mature mixed hardwoods and pines having relatively closed canopies, relatively open understory, and a high proportion of forest edge. Occupied tracts include both groves of trees along streams and bays and small woodlots located near agricultural fields. In some areas, particularly in southern Dorchester County, Maryland, occupied habitat includes tracts dominated by mature loblolly pine located adjacent to marshes and tidal streams. The woodland habitats now occupied by the Delmarva fox squirrel are consistent with those occupied by other subspecies of fox squirrel (Bakken 1952; Brown and Yeager 1945; Weigl et al., in press).

The picture of the Delmarva fox squirrel that emerges from the literature is one of a species relatively adept at utilizing a dissected, heterogeneous landscape dominated by agriculture and woodlot forestry. Fox squirrels are more cursorial than gray squirrels, and often are found on the ground several hundred meters from the nearest woodlot. They occupy larger home ranges than gray squirrels (30 ha vs. 3 ha), travel farther between captures (307 m vs. 119 m), and thus are generally more mobile (Flyger and Smith 1980). Fox squirrels more readily exploit agricultural crops such corn, oats, soybeans and fruit. They more frequently utilize forest edges. Fox squirrels would thus appear to be relatively well-adapted to exploit the landscape created by settlement of the coastal plain.

One might conclude that man's activities on the Delmarva Peninsula should have been to the benefit of the fox squirrel. Land clearing has created woodlots. Grazing and burning have opened up the understory. Agriculture has increased the availability of alternative food sources and perhaps stabilized the food supply. Indeed, Allen (1943) and Nixon and Hansen (1987) indicate that settlement and agriculture have worked to the advantage of the fox squirrel throughout the midwestern United States, resulting in increased abundance and an expanded geographic range.

Why has this not occurred with the Delmarva subspecies? Why has the abundance of this fox squirrel continued to decline throughout the period of the recorded literature (since approximately 1850)?

Taylor (1976) attributes the continued decline of the Delmarva fox squirrel to habitat destruction. While many of the landscape changes resulting from settlement might have benefited the fox squirrel, others have been detrimental. Taylor believes that extensive timber harvest has been particularly detrimental. The removal of mature hardwoods has reduced the availability of suitable den trees, removed reliable sources of concentrated hard mast, promoted the luxuriant growth of understory vegetation, and perhaps altered the competitive relationship between fox and gray squirrels to favor grays. Furthermore, coastal plain woodland management typically has involved both short timber rotations (i.e., frequent harvests) and reforestation with pure stands of loblolly pine. Finally, gradual urbanization has added yet another detrimental land-use practice.

Habitat Suitability

It is assumed that Present (i.e., occupied) sites are more "suitable" on the average than are Absent (i.e., unoccupied) sites. Present sites are regarded here as the "standard of excellence" by which to judge the habitat requirements of the Delmarva fox squirrel. Given that a number of unknown (and unknowable) ecological, biogeographical, and/or historical factors may actually be responsible for the absence of this subspecies from any particular site within the historic range, this assumption is correct only as a first approximation (ref. Hanski 1982). It clearly would be unwarranted if the distribution of squirrels among these 54 study sites were highly variable through time. Nevertheless, the chance presence of the squirrel on "unsuitable" sites and its absence from "suitable" sites because of factors other than habitat suitability per se can only make it more difficult to distinguish between Present and Absent sites. These analyses based on presence-or-absence population information thus circumvent many of the potential pitfalls associated with the use of population density as an indicator of habitat suitability (Van Horne 1983).

Given its present habitat, it seemed reasonable to propose that the capacity of a woodland to support a population of the Delmarva fox squirrel could be determined by habitat structure, forest composition and/or the land use and cover com-

Table 4.—Comparison of average "fox squirrel present" and "fox squirrel absent" study areas at the 1-, 2- and 4-square kilometer scales of observation. Testing for similarity of landscape dimensions listed in table 3.

Statistic	1-km²	2-km²	4-km²
Number "Present" areas	7	27	7
Number "Absent" areas	9	11	9
Chi-square	4.791	8.574	2.750
df	5	5	5
P	0.442	0.127	0.738

position of the surrounding landscape. We anticipated originally that each of these components of habitat suitability would prove to be important in its own way, and that each would have a perceptible influence on fox squirrel presence or absence in Maryland woodlots today. Our results indicate, however, that habitat structure is the component most likely to contribute meaningfully to the formulation of a predictive model of habitat suitability. Only the structure variables discriminate strongly between Present and Absent sites: Present sites have larger trees, less ground cover and less understory (fig. 2). These variables account for the greatest fraction of the explained variation, their dispersion matrices are effectively homogeneous, and they classify sites to the correct group (i.e., Present or Absent) at least as well as any of the variable sets examined.

