Influence of Forest Management and Microhabitat Conditions on Abundance of Southern Fox and Gray Squirrels

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Abstract: Squirrels (*Sciuris* spp.) are important game species; however, it is believed that southern fox squirrel *(S. niger)* populations in many regions are declining. Changes in forest management practices may have reduced habitat availability and diversity, thereby contributing to declining population trends. However, relationships among forest management practices, active management of wildlife habitats, and wildlife populations requires an understanding of relationships among forest communities and wildlife populations. We used linear regression to build predictive models of gray squirrel *(S. carolinensis)* and fox squirrel relative abundance based on winter and summer habitat conditions. Relative abundance of gray squirrels was greatest in older hardwood stands containing high basal areas, regardless of season. Southern fox squirrel abundance also was correlated with percentage hardwood, indicating the importance of the hardwood component to southern fox squirrels. Our data suggest that the hardwood component within mixed and pine-dominated stands is an important cue for habitat selection by southern fox squirrels and should be monitored when managing for sustainable populations of southern fox and gray squirrels.

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In Mississippi, squirrel (*Sciurus* spp.) hunting is second only to white-tailed deer *(Odocoileus virginianus)* hunting in popularity (Ross 1996). However, southern

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fox squirrel populations have declined because of decreased habitat availability and quality (Loeb and Moncrief 1993). The southern fox squirrel *(S. niger)* is more of a habitat specialist than the gray squirrel *(S. carolinensis)* (Flyger and Gates 1982) and, consequently, southern fox squirrels may be more sensitive to changes in habitat composition and structure than gray squirrels. In fact, declines in southern fox squirrel numbers have occurred in other southeastern states, and several states have listed subspecies of the fox squirrel as threatened or endangered (Flyger and Gates 1982).

Previous studies have suggested that patch size and cover type diversity influence distribution and abundance of fox squirrels (Brown and Batzli 1984, Taylor 1973). Southern fox squirrels are commonly associated with mature pine forests containing an oak (*Quercus* spp.) component (Weigl et al. 1989). Additionally, the loblolly pine *(Pinus taeda)* forests of the Piedmont region also may provide suitable habitat (Hilliard 1979). However, the highly variable seed crop of the southern pines are rarely considered in assessing quality of southern fox squirrel habitat (Ha 1983).

Gray squirrel abundance and distribution are affected by availability of hardwood sawtimber and den cavities (Flyger and Gates 1982). However, forest type conversions (i.e., hardwood to pine), reduced rotation lengths, large block plantations, and improved machinery have led to a decrease in both habitat diversity and abundance for many wildlife species (Speake 1970, Dickson and Huntley 1985, Ivey and Frampton 1987), particularly for southern fox and gray squirrels (Weigl et al. 1989, Ha 1983). The loss of suitable forested habitats from encroaching urbanization and continuing changes in forest management practices may significantly affect squirrel populations throughout the Southeast, particularly fox squirrels. However, the effects of these manipulations on southern populations is relatively unknown. Thus, our objectives were to 1) determine relative abundance of southeastern fox and gray squirrels on 12 pine-dominated sites across Mississippi and 2) relate relative abundance to forest stand conditions influenced by standard forest management practices.

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Methods

Study Areas

This study was conducted on 12 sites in Mississippi. Replication encompassed a representative sample of current southern fox squirrel habitat types across Mississippi with an emphasis on pine-hardwood forests and traditionally managed pine forests. Site criteria included a minimum of 150 forested ha, stand age of $\geq$50 years, pine basal areas of 11 m^2/ha, and known or suspected presence of southern fox squirrels. We sampled a range of habitat conditions by using these criteria. Our study sites encompassed 3 major forest types: loblolly pine-upland hardwood, longleaf pine *(P. palustris),* and loblolly-short leaf pine *(P. echinata).* For detailed descriptions of each study area, including species associations and vegetative characteristics of each site, see Ross (1996).

