HABITAT AND LANDSCAPE CHARACTERISTICS THAT INFLUENCE POPULATION DENSITY AND BEHAVIOR OF GRAY SQUIRRELS IN URBAN AREAS

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by
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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

HABITAT AND LANDSCAPE CHARACTERISTICS THAT INFLUENCE POPULATION DENSITY AND BEHAVIOR OF GRAY SQUIRRELS IN URBAN AREAS

presented by TOMMY S. PARKER

a candidate for the degree of Doctor of Philosophy

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

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Douglas Noltie

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To my
grandparents,
mother,
and
wife

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ABSTRACT

Recent trends in ecological studies have displayed increases in the studying of urban systems and wildlife. Investigations on various urbanized taxa have often described similar behavioral (reduced fear of humans, altered activity patterns, and increased intraspecific aggression) and population dynamics (higher densities and reduced dispersal) modifications. In addition to the presence of these changes in urbanized wildlife, little is known regarding the habitat and landscape features associated with these changes. The objective of my study was to identify habitat and landscape characteristics correlated with behavioral and life history adaptations of urban wildlife.

In the summer and fall of 2003 and 2004, I sampled gray squirrels (*Sciurus carolinensis*) at six urban parks for density, wariness, intraspecific aggression, and activity patterns. I then used combinations of each parks ecological characteristics (size, canopy cover, tree basal area, and number of trees) and the characteristics of the adjacent landscapes (tree cover, number of trees, building cover, and number of buildings) to develop models to predict gray squirrel wariness (fear of humans), intraspecific aggression, activity patterns, and density. Akaike's Information Criterion (AIC) was used to evaluate candidate models and determine the best approximating models. Density and canopy cover were the most efficient predictors for wariness (AIC = 48.42, W_i = 0.500); density, patch tree basal area, and matrix tree cover for aggression (AIC = 39.54, W_i = 0.567); patch size, canopy cover, and number of matrix trees for density (AIC = 57.40, W_i = 0.237), and density for activity (AIC = 34.02, W_i = 0.253).

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CHAPTER ONE

General Introduction

Introduction

As urbanization increases, the pertinent theory and practice of wildlife management will need to adapt. Ecological studies are increasingly addressing urban ecosystems and the wildlife therein. Across wildlife species, investigations of various urbanized populations often describe similar changes in behavioral characteristics and population demography relative to nonurban population, termed “synurbization”. However, little is known about the specific habitat and landscape attributes associated with these changes. My study will foster a greater understanding of wildlife and their behavior in urban habitats, assist managers and policy makers in managing urban wildlife, planners in designing urban areas, and ecologist in attaining a better understanding of how urban ecosystems function.

Previous studies have been conducted on the altered behavior (Flyger, 1970, 1974; Cook, 1980; Manski *et al.,* 1980; Gustafson and VanDruff, 1990) and population demography characteristics (Williamson, 1983; McPherson and Nilon, 1987; Atkinson and Shackleton, 1991; Quinn, 1992) of wildlife species in urban environments. These studies have described modifications in behavior (reduced fear of humans, altered activity patterns, and increased aggression) and population demographic attributes (elevated population density and reduced dispersal) in the subject taxa, suggesting that these changes are responses to attributes of the urban environment. However, how these behavioral and demographic changes specifically relate to the attributes of urban habitats and landscapes has remained largely unstudied.

In this dissertation, I asked the question, “Are urban habitat and landscape attributes associated with the synurbization of wildlife?” I hypothesized that squirrels in parks surrounded by greater levels of urbanization (more building cover and less tree cover) will exhibit higher population densities, increased rates of intraspecific aggression, increased activity levels, and reduced wariness. I quantified attributes of urban habitats (park size, canopy cover, total number of trees, and tree basal area) and their associated landscapes (tree cover, total number of trees, building cover, and total number of buildings) and developed models to predict density and behavior. Models were developed using ecological knowledge of gray squirrels and the described characteristics of species that have undergone synurbization.

Background

The synurbization of vertebrate species has been studied; across taxa, similar modifications in aggression, activity patterns, wariness, and population density have been shown. Gliwicz *et al.* (1994) examined two taxonomically distant vertebrate species, blackbird *(Turdus merula)* and striped field mouse *(Apodemus agrarius)*, and concluded that the effects of urban conditions upon wildlife are so strong that parallel changes in behavioral and life history characteristics occurred in both taxa. These authors further suggested that most vertebrate species experiencing synurbization would typically exhibit changes in diet composition, and nest site selection, reduced migratory behavior, and a reduced fear of man (Gliwicz *et al.,* 1994).

Cooke (1980) found that urban populations of song thrush (*Turdus philomelos*), blackbird (*T. merula*), robin (*Erithecus rubecula*), dunnock (*Prunella modularis*), starling (*Sturnus vulgaris*), greenfinch (*Carduelis chloris*), and house sparrow (*Passer* *domesticus*) allowed humans to approach closer before fleeing, suggesting a reduced fear of humans.

For gray squirrels, Manski *et al.* (1980) showed that the population density in Lafayette Park, Washington, D.C., ranged from 22.75/ha in the spring to 51.5/ha in the fall, the highest densities ever reported for the species and far in excess of those in less urbanized areas. Gray squirrels in this park were also more active throughout the day than were conspecifics in nonurban areas.

According to Shargo (1988) and Quinn (1992), coyotes (*Canis latrans*) in urban areas occupy smaller home ranges and exhibit different activity patterns in comparison to coyotes in nonurban areas. Urban coyotes also consumed foods of anthropogenic origin and showed a reduced fear of man, often being seen near homes and foraging in clear sight of humans and domestic pets (Shargo, 1988).

In an examination of the northern water snakes (*Nerodia sipedon*) and eastern garter snakes (*Tamnophis sirtalis*) along an urban section of the Raritan Canal, New Jersey, Burger (2001) found that relative to nonurban conspecifics, humans were allowed to approach these snakes within 200 cm, and that more than half of the snakes tested took greater than 60 seconds to respond to humans being within this radius.

Study Focus

In this study, I quantified attributes of urban habitats and landscapes and tested the strength of their association with the attributes of synurbization demonstrated by gray squirrels. The behaviors chosen for this study are those proposed by Gliwicz *et al.* (1990) as being common among urbanized species, i.e., reduced fear of man (wariness), altered levels of intraspecific aggression, modified activity patterns, and increased population density.

Previously investigations of gray squirrels in urban areas (Flyger, 1959; Manski *et al.*, 1980; Williamson, 1983; Gustafson and VanDruff, 1990) and other urbanized species (Gliwicz *et al.*, 1994) served as the framework in the methods used in this study. Following many of the procedures used in these earlier studies allowed me to more readily compare my results to theirs.

Subject Species

The gray squirrel is a medium-sized tree squirrel that does not display sexual dimorphism in size or color (Koprowski, 1994). Total body length is 380 – 525 mm and adult body mass ranges from 300 – 710 g (Schwartz and Schwartz, 1981). The dorsal pelage is dark to pale gray; the fur may be cinnamon colored on the hips, feet, and head; the ventral side is white or gray, to buff or cinnamon (Flyger and Gates, 1982). Ears are buff to gray or white, and the long, bushy tail is white to pale gray and 150 – 250 mm in length (Koprowski, 1994). Both melanism and albinism are common (Steele and Koprowski, 2001). The species' only natural sympatric congener is the fox squirrel *(S. niger)*, which is 20% larger and brown in color (Koprowski, 1994). The species is a familiar inhabitant of urban settings throughout large portions of the eastern United States (Thompson and Thompson, 1980), and is one of several native species of tree squirrels found in North America (fox squirrel; western gray squirrel, *S. griseus*; Abert's squirrel, *S. aberti*; Arizona gray squirrel, *S. arizonensis*; Mexican fox squirrel, *S. nayaritensis*; pine squirrel, *Tamisciurus hudsonicus*; Douglas' squirrel, *T. douglasii*).

The range of the gray squirrel in North America extends west to the edge of the deciduous forest and north into Canada (Koprowski, 1994). Historically, the species' range was restricted to the eastern areas of North America. However, as a result of numerous introductions, the species is currently present in California, Montana, Oregon, and Washington in the United States, and Quebec, New Brunswick, British Columbia, Manitoba, Nova Scotia, Ontario, and Saskatchewan in Canada (Robinson and Cowan, 1954). Gray squirrels are also present in Italy, England, Scotland, and Ireland as a result of intercontinental introductions (Lloyd, 1983).