Forest composition is highly variable among locations in eastern Maryland, but this variation seems to exert only a marginal influence on the likelihood of occurrence of fox squirrels on any given site. The composition variables classify sites as reliably as the structural variables, and they account for only a slightly lower fraction of the explained variation. They do not, however, discriminate strongly between Present and Absent sites and their dispersion matrices are strongly non-homogeneous. Of course, this conclusion is based on a comparison of two groups of sites, all of which are known to be "squirrel woods." Had there been a "tree squirrel absent" category of study area, forest composition might well have appeared to be more significant (cf. Nixon et al. 1978, Sanderson et al. 1976).

Landscape composition also varies among locations, but this variation seems not to be important on the average in discriminating between occupied and unoccupied sites today. The landscape variables account for a comparable fraction of the explained variation, they classify sites almost as reliably as the structural variables, and their dispersion matrices are homogeneous. They do not, however, discriminate meaningfully between Present and Absent sites. Given the suggested importance of landscape changes in bringing about the decline of the fox squirrel, this result was somewhat unexpected. The correct interpretation probably requires recognition that most of the Eastern Shore landscape has been altered, fragmented and homogenized. Most of the remaining woodlands are mere remnants of forest in a mosaic of agricultural fields, wetlands and suburban development. There may simply be little important variation remaining among these forest patches. At the same time, it must be recognized that a number of potentially important landscape variables—e.g., proximity to streams and ponds (McComb and Noble 1981) and proximity to roadways (Flyger and Lustig 1976)—were not considered in this analysis.

Management Implications

The Recovery Plan for the Delmarva fox squirrel calls for both the translocation of squirrels to suitable habitats throughout the historic range and the maintenance of occupied habitat (Taylor et al. 1983). Will objective, quantitative habitat analysis be helpful in evaluating potential release sites and planning prescriptive habitat management? Results of the analyses presented here provide some basis for optimism. A number of management implications follow from these results:

1. Of the variable sets examined, habitat structure is the best indicator of biological habitat suitability for the Delmarva fox squirrel at the present time. Even this minimal list of structure variables (table 1) has the power to discriminate meaningfully between occupied and unoccupied forest stands. Present sites have larger trees, less ground cover, and less understory than Absent sites. Significantly, these results corroborate the general habitat descriptions reported by Flyger and Lustig (1976).

2. In addition to this clear-cut discrimination, the structure variables exhibit the most desirable combination of statistical properties, including the highest variance explanation, homogeneity of dispersions, and high correct classification rates. These properties will simplify the formulation of a predictive classification model of habitat suitability.

3. Although the absence of meaningful discriminating information in forest composition and landscape dimensions was somewhat surprising, these results have the effect of simplifying the effort to quantify habitat suitability for the Delmarva fox squirrel. It would be imprudent to disregard forest composition and landscape attributes in the evaluation of potential release sites; these components of habitat suitability must be important at some level (Flyger and Lustig 1976). There appears to be little potential, however, for the variables analyzed here to contribute to a predictive model of habitat suitability.

4. The discriminating structure variables are easy and relatively inexpensive to measure. Including site reconnaissance, approximately one-half day of field time is required for a team of two ex-

perienced observers to collect a Taylor-type data set.

5. It should therefore be practical to pre-screen potential release sites for habitat suitability relative to Present sites. Objective pre-screening has not always been possible because no "standard of excellence" has been available.

6. It also should be practical to plan, implement and evaluate prescriptive habitat management for the benefit of the Delmarva fox squirrel on occupied sites or potential release sites. The important measures of habitat structure (e.g., understory vegetation density) tend to be variables which are amenable to silvicultural manipulation (Nixon et al. 1980).

Conclusions

We anticipated at the outset that each of three potentially important components of habitat suitability—forest habitat structure, forest tree species composition, and surrounding landscape dimensions—would influence the present occurrence of the Delmarva fox squirrel in forest stands on the Eastern Shore of Maryland. The analyses reported here produced a number of surprises.

Habitat structure is the only component that both discriminates between occupied and unoccupied sites in a meaningful way and exhibits a combination of statistical properties favorable for the formulation of a predictive classification model of habitat suitability.

The analysis of habitat structure provides a basis for optimism that such a model would prove useful both for pre-screening potential release sites and for planning, implementing and monitoring prescriptive habitat management.

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