Squirrel Census

We conducted time area counts (Uhlig 1955, Bouffard and Hein 1978) in October/November 1994 and 1995 to coincide with hard mast maturation (Burns et al. 1954, Nixon and McClain 1969, Weigl et al. 1989). We considered these months as the peak of annual squirrel activity (Allen 1942, Baumgartner 1943, Flyger and Gates 1982). We attempted to conduct all time area counts prior to the opening of harvest seasons. Depending on topography of individual study sites, we sampled 20 stations spaced 200 m apart. We began sampling stations ≥100 m from primary or frequently traveled roads and continued sampling into stand interiors. Spacing was such that counting of an individual more than once was minimized. Observation time consisted of 4 minutes/station, with 2–3 minutes of "settle down" time in addition to the 4-minute sample. Time area counts were conducted once/site/year. Previous research has identified problems inherent in standard time area counts (Marshall 1967, Laubhan 1987), including double counting and difficulties in identifying individual squirrels by vocalizations. To address these concerns, we partitioned squirrel sightings during time area counts into gray, southern fox, and unknown squirrel categories. We used only positively identified gray and southern fox squirrel visual observations as dependent variables in subsequent analyses.

Habitat Assessment

We evaluated habitat conditions twice/year at each site. The 2 periods were maximum foliage in summer and minimal foliage in late winter. These time periods coincided with presumed periods of greatest and least squirrel travel movements (Flyger and Gates 1982). Measurements included 1) stand age, 2) pine and hardwood basal areas (BA), 3) diameter at breast height (DBH), 4) understudy abundance, 5) horizontal structure, and 6) percentage canopy closure. We determined stand age from Forest Service data, private landowner information, and/or increment boring of 10 randomly selected dominant trees. We determined BA for all woody vegetation by using 5- and 10-factor prisms (Hayes et al. 1981). The 10-factor prism predominantly included dominant canopy, sawtimber-size trees. The 5-factor prism included the shrub component (woody vegetation <10 cm dbh and <10 m in height). We determined canopy closure (>15 m) using a forest densiometer (Lemmon 1956). We determined understory plant abundance (plants <1.3 m high) using the line intercept method with 6 m of tape/plot and 20 plots/study area (Canfield 1941). From line intercepts sampled in 2.5-cm increments, we determined the ratio of bare ground to grass, vine, forb, and woody species abundance. We assessed horizontal vegetative structure for 20 random plots/study area using a Nudd's density board with 4 readings/plot in the cardinal directions (Nudds 1977, Hayes et al. 1981).

We tabulated hard mast abundance by sampling 20 randomly located stations/study area during October/November, immediately following time area counts. At each station, 4 1-m^2 hoops were placed in the 4 cardinal directions from plot center. After completing a time area count, acorns within each hoop were collected, counted, and identified to species. We recognize that acorn depredation by squirrels and other species could influence our estimates of hard mast abundance. However, we assumed that this potential influence was similar across areas.

Statistical Analysis

We used multiple linear regression to build separate predictive models for gray and southern fox squirrel abundance. We included in model selection 8 variables describing the overstory, 10 variables describing the understory, 3 variables describing the midstory, and 6 variables describing food resources (Table 1). We used correlation matrices to screen variables and eliminate from consideration highly correlated pairs. We considered pairs to be correlated if $r \geq 0.6$.

We performed multiple regression analysis using stepwise selection to predict relative squirrel abundance (partitioned by species). We conducted separate analyses

Table 1. Habitat variables by stand position used in multiple regression analyses to predict squirrel abundance on 12 sites in Mississippi, 1993–1995.