Study Topic

Gray squirrels located in small urban parks in Baltimore, Maryland were chosen as subjects for this study. Eastern gray squirrel was selected as a study species because they are abundant in urban areas, well adapted to life in urban habitats, and have been the subject of numerous investigations in both urban (Flyger, 1970, 1974; Bouffard, 1978; Manski *et al.*, 1980; Lloyd, 1983; Williamson, 1983; Gustafson and VanDruff, 1990; Hein, 1997; Steele and Koprowski, 2001) and non-urban areas (Robinson and Cowan, 1954; Flyger, 1959; Bouffard, 1978; Keymer, 1983; Rushton *et al.*, 1997; Gurnell *et al.*, 2001).

Gliwicz *et al.* (1994) is widely accepted as a key study concerning the effects of urbanization on the behavior and life history characteristics of wildlife. In this dissertation, I use gray squirrels to study the adaptations exhibited by urban wildlife as described Gliwicz *et al.* (1994), and examine the relationship of these changes to habitat and landscape attributes. Chapter two will address the relationship between population abundance and the behavior of gray squirrels. Chapter three will discuss the ability of habitat and landscape characteristics to predict density and behavior of gray squirrels in urban environments. Finally, chapter four will summarize the findings of this dissertation.

This dissertation is written according to the style as outlined in the instructions to authors for *Urban Ecosystems*, to which selected chapters will be submitted for publication. A detailed description of the pertinent study sites, methods, results, discussion, and references will be provided in each chapter.

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CHAPTER TWO

Gray Squirrel Abundance and Behavior in Urban Areas

Introduction

Urban and suburban areas are landscapes specifically designed for humans and human activities. Although once considered to be habitats for a few select species of wildlife, urban areas have been shown to be utilized by a larger number of taxa than previously suggested (Ditchkoff *et al.,* 2006). As more areas become urbanized, human and wildlife interactions will occur more frequently. In anticipation of this, urban areas and the wildlife that inhabit urban landscapes have been receiving greater attention from ecologist (Adams, 2005; Ditchkoff *et al*., 2006).

Increased density, increased intraspecific aggression, and a reduced fear of humans, are the more observable and frequently described characteristics of urban wildlife. It has been hypothesized that regardless of species, wildlife populations undergoing synurbization (the process of becoming urbanized) will show increased population densities, a reduced fear of man (wariness), and increased levels of intraspecific aggression (Gliwicz *et al*., 1994). These characteristics have been described in urban populations of gray squirrels (*Sciurus carolinensis*; Flyger, 1970), rock doves (*Columba livia*; Cooke, 1980), coyote (*Canis latrans*; Shargo, 1988), striped field mouse (*Apodemus agrarius;* Gliwicz *et al*.,1994), blackbirds (*Turdus merula;* Gliwicz *et al*.,1994), raccoons (*Procyon lotor*; Smith and Engeman, 2002), and northern water snakes (*Nerodia sipedon*; Burger, 2001). However, when reviewing the literature on urban wildlife, I found instances where some wildlife populations in urban areas have not developed the increased population densities, yet they do display a reduced fear of man and increased intraspecific aggression (Flyger, 1955, 1970; Shargo, 1988; Burger, 2001). The main goal of this dissertation is to develop models of habitat and landscape attributes that are associated with the density, wariness, and intraspecific aggression of urbanized wildlife; however, it seems that a logical starting point was to assess the relationship between population density and these behaviors. Examining this relationship may be a critical component in achieving the overall goals of the study.

The eastern gray squirrel (*Sciurus carolinensis*), a species that is commonly associated with urban areas, was used as the subject species for this study. The species' history in urban areas, human habituation to their presence, and previous research on the species in this setting, make gray squirrels ideal for population density and behavioral studies in urban habitats.

Substantial work has been conducted on the factors that influence squirrel abundance in urban areas. Williamson (1983) identified the features of urban habitats that are important for gray squirrel abundance. McPherson and Nilon (1987) developed a habitat suitability index model (HSI) to assess urban habitats for factors that may limit gray squirrel abundance. Hein (1997) described population density, Thompson and Thompson (1980) and Bowers and Breland (1996) the food habits, Manski *et al.* (1980) the activity patterns, and Merwe *et al.* (2006) gray squirrel distribution over varying landscape types in urban habitats. However, studies of the behaviors exhibited by urban wildlife (i.e., decreased wariness and increased intraspecific aggression) have been limited.

I studied gray squirrel populations in small urban parks. Small urban parks are systems for a study of this type because they are common in urban areas and play an important role in offering opportunities for human and wildlife interactions (Nilon *et al.*, 1999). I used a park with a documented high abundance of gray squirrels, Lafayette Park, Washington, D.C., and six urban parks in Baltimore, MD with unknown squirrel abundances. The squirrel abundance in Lafayette Park has been reported to exceed 31.3 individuals per hectare, and has been the subject of several studies regarding their elevated abundance (Manski *et al.,* 1980) and their management needs (Hadidian *et al.*, 1988; Steele and Koprowski, 2001). Other studies of gray squirrels in urban parks, including those located in Baltimore, have shown squirrel abundance to be 3 – 10 individuals per hectare (Flyger, 1970, 1974; Koprowski, 1994; Steele and Koprowski, 2001). Thus, the use of Lafayette Park, in conjunction with the Baltimore parks, allows me to study the relationship between density and behavior over varying levels of squirrel abundance.

In addition to evaluating the relationship between density and behavior of gray squirrels, I was also interested in how squirrel abundance relates to the habitat suitability of parks. Understanding the relationship between park habitat suitability and gray squirrel density and behavior is important because it may provide insights into the drivers of squirrel abundance in urban habitats. I used the gray squirrel habitat suitability index (HSI) model developed by McPherson and Nilon (1987) to evaluate each park. HSI models predict the suitability of habitat for a species based on a set of literature-based habitat attributes that are associated with the species' requirements. This HSI model, as do all HSI models, provides a conceptual framework for researchers and managers to measure and compare the quality of habitats for a particular wildlife species (McPherson and Nilon, 1987).

In this chapter of my dissertation I ask the following questions: (1) What is the relationship between gray squirrel abundance and habitat suitability? (2) What is the relationship between gray squirrel abundance and wariness of humans? (3) What is the relationship between gray squirrel abundance and intraspecific aggression? We hypothesized that squirrels in parks with higher abundances will have a greater reduction in wariness and increased intraspecific aggression.

Methods

Study Area

Lafayette Park

Lafayette Park is located adjacent to the White House in downtown Washington, D.C. The park has an area of 3.3 ha and is listed on the National Register of Historic Places (Olszweski, 1964). Lafayette Park, which is part of the National Park System, has been managed since 1933 with the primary objective being to protect and preserve the historic landscaping themes established in 1853 by Andrew Downing (Olszweski, 1964; Hadidian *et al.*, 1988). The park has a canopy cover of 60%, comprised of both native and exotic tree species; the grounds are 50% manicured turf, 34% brick walkways, and 10% flower beds (Hadidian *et al.*, 1988).

Baltimore Parks

I first obtained a list of municipal parks from the Parks and People Foundation of Baltimore and identified parks of approximately the same area of Lafayette Park 2 - 7 ha. I also chose parks of this size because they are common in urban areas, and offer numerous opportunities for human wildlife interaction (Nilon *et al.*, 1999). I then visited each park and selected ones with canopy covers of 40 - 65%. A canopy cover of 40 - 65%

has been identified as an important habitat component for gray squirrels in urban areas (Williamson, 1983); therefore I also used this criterion in the selection process. The six urban parks in Baltimore I chose were: Federal Hill Park, Irvin Luckman Park, Stoney Run Park, Lakeland Park, Burdick Park, and Carroll Park (Table 2.1).

Squirrel Habitat Suitability Index (HSI)

I assessed each park's ability to provide food and cover resources using a gray squirrel habitat suitability index (HSI) model developed by McPherson and Nilon (1987). This HSI model is designed to measure the quality of habitat for gray squirrels at a given point in time and uses the average tree diameter and tree canopy closure as indicators of food availability or quantity and the number of preferred and supplemental plant species as indicators of food quality (McPherson and Nilon, 1987). The limiting factors, for urban gray squirrel populations, can be the availability of preferred winter food species or the amount of tree cover. Preferred winter food species are those that produce hard mast: oak, hickory, walnut, pecan, beech, maple, pine, and horsechestnut (Table 2.2). Supplemental food species are dogwood, spruce, hemlock, and Douglas-fir (Table 2.2).