Variable
Tree diameter at breast height (dbh)
Stand overstory basal area — obtained with 10-factor prism
Stand midstory basal area — obtained with 5-factor prism
Pine overstory basal area — obtained with 10-factor prism
Pine midstory basal area — obtained with 5-factor prism
Canopy closure — measured with forest densiometer
Percentage stand pine (*N* pine trees/total trees)
Percentage stand hardwood (1–%pine)
Distance to nearest tree (point-center quarter method)
Stand age (years)
Horizontal density (Nudds board)
Percentage understory vine (line intercept)
Percentage woody understory (line intercept)
Percentage understory forb (line intercept)
Percentage understory grass (line intercept)
Percentage understory debris (line intercept)
Percentage understory bare ground (line intercept)
Percentage understory snag occurrence (line intercept)
Percentage understory log occurrence (line intercept)
Percentage understory fungi (line intercept)
Red oak mast abundance (hoop method)
White oak mast abundance (hoop method)
Hickory mast abundance (hoop method)
Total mast abundance (hoop method)
Percentage soft mast producing hardwood component (point-center quarter method)
Percentage hard mast producing hardwood component (point-center quarter method)
Percentage mast producing hardwood component (point-center quarter method)

for summer and winter data sets. The stepwise multiple regression analysis included non-autocorrelated habitat characteristics as independent variables to predict relative squirrel abundance. Each independent habitat variable used in each of the regression analyses was composed of a mean value derived from the 20 sample plots/study area/habitat assessment period. We regressed these variable means against abundance of each squirrel species. All count, data, gray and southern fox squirrel time area counts, and hard mast counts (partitioned by species) were square-root transformed prior to regression. All habitat data expressed in percentages were arcsin square-root transformed prior to regression.

We used multicollinearity diagnostics to reduce over-specification of regression models. Variance inflation factors ≥ 10 and condition numbers $\geq 1{,}000$ were used to indicate variables for removal. We also used Akaike's Information Criterion (AIC) scores to select the model that best fit the data with a lower AIC score indicating a better fitting model (Burnham and Anderson 1992).

To examine functional relationships of the regression models, variables not assessed were held constant while varying the independent variables of interest from their observed minima to their maxima. We chose to examine functional relationships of variables that could feasibly be manipulated on sites throughout the Southeast. For example, to assess the relationship between squirrel abundance and hardwood BA, all other significant independent variables in the model were held constant at means while varying hardwood BA in increments of 15-m^2.

Results

Variable Reduction

By examining correlation matrices, we eliminated 15 of 27 possible habitat variables. The 12 remaining variables used to predict relative squirrel abundance were horizontal density (%), percentage canopy closure (>5 m), total BA (m^2/ha), percentage hardwood BA (m^2/ha), frequency of occurrence of understory debris, red oak mast abundance, percentage understory snag occurrence, stand age (years), percentage woody understory (line intercept), percentage soft mast producing hardwoods in the overstory, total mast abundance, and percentage hard mast producing hardwoods in the overstory.

Winter Gray Squirrel Model

Four habitat variables accounted for 86% of variability in gray squirrel relative abundance) $F_{4,7}=19.29$; $P<0.001$).

$$Y= 26.155 + 0.02X1 + 0.33X2 + 0.32X3 + 0.08X4 \qquad \text{(Equation 1)}$$

where: Y=relative gray squirrel abundance; X_1=stand age (years); X_2=total basal area (m^2/ha); X_3=red oak mast abundance; and X_4=total mast abundance.

Total mast abundance (partial $R^2=0.31$, hereafter reported as percentages of variation explained), red oak mast abundance (29%), total BA (20%), and stand age

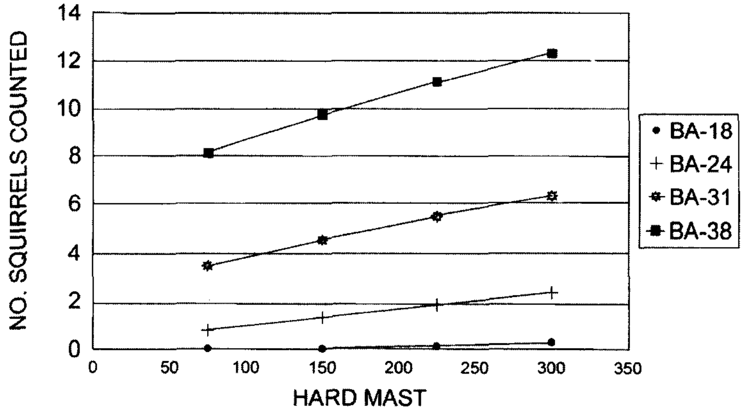

Figure 1. Relationship of winter hard mast abundance and stand basal area (BA = m^2/ha) to gray squirrel abundance, 1994–1995, in selected stands in Mississippi.

(11%) were determined to be significant predictor variables. Equal gray squirrel observations (Fig. 1) did not occur over a range of stand BA when BA and hard mast were used as predictor variables. As BA increased from 31 to 38 (a 21% gain), gray squirrel observations increased from 6 to 12 (a 100% gain). Contrasted to the BA increase from 24 to 31 (a 27% gain), gray squirrel observations increased from 2 to 6 (a 300% gain).

Winter gray squirrel relative abundance increased with increasing BA, mast abundance, and stand age. The largest effects on gray squirrel abundance from winter stand measurements were from total hard mast mean counts exceeding 100 acorns, red oak mast mean counts exceeding 80 acorns, stand ages exceeding 80 years, and stand BA exceeding 31 m^2/ha.

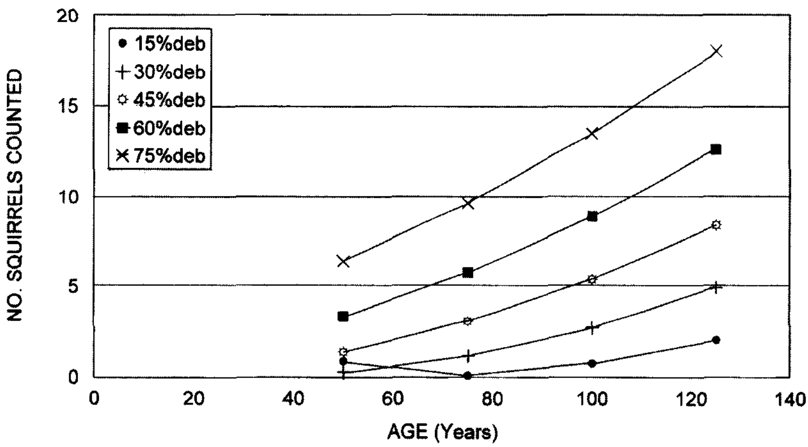

Figure 2. Relationship of stand age (years) and percentage understory debris (deb) to gray squirrel abundance, 1994–1995, in selected stands in Mississippi.

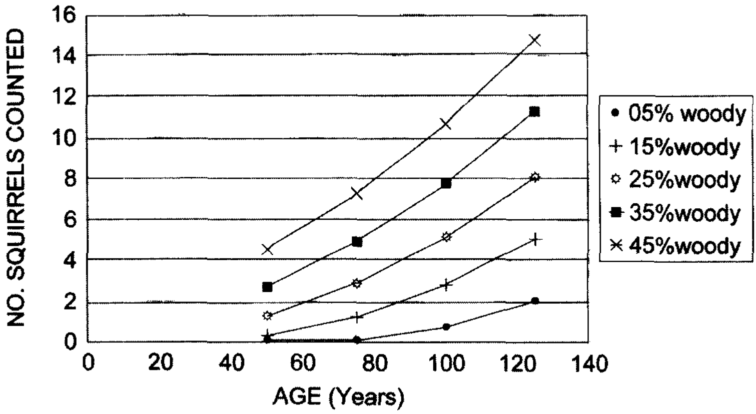

Figure 3. Relationship of stand age (years) and percentage woody understory to gray squirrel abundance, 1994–1995, in selected stands in Mississippi.

Summer Gray Squirrel Model

Five habitat variables accounted for 81.74% of the variance in gray squirrel relative abundance ($F_{5,16}=14.33$; $P=0.001$).

$$Y=-6.23+4.33X_1+0.17X_2+12.06X_3+0.02X_4+4.71X_5 \quad \text{(Equation 2)}$$

where: Y=relative gray squirrel abundance; X_1=frequency of understory debris (inches); X_2=red oak hard mast abundance (measured during fall); X_3=percentage snag (inches); X_4=stand age (yr); and X_5=frequency of occurrence of woody understory.