HSI scores were calculated by adding the scores from the preferred winter food trees (possible score = 1-10), percent canopy closure (possible score = 1-5), number of preferred food plants (possible score = 1-5), number of supplemental food plants (possible score = 1-5), and average DBH of park trees (possible score 1-10). Scores for each category were summed, divided by the maximum score possible (35), and multiplied by 100 (McPherson and Nilon 1987). The resulting number is the HSI score for the park.

Scores for winter foods were determined by summing the scores for preferred winter food trees, percent canopy closure, number of preferred food plants, and number of supplemental food plants, then dividing the resulting number by the maximum score possible (35), and multiplying by 100. Scores for tree cover were calculated by dividing the score for average DBH of park trees by the maximum score possible for the category (10) and multiplying by 100. The category with the lowest score, winter food or tree cover, is the limiting factor for the park.

Squirrel Abundance

Time area counts were used to determine an index of abundance for each park during four sampling periods: summer, July – August 2003 and 2004, and fall, October – November 2003 and 2004 (Flyger, 1959). This method, while providing a conservative estimate, is considered ideal for urban areas because it eliminates the use of traps in areas of high human activity and may be conducted rather inconspicuously to the public (Hein, 1997; Steele and Koprowski, 2001).

I divided each park into equal sized quadrants, established two vantage points within each quadrant, and recorded the distance from the vantage points to the outer edge of the park. Two vantage points were selected so that one would be available if a park visitor occupied the other. The distance from the vantage points to the edge of the park was used to estimate the distance from the vantage point to each squirrel counted. A random numbers generator was used to predetermine the sampling order of parks and quadrants within each park.

Time area counts lasted 15 minutes and the number of squirrels visible within the quadrant, the average distance to each squirrel counted, and the percentage of the quadrant that was observable was recorded. The index of abundance was determined for each location using the equation:

$$P = \frac{AZ}{(v)\,\pi\, Sy^2}$$

where, P is squirrel population, A is total area of park, Z is number of squirrels counted, v is percent of quadrant visible, S is number of 15 minute observational periods, and y is the average distance to the counted squirrels. This method estimates abundance based on the number of observational periods conducted at each location, and thereby provides an index of abundance for each season the location was sampled. This was also a good technique to use given that no comparisons were made across locations (Flyger, 1959). Counts were conducted from sunrise to four hours after sunrise and four hours prior to sunset until sunset. These are the times when urban squirrels are most active, and thus provide the best opportunities to count all the squirrels present in each quadrant (Manski *et al.*, 1980; Gustafson and VanDruff, 1990).

Wariness

Wariness was quantified using a standardized threat stimulus. An observer approaching an individual gray squirrel on the ground, directly and at constant pace, without vocalization or other deliberate auditory stimulation, was used as the threat stimulus (Gustafson and VanDruff, 1990). The distance between the squirrel and the approaching threat stimulus at the instant the squirrel fled was measured with a rolling tape measure and recorded as the startle distance.

A random numbers generator predetermined the order in which the quadrants within each park were sampled for squirrel wariness. Once a quadrant was selected, the third squirrel visible within that quadrant was sampled. This eliminated testing squirrels that were atypically bold, and thus more visible. Additionally, to avoid conditioning squirrels to my presence, no quadrant was sampled in consecutive order.

Intraspecific Aggression

Gray squirrels were observed for acts of aggression continuously throughout the day by listening for chatter and watching for squirrel chases either on the ground or through the tree canopy. Squirrel intraspecific encounters that involved an agonistic action (chasing, biting, chattering, or rapid tail flicking) that elicited an agonistic or submissive response (fleeing, dropping of head or tail) were counted as an aggressive act (Gustafson and VanDruff, 1990). Repeat encounters between the same individuals were excluded because they constituted nonindependent observations. If a role reversal occurred in instances that involved the individuals, it was considered as a new act of aggression and was recorded as such (Gustafson and VanDruff, 1990). Adults are dominant in the social system of the gray squirrel; therefore, only acts of aggression between adult squirrels were recorded. Adult squirrels were distinguished from juveniles by the size and coloration of their tails. Quadrant and time of occurrence were recorded for each act of aggression. The average number of aggressive acts per hour was calculated for each location by dividing the total number of aggressive acts by the total number of hours observed.

Data Analysis

I used a linear regression analysis (SAS Institute, 2005) to examine the relationships between habitat suitability and squirrel abundance, squirrel abundance and wariness, and squirrel abundance and intraspecific aggression. I selected the linear regression because it was the most robust regression analysis that may be used with a single independent variable (Tabachnick and Fidell, 2001) and it was the best fit line for the data. I averaged the index of abundance estimates for each location across seasons then ran a linear regression with abundance as the dependent variable and HSI scores as the independent variable to assess the relationship of squirrel abundance and habitat suitability.

Data were grouped by locations with density, wariness, and intraspecific aggression averaged across seasons. I then analyzed the data using abundance as the independent variable and wariness and aggression as dependent variables (in separate analyses) to evaluate the relationship between abundance and these behaviors. I reviewed the R^2_{adj} and P-values to determine how efficiently density performed as a predictor for each behavior.

Results

Squirrel Habitat Suitability Index (HSI)

Lafayette Park scored an HSI = 57. Among Baltimore parks, HSI scores ranged from HSI = 51 (Federal Hill) to HSI = 71 (Irving Luckman). Cover suitability was the limiting factor at all parks except Lakeland Park (Table 2.3).

Squirrel Abundance

Squirrel abundance ranged from 38.2/ha (Summer 2003) to 49.1/ha (Fall 2003) in Lafayette Park and 2.0/ha (Carroll Park, fall 2003) to 13.1/ha (Federal Hill, summer 2003) in Baltimore (Table 2.4). Results of the linear regression analysis showed no relationship between habitat suitability and average squirrel abundance values ($R^2_{adj} = -0.50$, $P = 0.437$, $df = 6$).

Wariness

The average startle distance for gray squirrels in Lafayette Park was 2.25 ± 0.04 m. Distances varied at this location from 1.82 ± 0.05 m (fall 2004) to 2.77 ± 0.30 m (summer 2003). The startle distances for Baltimore parks ranged 4.64 ± 0.174 m (Federal Hill) to 12.50 ± 0.441 m (Stoney Run).

There was a negative association between mean squirrel abundance and mean startle distance for Lafayette Park and all Baltimore parks (Table 2.6). All regressions returned significant *P-values*, with the exception of Stoney Run Park, (Table 2.6). There was a negative relationship between density and startle distance in Baltimore parks across seasons ($R^2_{adj} = 0.71$, $P < 0.00$, $df = 23$) (Figure 2.1).

Intraspecific Aggression

Lafayette Park was observed for 100 hours for acts of intraspecific aggression among gray squirrels. Mean values ranged from 1.82 ± 0.05 to 2.77 ± 0.30 at this location. In Baltimore a total of 608 hours of observations were completed with means ranging from 2.20 ± 1.30 (Carroll Park) to 6.40 ± 1.35 (Lakeland Park).

There was no relationship between gray squirrel density and mean values for aggression in Lafayette Park (Table 2.6). There was a positive relationship between density and mean aggression values for the Baltimore parks. There was a positive relationship between density and intraspecific aggression in Baltimore parks across seasons. ($R^2_{adj} = 0.68$, $P < 0.00$, $df = 23$) (Figure 2.2).

Discussion

Gray squirrel abundances in Lafayette Park were similar to those previously reported for this location. Manski *et al.* (1980) and Hadidian *et al.* (1988) suggested that the high squirrel abundance in this park was a consequence of the availability of supplemental foods of anthropogenic origin, which comprised 35% of these squirrels' diets. Results of the HSI model for Lafayette Park also suggest that the available natural food and cover resources in this park are insufficient to support such a high abundance of squirrels. The current landscaping remains identical to that of the Manski *et al*. (1980) study. Therefore, without the addition of any natural food resources it appears that foods provided by humans continue to sustain this population.

Foods provided by humans may be fed directly to squirrels, which is the case in Lafayette Park (Hadidian *et al*., 1988), or provided indirectly from bird feeders, flowers, or trees located throughout the yards of homes located in close proximity to the park (Williamson, 1983). The latter, being the likely source for most neighborhood parks and the Baltimore parks used in this study. Regardless of the source, anthropogenic foods provide resources that may help to elevate squirrel population densities to levels higher than populations without these supplemental foods (Hadidian *et al*., 1988, Koprowski, 1994). This explains the absence of a correlation between habitat suitability and squirrel abundance; which was further evident in the two locations with the highest population densities, Layfayette Park and Federal Hill Park, also having the two lowest HSI scores (Table 2.3).