Percentage debris (30%) and relative amount of red oak mast (21%) were selected as significant predictor variables. Once stand ages exceeded 100, gray squirrel abundance ranged from 7 to 11, depending on total number of red oak acorns. Gray squirrel abundance increased as stand age, percentage understory debris, and percentage woody understory increased (Figs. 2, 3).

Winter Southern Fox Squirrel Model

Two independent variables accounted for 58% of variability in southern fox squirrel abundance ($F_{2,9}=6.20$; $P=0.020$)

$$Y=-4.35+0.25X_1+0.22X_2 \quad \text{(Equation 3)}$$

where: Y=relative southern fox squirrel abundance; X_1=horizontal visibility; and χ_2=total BA (m^2/ha).

Percentage understory visibility (33%) and total BA (25%) were selected as significant predictor variables. Relative southern fox squirrel abundance increased when BA exceeded 31 m^2/ha and understory visibility (measured in paces with a Nudds horizontal density board) was 8 paces or greater (approx. 10 to 15 m) (Fig. 4).

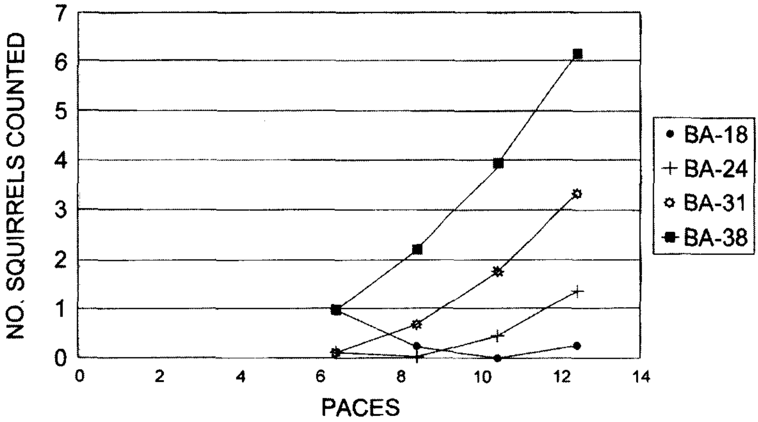

Figure 4. Relationship of winter Nudds board sampling (paces) and stand basal area (BA = m^2/ha) to fox squirrel abundance, 1994–1995, in selected stands in Mississippi.

Summer Southern Fox Squirrel Model

Two habitat variables (total BA and percentage hardwood) accounted for 43% of variability in southern fox squirrel abundance ($F_{2,19}$=7.18; P=0.005).

$$Y = -2.47 + 0.16X_1 + 1.41X_2 \qquad \text{(Equation 4)}$$

where: Y=relative southern fox squirrel abundance; X_1=total BA (m^2/ha); and X_2=percentage hardwood BA (m^2/ha).

Total BA obtained by 10-factor prism (26%) and percentage of hardwood BA (17%) were selected as significant predictor variables. Equal southern fox squirrel observations (N=1) were recorded when decreasing BA of 38 (N=m^2/ha, 31 m^2/ha,

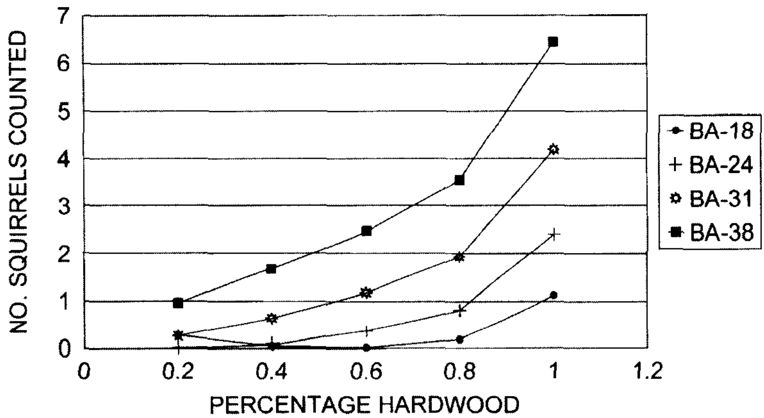

Figure 5. Relationship of percentage stand hardwood and stand basal area (BA = m^2/ha) to fox squirrel abundance, 1994–1995, in selected stands in Mississippi.

and 18 m^2/ha occurred in conjunction with increasing stand hardwood percentages of 20, 60, and 100, respectively. Southern fox squirrel relative abundance increased with increasing percentage hardwood and total BA within stands (Fig. 5). As percentage hardwood within stands exceeded 80%, southern fox squirrel relative abundance dramatically increased for all BA sampled. The difference in southern fox squirrel abundance was greatest between BA 31 m^2/ha and 38 m^2/ha.

Areas that consistently yielded southern fox squirrel sightings exhibited 3 consistently similar stand characteristics: stand age approached 100 years, stand hardwood component approached 60%, and total BA approached 27 m^2/ha. Two areas in particular accounted for >39% of southern fox squirrel sightings (13 of 33) and >30% of gray squirrel sightings. Overall, they combined for 33% of total squirrel sightings out of 10 areas during this study. In contrast, 2 sites meeting the age requirement, but not containing the desirable hardwood component or the BA, accounted for 8% of gray squirrel sightings, 3% of southern fox squirrel sightings, and 7% of total squirrel sightings during time area counts.

Discussion

Southern fox squirrel habitat has consistently been identified in the literature as having a significant pine component associated with a sparse, open understory mixed with some hardwoods. Previous studies have associated fox squirrel numbers with various habitat stand characteristics such as understory density (Allen 1942, Brown and Yeager 1945, Taylor 1973, Laubhan 1987), hard mast production (Nixon and McClain 1969, Kantola 1986), percentage canopy closure (Laubhan 1987), ground litter (Laubhan 1987), horizontal density (Laubhan 1987, Powers 1993), and BA (Powers 1993). Several studies have identified a hard mast producing hardwood component as being used more than expected (or used greater than availability) relative to habitat availability (Hilliard 1979, Kantola 1986, Weigl et al. 1989, Powers 1993). We recognize that our models for southern fox squirrel abundance only explained approximately 50% of overall variability in southern fox squirrel abundance. However, southern fox squirrel abundance in this study was positively correlated with percentage hardwood, not pine, indicating that the hardwood component of pine-hardwood mixtures may be the more important of the 2 components. This contrasted with previous southern fox squirrel literature which suggested a greater importance of pine components (Allen 1982). In light of current declining southern fox squirrel populations, intensive forest management practices (i.e., shorter rotation lengths, hardwood suppression, large block pine plantations) will only increase the importance of maintaining the hard mast producing hardwood component to southern fox squirrel populations.

Greater southern fox squirrel observations occurred at lower BA as the stand percentage of hardwood occurrence increased. This has direct management implications for landowners wanting to increase southern fox squirrel populations, especially in intensively managed pine forests where mature stand BA is typically 22 m^2/ha or less. To positively impact southern fox squirrel observations in stands with low BA, the percentage of the stand composed of mast producing hardwoods must be increased. The southern fox squirrel, being of much greater body size than the gray squirrel, and with large energy needs, is more of a ground foraging animal (Flyger and Gates 1982, Weigl et al. 1989). This may account for the correlation between winter southern fox squirrel abundance and understory visibility. This correlation also may have been a function of shading effect caused by the hardwood stand component we found to be correlated with southern fox squirrel abundance.

Most fox squirrel habitat studies, both midwestern and southeastern, have emphasized the importance of a variety of food sources because of hard mast crop variability (Ha 1983, Kantola 1986, Weigl et al. 1989, Powers 1993). This diversity of food sources is deemed especially important to the southern fox squirrel because of lower total tree species diversity and lower diversity of hard mast bearing species (Oosting 1956, Braun 1964). The cone crop of southern pines is highly variable, similar to hard mast producing species. Red and white oaks yield heavy acorn crops on average once every 4 years (Barrett 1931) and large cone yields of southern pines may occur as little as once every 5–7 years (Schopmeyer 1974, Ha 1983, Powers 1993). Many factors have been reported to affect hard mast production including tree diameter, BA, crown diameter, water availability, site position, and soil characteristics (Christisen and Korschegan 1955). In our study, stands containing mixed hardwood and pine clearly showed strong squirrel associations and extreme variability of seed production may necessitate mixed stands of mast producing trees for squirrels, particularly southern fox squirrels (Christisen and Korschegan 1955, Goodrum et al. 1971, Christisen and Kearby 1984). This association indicates a need for heterogeneous habitat within the Southeast to satisfy basic southern fox and gray squirrel requirements.