The lack of a relationship between habitat suitability and squirrel density suggests that other factors inside and outside parks are contributing to squirrel abundance in small urban parks. In the following chapter I will investigate the role of park habitat features and features of the land use matrix surrounding the parks that may explain differences in squirrel density.

The results of the linear regression analyses relating abundance to wariness and abundance to aggression demonstrates that as gray squirrel abundance increases, squirrel wariness decreases and intraspecific aggression increases. Gray squirrels in Lafayette Park, which were the least wary of any that were studied, may be less wary because of the high squirrel abundance. In the social system of gray squirrels, auditory cues are used to warn of predators and other threats (Schwartz and Schwartz, 1981; Koprowski, 1994); therefore, squirrels in high abundance populations may be less wary because more individuals are present to observe and provide warnings of predators or other threats. This may allow animals to focus more on securing food.

In addition, given the proximity of Lafayette Park to the White House, squirrels in this park are frequently exposed to high numbers of humans and levels of human activities (Manski *et al.*, 1980). In response to this, squirrels may become skillful in determining distances in which humans may approach before they become, or are perceived as, a threat. There were no attempts at quantifying the number of park visitors at each park. However, the Baltimore parks in this study may have fewer visitors than Lafayette Park but, the squirrels in these parks also experience humans and human activity, producing similar results. Federal Hill Park, which from personal observations, seemed to have a high number of visitors throughout daylight hours. This location also had low numbers for squirrel wariness.

Increased abundance, while providing more individuals to warn of threats, may also create increased intraspecific competition for food resources. This may influence individual squirrels to not only be less wary of threats, but also to exhibit more aggressiveness. Williams (1983) found that the more aggressive squirrels in urban habitats were able to secure more food resources than less aggressive squirrels. Although gray squirrels do not defend a specified territory, they do protect areas that are important for food resources (Flyger, 1974; Koprowski, 1994; Steele and Koprowski, 2001). In response to higher densities, the need to protect these areas that provide food resources may be increased.

I found that there are differences among Baltimore Parks in density, wariness, and intraspecific aggression. In the following chapter I will investigate how these relationships can be explained by differences in park habitat features and in the characteristics of the matrix surrounding each park.

The results of this study demonstrate a strong association between squirrel abundance and reduced wariness and increased intraspecific aggression. Future research should be carried out that incorporates those factors that influence population density in urban landscapes. Although this study did not include other species, there have been numerous studies indicating similar adaptations in other urbanized species. In order to gain a better understanding of the drivers for the behavioral adaptations displayed by urban wildlife, the results of this study should be tested on other species that live in close association with humans.

Several studies on urban wildlife have provided insights into the adaptations made by wildlife that have undergone synurbization (Flyger, 1955, 1970; Cook, 1980; Shargo, 1988; Gliwicz *et al*., 1994; Burger, 2001; Smith and Engeman, 2002; Ditchkoff *et al.*, 2006). These studies have described reduced wariness and increased intraspecific aggression in various urbanized species; however, a driver for these changes has not been described. While the mechanisms for synurbization may have several drivers associated with the attributes of urban landscapes, the results of this study suggest that density may be a driver for reduced wariness and increased intraspecific aggression exhibited by urbanized wildlife. However, it should be noted that animal behaviors are often correlated with numerous biotic and abiotic factors. Those factors which influence population densities of urban wildlife may also influence behavior.

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Table 2.1. Habitat characteristics of Lafayette Park located in Washington, D.C., USA, and six urban parks located in Baltimore, MD, used to study the influence of squirrel density on squirrel wariness and intraspecific aggression.

Location	Park size (ha)	Canopy cover (%)
Lafayette Park	3.3	60
Baltimore Parks		
Federal Hill	3.9	60
Irving Luckman	2.2	65
Stoney Run	2.7	45
Lakeland	4.9	50
Burdick	4.2	45
Carroll	6.9	40

Table 2.2. Gray squirrel habitat suitability index (HSI) model.

Characteristic	*Possible Score*
I. Winter food.	
A. Average tree diameter of preferred food plant species (cm dbh).	
1. Greater than 25.0	10
2. 15.1 - 25.0	7 - 9
3. 7.6 - 15.0	3 - 6
4. < 7.6	1 - 2
B. Percentage of canopy closure.	
1. 40 - 60	5
2. 60 - 70, 30 - 40	2 - 4
3. Greater than 70, less than 30	1
C. Number of preferred food plant species.	
1. More than 10	5
2. 6 - 9	3 - 4
3. 5	2
4. Less than 5	1
D. Number of supplemental food plant species.	
1. More than 5	5
2. 3 - 5	3 - 4
3. 2	2
4. Less than 2	1
II. Tree Cover	
A. Average tree diameter (cm dbh).	
1. Greater than 45.7	10
2. 38.1 - 45.7	8 - 9
3. 25.4 - 38.0	6 - 7
4. 15.0 - 25.3	2 - 5
5. Less than 15.0	1
HSI Calculation.	
1. Maximum score	35
2. Actual score	__
3. (2) / (1) x 100	__
Limiting Factors	
A. Winter Food.	
1. Maximum score: A + B + C + D	25
2. Actual score: A + B + C + D	__
3. (2) / (1) x 100	__ Food
suitability	
B. Tree Cover	
1. Maximum score: A	10
2. Actual score: A	__
3. (2) / (1) x 100	__ Cover
suitability	
Limiting factor is the lowest suitability value.	

Taken from (McPherson and Nilon, 1987)

Table 2.3. Habitat suitability scores of Lafayette Park and six urban parks located in Baltimore, MD.

	Location						
Characteristic	Lafayette	Federal Hill	Irving Luckman	Stoney Run	Lakeland	Burdick	Carroll
Food							
Average Diameter	6	9	8	9	9	9	8
Canopy Closure	5	5	4	5	5	5	5
Preferred Spp.	5	1	3	3	2	3	2
Supplemental Spp.	2	1	4	1	1	1	1
Food Total	18	16	19	18	17	18	16
Food Suitability	72	64	76	72	68	72	64
Cover							
DBH	2	2	6	5	7	6	5
Cover Total	2	2	6	5	7	6	5
Cover Suitability	20	20	60	50	70	60	50
Actual Score	20	18	25	23	24	24	21
HSI	57	51	71	66	69	69	60

Table 2.4. Summer and fall index of abundance (individuals/ha) for gray squirrels located in Lafayette Park, Washington, D.C., and six urban parks located in Baltimore, MD.

	2003		2004	
Location	Summer	Fall	Summer	Fall
Lafayette Park	38.2	49.1	44.3	46.3
Baltimore Parks				
Federal Hill	13.1	11.9	8.5	10.4
Irvin Luckman	2.9	2.7	5.2	8.9
Stoney Run	3.7	2.9	2.2	3.0
Lakeland	3.2	7.2	9.5	11.6
Burdick	5.6	5.2	6.1	7.9
Carroll	2.4	2.0	4.8	6.7

Table 2.5. Results of gray squirrel wariness and aggression in Lafayette Park, Washington, D.C. and six urban parks in Baltimore, MD. Wariness (= startle distance) expressed in meters, followed by the SE, and the number of animals sampled. Aggression data is expressed in number of aggressive acts per hour, followed by the SE, and (n) which represents the total number of daylight hours observed.

	2003		2004		
Location	Summer	Fall	Summer	Fall	Location Total
Lafayette Park					
Wariness	2.77 ± 0.30 (n = 31)	2.21 ± 0.11 (n = 32)	2.18 ± 0.08 (n = 31)	1.82 ± 0.05 (n = 30)	2.25 ± 0.04 (n = 124)
Aggression	11.75 ± 0.31 (n = 29)	15.40 ± 0.09 (n = 24)	16.20 ± 0.13 (n = 22)	27.40 ± 0.43 (n = 25)	17.69 ± 0.22 (n = 100)
Federal Hill					
Wariness	5.05 ± 0.34 (n = 32)	4.96 ± 0.31 (n = 38)	4.55 ± 0.39 (n = 35)	4.00 ± 0.35 (n = 30)	4.64 ± 0.17 (n = 135)
Aggression	7.10 ± 1.06 (n = 28)	5.30 ± 0.87 (n = 24)	3.20 ± 0.52 (n = 30)	5.40 ± 0.83 (n = 25)	5.25 ± 0.80 (n = 107)
Irvin Luckman					
Wariness	10.08 ± 0.82 (n = 30)	11.14 ± 0.64 (n = 37)	7.03 ± 0.40 (n = 37)	5.42 ± 0.24 (n = 31)	8.40 ± 0.36 (n = 135)
Aggression	2.30 ± 0.25 (n = 27)	2.10 ± 0.21 (n = 22)	5.40 ± 0.90 (n = 29)	4.90 ± 0.88 (n = 23)	3.70 ± 0.86 (n = 101)
Stoney Run					
Wariness	14.48 ± 0.88 (n = 34)	10.05 ± 0.21 (n = 39)	12.84 ± 0.33 (n = 37)	12.66 ± 0.22 (n = 32)	12.50 ± 0.44 (n = 142)
Aggression	2.50 ± 0.20 (n = 28)	1.80 ± 0.19 (n = 23)	2.10 ± 0.34 (n = 27)	2.70 ± 0.12 (n = 22)	2.30 ± 0.20 (n = 100)
Lakeland					
Wariness	13.94 ± 0.65 (n = 35)	11.36 ± 0.52 (n = 36)	6.79 ± 0.64 (n = 37)	4.40 ± 0.20 (n = 30)	9.12 ± 0.43 (n = 138)
Aggression	3.50 ± 0.47 (n = 27)	5.00 ± 0.62 (n = 20)	7.20 ± 1.01 (n = 26)	9.70 ± 1.23 (n = 21)	6.40 ± 1.35 (n = 94)

Table 2.5. (Continued)

	2003		2004		
Location	Summer	Fall	Summer	Fall	Location Total
Burdick					
Wariness	12.35 ± 1.21 (n = 35)	11.89 ± 0.92 (n = 34)	9.01 ± 0.84 (n = 38)	8.25 ± 0.66 (n = 30)	10.37 ± 0.48 (n = 137)
Aggression	6.00 ± 1.02 (n = 29)	4.00 ± 0.79 (n = 22)	5.30 ± 0.98 (n = 27)	3.60 ± 0.82 (n = 22)	4.70 ± 0.56 (n = 100)
Carroll					
Wariness	16.65 ± 1.18 (n = 35)	13.10 ± 0.71 (n = 38)	10.95 ± 0.57 (n = 33)	8.63 ± 0.45 (n = 31)	12.33 ± 0.46 (n = 137)
Aggression	0.00 ± 0.00 (n = 28)	0.00 ± 0.00 (n = 24)	4.20 ± 0.90 (n = 29)	4.80 ± 0.92 (n = 20)	2.20 ± 1.30 (n = 101)

Table 2.6. Results of linear regression analyses of gray squirrel density and wariness, and density and aggression for Lafayette Park, located in Washington, D.C., USA and six urban parks of Baltimore, MD, USA. Significant *P*-values at the 0.05 level, are indicated with an asterisk (*).

	Wariness				Aggression			
Location	R^2_{adj}	*df*	*P*	*Linear Model*	R^2_{adj}	*df*	*P*	*Linear Model*
Lafayette Park	0.78	3	0.02*	5.21 – 0.06 density	0.48	3	0.52	13.98 + 0.71 density
Baltimore Parks								
Federal Hill	0.62	3	0.04*	3.00 – 0.15 density	0.84	3	0.05*	3.55 + 0.78 density
Irving Luckman	0.85	3	0.05*	12.76 – 0.88 density	0.41	3	0.22	1.35 + 0.47 density
Stoney Run	0.40	3	0.59	8.96 + 1.20 density	0.46	3	0.54	1.37 + 0.31 density
Lakeland Park	0.93	3	0.03*	18.38 – 1.17 density	0.89	3	0.04*	0.62 + 0.73 density
Burdick Park	0.57	3	0.05*	19.36 – 1.45 density	0.50	3	0.05*	7.65 + 0.47 density
Carroll Park	0.64	3	0.01*	19.37 – 1.45 density	0.89	3	0.04*	7.65 + 0.47 density
Baltimore Parks Combined	0.72	23	< 0.01*	15.21 – 0.92 density	0.60	23	< 0.01*	0.84 + 0.52 density
All Parks Combined	0.75	27	< 0.01*	11.14 – 0.23 density	0.81	27	< 0.01*	1.71 + 0.37 density

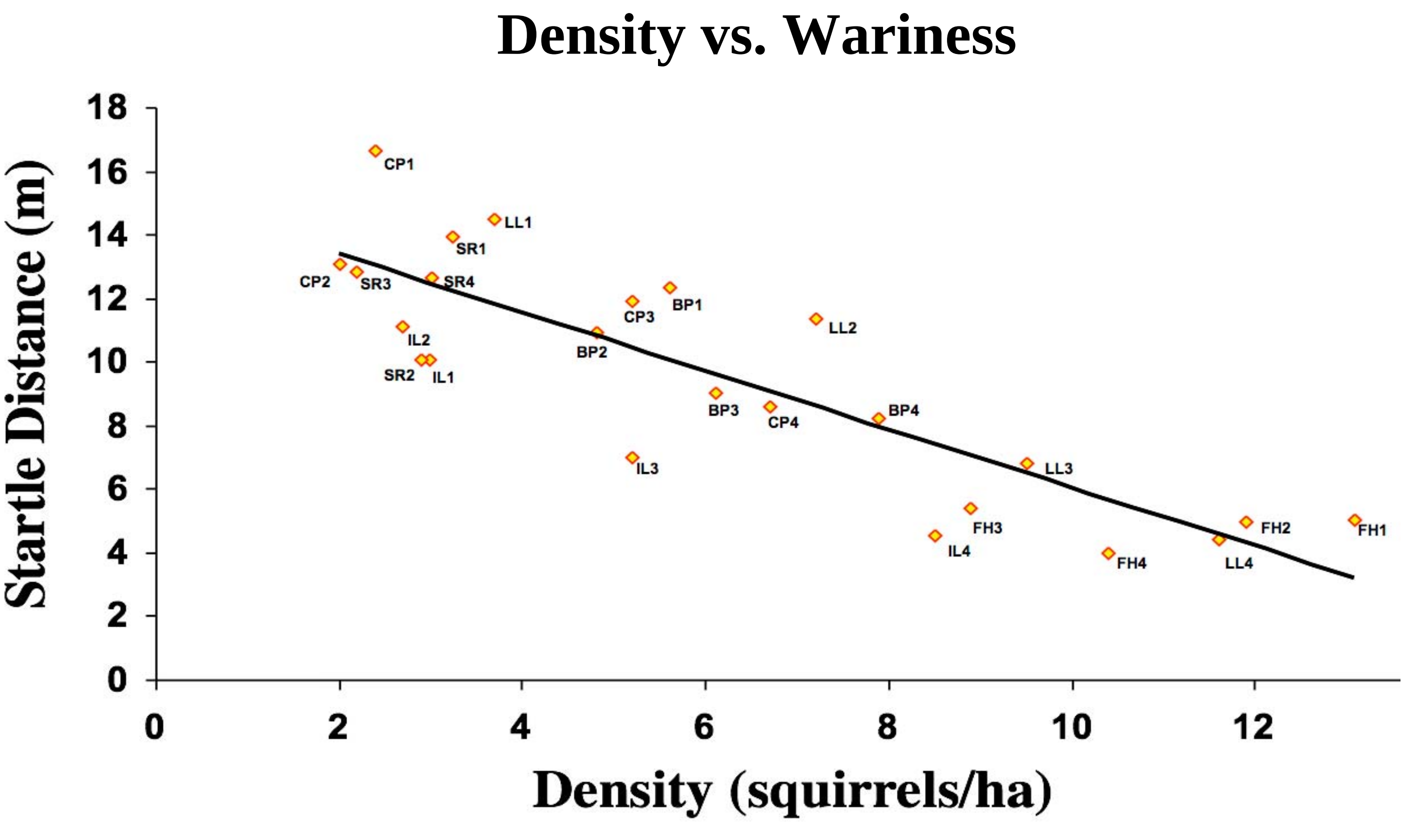

Figure 2.1. Results of linear regression analysis of gray squirrel density and wariness. Location abbreviation (FH = Federal Hill Park, IL = Irvin Luckman Park, SR = Stoney Run Park, LL = Lakeland Park, BP = Burdick Park, CP = Carroll Park) is followed by sample seasons (1 = summer 2003, 2 = fall 2003, 3 = summer 2004, 4 = fall 2004). $R^2_{adj} = 0.71$, $P < 0.00$, n = 24, and $df = 23$.