Increasing total BA has been reported to be more suitable for gray squirrel relative abundance (Allen 1987). Gray squirrels often inhabit dense hardwood stands with a continuous canopy throughout, whereas southern fox squirrels often inhabit sparsely wooded, fire-climax, pine forest ecosystems with a discontinuous canopy (Flyger and Gates 1982). Large gray squirrel populations often have been attributed to an abundance of large blocks of continuous, mature hardwoods (Uhlig 1955, Allen 1987). In our study, gray squirrel relative abundance increased when percentage understory debris exceeded 60%. We observed a linear relationship between gray squirrel relative abundance and stand age. These observations are supported by previous studies. Similarities of variable correlation for gray and southern fox squirrel relative abundance in virtually all models we constructed, including total BA, percentage hardwood, and percentage debris, agreed with the HIS models of Allen (1982, 1987) and Laubhan (1987). This indicated that areas most favorable for southern fox squirrels also represented the most suitable habitat for gray squirrels.

Summary and Management Implications

Gray squirrel abundance was correlated to stand age, hard mast abundance, presence of woody plants and debris in the understory. Older hardwood stands containing high BA were important for relative gray squirrel abundance, regardless of season. Southern fox squirrel abundance was positively correlated with horizontal understory visibility, percentage hardwood, and BA. Equation 4 suggested that higher stand hardwood BA was very important to southern fox squirrels, contrary to what has been reported in the literature. Current forestry practices on pine-dominated sites rarely include BA exceeding 22 m^2/ha and hardwood percentages exceeding 60%; levels at which southern fox and gray squirrel abundance seemed to show significant increases in our models. While this study along with others (Ha 1983, Edwards 1986, Kantola 1986, Weigl et al. 1989, and Powers 1993) indicated a greater than expected correlation to the stand hardwood component, the stand pine component may significantly impact southern fox squirrel numbers. Energy requirements and other habitat needs of the southern fox squirrel cannot easily be met by intensively managed pine forests if mast producing hardwoods such as the understory "scrub" oaks described by Ha (1983), Kantola (1986), Weigl et al. (1989), and Powers (1993) are not present for food and shelter requirements.

On our study areas, many sites containing pines of the desired age were maintained under strict hardwood repression regimes. Consequently, understory mast producing hardwoods such as those discussed by Kantola (1986) and Weigl et al. (1989) as being important for southern fox squirrels were nonexistent. Additionally, resulting pine stands produced by current forestry practices are usually harvested much too young to meet cavity production requirements or optimum seed production for suitable long term southern fox and gray squirrel habitat. Even when allowed to reach ages where optimum seed production can be obtained, the southern pine cone crop is highly variable. The southern pine cone crop appears in late summer, a critical period of food availability for the fox squirrel (Ha 1983, Kantola 1986, and Weigl et al. 1989). This variable nature of food availability in the southeast underscores the importance of maintaining a diversity of habitat components to support viable southern fox squirrel populations.

The variability associated with absolute southern fox squirrel time area counts could only partially be explained through stand habitat characteristics. However, our data suggested that by altering current forest management practices in Mississippi, southern fox squirrel abundance can be influenced through habitat manipulation. In contrast, variability associated with absolute gray squirrel time area could be adequately explained through easily measurable stand habitat characteristics. Specifically, to create the greatest influence on gray squirrel relative abundance for the smallest change in BA, management strategies should be concentrated around stand BA between 24 and 31 m^2/ha.

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