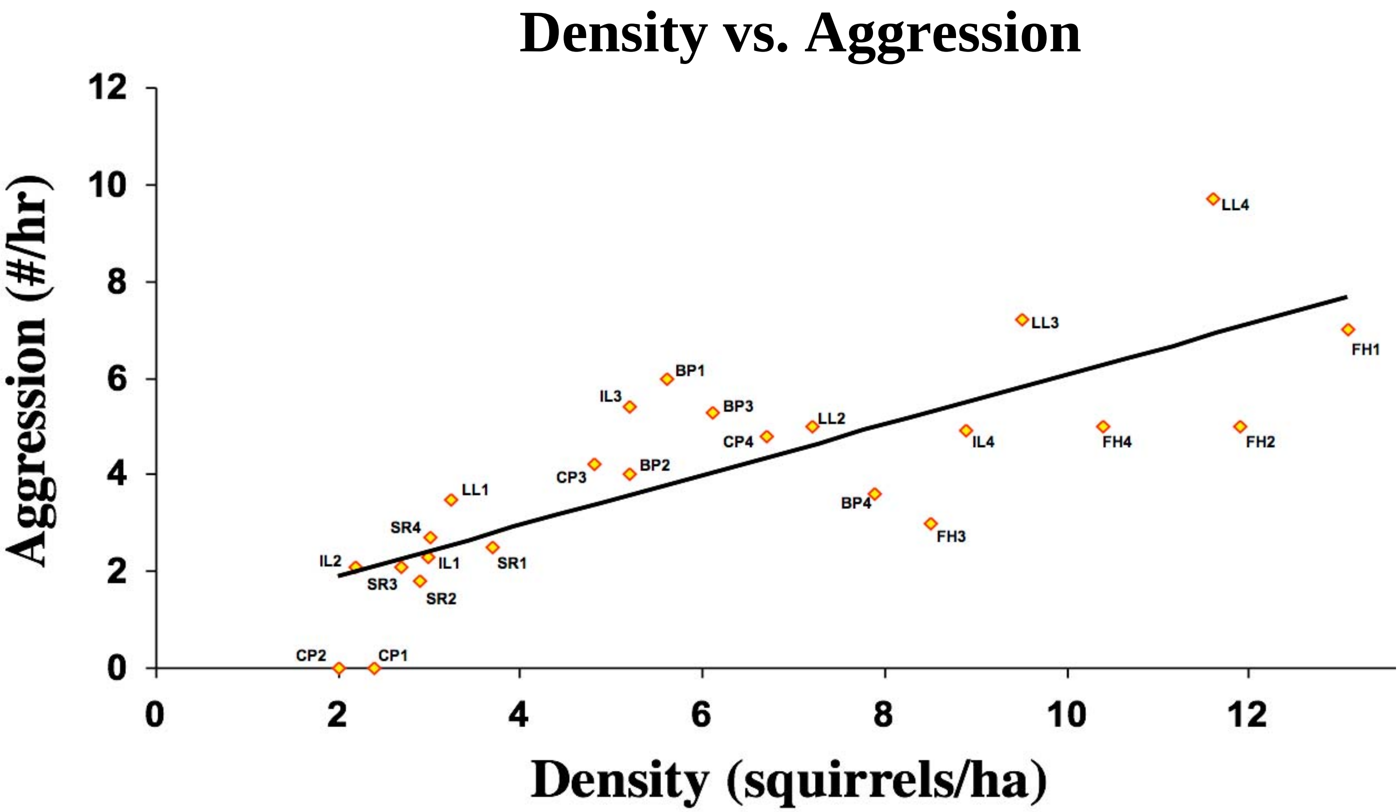

Figure 2.2. Results of linear regression analysis of gray squirrel density and intraspecific aggression. Location abbreviation (FH = Federal Hill Park, IL = Irvin Luckman Park, SR = Stoney Run Park, LL = Lakeland Park, BP = Burdick Park, CP = Carroll Park) is followed by sample seasons (1 = summer 2003, 2 = fall 2003, 3 = summer 2004, 4 = fall 2004). $R^2_{adj} = 0.68$, $P < 0.00$, n = 24, and $df = 23$.

CHAPTER THREE

Habitat and Landscape Characteristics Correlated with Urban Gray Squirrel Population Density and Behavior

Introduction

Urban areas are dynamic systems that have been focal points for economic, sociological, and ecological studies. Ecologists have recognized the opportunities provided by urban areas and have shifted their focus to questions regarding anthropogenic impacts on the environment. Thus, city planners and wildlife mangers are collaborating with scientist in hopes of gaining a better understanding of how animals use urban resources. A major intellectual challenge facing modern ecologists is to discover those forces that determine the types and abundance of species found in a given community (Adams, 2005). This holds true for species found in both pristine and urban habitats.

Urban landscapes are designed and managed primarily for human use. These environments contain areas of diverse character that vary temporally and spatially (Johnson *et al*., 2004). While cities may offer abundant resources for wildlife, securing these resources may come at great cost. Animals maneuvering through urban landscapes are vulnerable to negative human interactions, namely collisions with vehicles or encounters with domestic pets. Thus, understanding landscape-level effects has become essential to understanding ecological patterns and processes in urban ecosystems and how animals utilize resources in urban ecosystems (Gustafson, 1998).

Several studies have been conducted on wildlife in urban systems concerning behavior (Flyger, 1970, 1974; Cook, 1980; Manski *et al.,* 1980; Gustafson and VanDruff, 1990) and population dynamics (Williamson, 1983; McPherson and Nilon, 1987; Atkinson and Shackleton, 1991; Quinn, 1992). Some of these studies have described changes in the behavior (reduced fear of humans, altered activity patterns, increased aggression) and population density of various taxa, suggesting that these changes represent adaptations to urban surroundings (synurbization). However, there is little known about what specific attributes of urban settings prompt these behavioral and life history changes. Currently, there are no published studies exploring the habitat and landscape characteristics associated with the synurbization of wildlife.

In the previous chapters of this dissertation, I showed the existence of a negative association between gray squirrel population density and wariness, and a positive association between population density and intraspecific aggression. However, my results showed no relationship between population density and habitat suitability, even though the habitat suitability index (HSI) model that I used considered habitat features that have been shown to be important for gray squirrel abundance in urban areas (McPherson and Nilon, 1987). This suggests that alternative attributes of urban environments, on the landscape scale, may be the bases for the high population densities of gray squirrels. Also, given the relationship between population density and the behaviors discussed in chapter two, these additional landscape attributes may also be indirectly influencing squirrel behavior.

The purpose of this study is to determine the degree to which the habitat and landscape features of urban environments can be used as predictors of squirrel densities and behavior. I quantified four characteristics of urbanized gray squirrels (higher population densities, reduced fear of man (wariness), increased intraspecific aggression (aggression), altered activity patterns), and test whether less tree cover and more building cover in the urban landscape surrounded the parks are associated with reduced wariness, and increased density, intraspecific aggression, and activity.

Methods

Study Area

The city of Baltimore, Maryland, USA, is located in the northeastern portion of the state. Baltimore was founded in 1729, has a population of 636,251, and currently owns and maintains 347 municipal parks that total 2,556 ha within the city limits (U.S. Census Bureau, 2004). As the largest city in the state, Baltimore occupies an area of 210 km^2. The southern boundaries of the city are dissected by the Patapsco River, which empties into Chesapeake Bay. Elevations range from sea level to 149 m (NOAA, 2006). All four seasons are pronounced, with summers being moderately hot and the winters cool. During the sampling period, the average daily temperatures were 24.3°C for July – August and 12.9°C for October – November. Minimal precipitation occurred during these times: 180 mm (July-August) and 166 mm (October-November; NOAA, 2006).

Site Selection

Parks 2 – 7 ha in size, with a tree cover of 40 – 65%, and that had no other parks or forested patches within 2 km of the park edges were selected for this study. An area of 2 – 7 ha was chosen because this is a common park size in urban neighborhoods and offers adequate opportunity for human and wildlife interactions (Nilon *et al.*, 1999). A canopy cover of 40 - 65% has been identified as an important habitat attribute for gray squirrels in urban areas (Williamson, 1983).

The matrix surrounding each park was considered in the study site selection process. Gray squirrels have been observed moving up to 0.48 km between urban parks (Manski *et al*., 1980). Because of this, I considered a 2 km radius from the outer perimeter of each park as the matrix within which each park occurred. Parks that had one or more parks situated within this 2 km radius were not used as study sites, thus reducing the possibility of individual squirrels being sampled in multiple parks. Based on these criteria, in July 2003, I selected six study sites throughout Baltimore: Federal Hill Park, Irvin Luckman Park, Stoney Run Park, Lakeland Park, Burdick Park, and Carroll Park (Table 3.1). Using ArcView GIS, the percent tree cover, total number of trees, percent building cover, and total number of buildings in the 2 km area adjacent to each park was determined.

Park Characteristics

Percent canopy cover, tree basal area, tree species composition, and tree density were measured in each park at the onset of the study in August 2003 (Table 3.1). These characteristics are known to affect the population density of gray squirrels in urban areas (Flyger, 1970; Williamson, 1983; Bowers and Breland, 1996).

A spherical densitometer was used to measure canopy cover at each study site. Diameter at breast height (DBH) of individual trees was measured using diameter tape; this measure was then converted to tree basal area using the stand basal area formula. Each tree was identified to species using The Audubon Society Field Guide to North American Trees (1980). Tree abundance was determined by totaling tree numbers by study site. At the beginning of each sampling season, study sites were visually examined for the removal or addition of trees.

Matrix Characteristics

I used digitized 2000 LANDSAT satellite images of Baltimore to quantify each park's surrounding landscape (matrix). These images were digitized and provided to us by the Parks and People Foundation of Baltimore. I then used these images to determined the percent tree cover, total number of trees, percent building cover, and total number of buildings for the 2 km radius surrounding the edge of each park (Table 3.1). I calculated percent tree cover (tree cover) by dividing the total area of the matrix covered by trees by the total area of the matrix, then multiplying this number by one hundred. Percent building cover (building cover) was calculated using the same technique, dividing the total area covered by buildings by the total area of the matrix, then multiplying this number by one hundred. The total number of matrix trees (matrix trees) and total number of matrix buildings (building number) were derived by summing the number of occurrences for each within the matrix.

Squirrel Abundance

Time area counts were used to determine the index of abundance for each study site during four sampling periods: summer, July – August 2003 and 2004, and fall, October – November 2003 and 2004 (Flyger, 1959). This method, while providing a conservative estimate, is considered ideal for urban areas because it eliminates the use of traps in areas of high human activity and may be conducted rather inconspicuously to the public (Hein, 1997; Steele and Koprowski, 2001).

I divided each park into equal sized quadrants, established two vantage points within each quadrant, and recorded the distance from the vantage points to the outer edge of the park. Two vantage points were selected so that one would be available if a park visitor occupied the other. The distance from the vantage points to the edge of the park was used to estimate the distance from the vantage point to each squirrel counted. A random numbers generator was used to predetermine the sampling order of parks and quadrants within each park.

Time area counts lasted 15 minutes and the number of squirrels visible within the quadrant, the average distance to each squirrel counted, and the percentage of the quadrant that was observable was recorded. The index of abundance was determined for each location using the equation:

$$P = \frac{AZ}{(v)\,\pi\, Sy^2}$$

where, P is squirrel population, A is total area of park, Z is number of squirrels counted, v is percent of quadrant visible, S is number of 15 minute observational periods, and y is the average distance to the counted squirrels. This method estimates abundance based on the number of observational periods conducted at each location, and thereby provides an index of abundance for each season the location was sampled. This was also a good technique to use since I will not be comparing density across locations (Flyger, 1959). Counts were conducted from sunrise to four hours after sunrise and four hours prior to sunset until sunset. These are the times when urban squirrels are most active, and thus provide the best opportunity to count all the squirrels present in each quadrant (Manski *et al.*, 1980; Gustafson and VanDruff, 1990).

Squirrel Behavior: Wariness, Intraspecific Aggression, and Activity

Gray squirrel behavior was assessed by measuring squirrel wariness, intraspecific aggression (aggression), and activity. When compared to nonurban conspecifics, these behaviors have been shown to differ in urban wildlife populations (Cooke, 1980; Gustafson and VanDruff, 1990, Gliwicz *et al*., 1994) regardless of taxa and geographic location (Gliwicz *et al.,* 1994). We measured all squirrel behaviors in the summer and fall 2003 and 2004, from sunrise to four hours after sunrise, and four hours prior to sunset until sunset.

Wariness

Wariness was quantified using a standardized threat stimulus. An observer approaching an individual gray squirrel while on the ground, directly and at constant speed, without vocalization or other deliberate auditory stimulus, was used as the threat stimulus (Gustafson and VanDruff, 1990). The distance between the squirrel and the approaching threat stimulus at the instant the squirrel fled was measured with a rolling tape measure and recorded as the startle distance.

A random numbers generator predetermined the order in which the quadrants within each study site were sampled for squirrel wariness. Once a quadrant was selected, the third squirrel visible within that quadrant was sampled. This eliminated testing squirrels that were atypically bold, and thus more visible. Additionally, to avoid conditioning squirrels to my presence, no quadrant was sampled in consecutive order. I calculated the average startle distance by location and season.

Intraspecific Aggression

Gray squirrels were observed for acts of aggression continuously throughout the day by listening for chatter and watching for squirrel chases either on the ground or through the tree canopy. Gray squirrel intraspecific encounters that involved an agonistic action (chasing, biting, chattering, or rapid tail flicking) that elicited an agonistic or submissive response (fleeing, dropping of head or tail) were counted as an aggressive act (Gustafson and VanDruff, 1990). Repeat encounters between the same individuals were excluded because they constituted nonindependent observations. If a role reversal occurred in instances that involved the individuals, it was considered as a new act of aggression and was recorded as such (Gustafson and VanDruff, 1990). Adults are dominant in the social system of the gray squirrel; therefore, only acts of aggression between adult squirrels were recorded. Adult squirrels were distinguished from juveniles by the size and coloration of their tails. Quadrant and time of occurrence were recorded for each act of aggression. The average number of aggressive acts per hour was calculated for each location by dividing the total number of aggressive acts by the total number of hours observed.

Activity

The third gray squirrel seen within a quadrant, which was predetermined by a random numbers generator, was selected as the focal animal. This approach was taken to reduce the probability of studying only the most visible squirrels within each park and mirrors the technique employed by Manski *et al.* (1980) to assess urban gray squirrel activity. Each focal animal was videotaped using a digital video camera for 15 minutes, after which, a new quadrant and focal animal was selected. Videotaping begin at sunrise and ran consecutively until sunset.

Squirrel activity was examined during the summer and fall of 2003 and 2004. Observed activities were categorized and tabulated as: feed (the process of consuming a food item); forage (the behavior associated with searching for food); store (the behavior associated with burying food); rest (sleeping and loafing); groom (scratching, licking, and biting oneself or another squirrel); chase (the behavior associated with the pursuit of and/or flight from another squirrel or squirrels); movement (other locomotion not used in the above categories); observe (the act of stopping and visually inspecting surroundings); and other (behavior not described in the above categories). Gray squirrels in urban areas are more active than their nonurban conspecifics (Flyger, 1970). Therefore, I used a method to compare how active squirrels are across locations. I used an index of activity (IA) to how active squirrels were at each location. The index of activity was calculated by summing the occurrences of all activities for each park, then dividing this number by the total observation time at that park.

Model Development

The purpose of this study is not to test if the variables chosen have an effect greater than zero (a null hypothesis test). However, I am attempting to ascertain which combination of variables best approximate the biological system of the synurbization of gray squirrels. The technique of model ranking being used in this study, the information-theoretical approach, is an alternative to model selection via null hypothesis testing (Burnham and Anderson, 1998; Anderson *et al*., 2000). This technique also avoids the inclusion of variables that have little or no justification in the model but might give spurious results (Hoving *et al*., 2004).

I constructed models that are likely to describe population density, wariness, aggression, and activity levels of gray squirrels in urban areas. Models were based on published literature and ecological knowledge of the species and included habitat and landscape attributes. Also, based on my findings regarding the relationship between density and behavior, models were included that used density as a single predictor variable, as well as models with density, habitat attributes, and landscape attributes to test their association with behavior. Before constructing the models, a correlation analysis was conducted in an attempt to avoid using variables that may be intercorrelated. After the models were constructed, the best approximating models were determined through the use of Akaike's Information Criterion (AIC).

Correlation Analysis

An evaluation of correlations among habitat attributes, landscape attributes, density, wariness, aggression, and activity was conducted using a Pearson's Correlation Analysis with a two-tailed test for significance (Tabachnick and Fidell, 2001). This analysis was used to better understand the relationships between habitat and landscape variables and as a guide for selecting variables to explain squirrel density and behavior.

Linear Regression Analysis

I performed multiple regression analyses to model squirrel density, wariness, aggression, and activity in urban parks. In the density regression analyses, I used density as the dependent variable, and park size (size), park tree canopy (canopy), tree basal area within the park (basal area), number of trees within the park (tree number), matrix building cover (building cover), number of buildings in matrix (building number), matrix tree cover (tree cover), and number of trees in matrix (matrix trees) as independent variables. Dependent variables for behavior regression analyses were: wariness, aggression, and index of activity (activity). Independent variables for behavior regression analyses were: size, canopy, basal area, tree number, building cover, building number, tree cover, matrix trees, and squirrel density.

Candidate Models

Models for squirrel density and behavior were developed a priori. Results from the correlation analysis were used to evaluate the combination of variables used in each model. Models that contained significantly and correlated variables were reconstructed to include only one of the variables. In the rare cases in which this could not be accomplished, the model was removed from the group.

Each set of candidate models included what I have termed my “standard set” of models: global, null, habitat attributes, and landscape attributes. A global model containing all variables and a null model containing no variables were used to contrast the predictive power of the selected variables. I hypothesized that a combination of park and landscape characteristics would be the best predictors of squirrel density, wariness, aggression, and activity. Therefore, I included models that would examine the predictive ability of habitat attributes and landscape attributes separately, as well as models that used combinations of these variables.

Results

Squirrel Abundance

Gray squirrel abundance varied from 2.0/ha for Carroll Park during fall 2003 to 13.1/ha for Federal Hill in summer, 2003 (Table 3.4). The average squirrel density, by season, was 5.1/ha (summer, 2003), 5.3/ha (fall, 2003), 6.1/ha (summer, 2004), and 8.1/ha (fall, 2004).

Wariness

A total of 824 squirrels were sampled for wariness (Table 3.5). Startle distances ranged from 4.64 ± 0.174 m (Federal Hill) to 12.50 ± 0.441 m (Stoney Run). The remaining results for wariness in Baltimore parks were Irving Luckman: 8.40 ± 0.36 m, Lakeland: 9.12 ± 0.43 m, Burdick: 10.37 ± 0.48, and Carroll: 12.33 ± 0.46 m. Seasonal averages for startle distance were summer 2003: 12.10 ± 0.444 m, fall 2003: 10.37 ± 0.3237 m, summer 2004: 8.53 ± 0.348 m, and fall 2004: 7.31 ± 0.293 m.

Intraspecific Aggression

A total of 608 hours of observations were completed to assess gray squirrel aggression (Table 3.5). The number of aggressive acts per hour ranged from 0.0/hr in Carroll Park during summer 2003 to 9.70 ± 1.23/hr in Lakeland Park during fall 2004. Seasonal averages for aggression were summer 2003: 3.6 ± 1.063/hr, fall 2003: 3.0 ± 0.847/hr, summer 2004: 4.6 ± 0.736/hr, and fall 2004: 5.20 ± 0.989/hr.

Activity

A total of 7,560 minutes, 504 focal animals, of video was analyzed for gray squirrel activity. The average IA score for the study was 0.229 ± 0.004, ranging 0.193 ± 0.024 (fall 2004, Federal Hill) to 0.285 ± 0.003 (summer 2004, Irvin Luckman).

Candidate Models

Results of the correlation analysis yielded 22 significant correlations, six at the $P < 0.05$ level and sixteen at the $P < 0.01$ level. Four significant correlations were positive: building number and matrix tree cover, building number and matrix tree number, park size and building cover, and matrix tree number and matrix tree cover; and five were negative: park size and park canopy, park size and matrix tree cover, park canopy cover and building number, park canopy cover and matrix tree number, and matrix building cover and matrix tree cover (Table 3.2). I concluded the correlation between matrix tree number and matrix tree cover and matrix was of ecological relevance and each of these variables would contribute similar information to any model in which both variables were used. Based on these results I did not use these variables together in any models.

Density

I evaluated eight candidate models for their ability to predict squirrel population density in urban parks. The best approximating models, those with the lowest AIC scores, were models *D1* (AIC = 57.40), *D2* (AIC = 57.59), *D3* (AIC = 57.65), and *D4* (AIC = 57.66). Models with the highest AIC values were the global, null, park, and matrix models (Table 3.3).

Models *D1*, *D2*, *D3*, and *D4* included combinations of patch and matrix characteristics. Park size was a common predictor variable in the models that showed similar levels of support. Model *D1* included patch size, matrix building cover, and matrix tree cover as the variables that best predict squirrel population density; however, models *D2* ($\Delta_i = 0.19$), *D3* ($\Delta_i = 0.24$), and *D4* ($\Delta_i = 0.26$) had scores that suggest there is substantial support for each model. Attempts at model averaging resulted in AIC scores that were higher than the AIC score of each individual model; therefore, I have chosen to report the models as they were constructed, with the understanding that these scores are relatively similar.

Wariness

I determined the best predictive model for wariness was model *W1* that utilized canopy cover and density as predictors (Table 3.3). Model *W1*, yielded an AIC = 48.42 and $W_i = 0.500$; other models had higher AIC scores (AIC ≥ 50.09), relatively less support, $W_i \leq 0.216$, and contained more parameters. Density was effective as a predictor of squirrel wariness when combined with additional variables; however, when evaluated alone, it was the third most supported model (Table 3.3). When I combined density with patch canopy cover it yielded the model with the lowest AIC score and the strongest support.

Intraspecific Aggression

Model *A1*, the best approximating model for aggression, yielded an AIC = 39.54, $W_i = 0.567$, and used tree basal area, matrix tree cover, and density as predictors. This model also has the highest W_i of all models throughout the study. Models with the least amount of support ($W_i = 0.000$) were those in my standard set (Table 3.3).

Models *A1* and *A2* had similar AIC scores, (Table 3.3). However, a greater distinction between the models was observed when evaluating the W_i for the models. Squirrel density and park basal area were used as predictors in both models. Matrix tree cover, in model *A1*, and patch size, in model *A2*, were the variables that differed in the sets of predictor variables.

Activity

Model *P1*, which used squirrel population density as the only predictor, was the best approximating model and yielded approximately twice the support of the second best approximating model, *P2* (Table 3.3). It should be noted that models *P1, P2, P3,* and *P4* all yielded $\Delta_i \leq 1.99$, which are small enough to warrant closer evaluations of the remaining models in this set. Model *P2*, the second most supported model, and models *P3* and *P4*, all had a Δ_i that suggest these models had substantial support, although not as much as model *P1*. However, model *P3* was the unique model in this group because of the number of variables used, four, and the absence of the density variable.

Discussion

The densities and behaviors reported in this study are within the range of those previously reported for the species in urban areas (Flyger, 1955, 1959; Manski *et al*., 1980; Koprowski, 1994) and are common for similar studies conducted on other urbanized wildlife (Cooke, 1980; Gliwicz *et al.,* 1994). The results of this study demonstrate that both habitat and landscape attributes can be used as predictors of squirrel population density and behavior. Previous studies have developed squirrel population density models using variables that focus primarily on the ability of an area to produce food and cover. I am suggesting that these models should be expanded to include variables such as tree cover and building cover of the adjacent landscape. Models for squirrel wariness, aggression, and activity, also benefit from including combinations of habitat and landscape features along with density.

Federal Hill, which had the highest squirrel population density during the summer and fall 2003, is located in a heavily urbanized area of downtown Baltimore. Not surprisingly, the area surrounding this park has the lowest amount of tree cover of any of the parks in this study (Table 3.1). Upon visual examination of the matrix tree cover, I found that many of these trees were newly planted street trees that were far younger than the 8 - 30 years needed for squirrel den cavity formation (Baumgartner, 1939). Additionally, the crowns of these trees were not large enough to support leaf nests or to provide adequate amounts of mast, which could be used as food resources (Williamson, 1983). Conversely, Stoney Run, which consistently exhibited low squirrel population densities throughout the study, has a matrix abundant in large, walnut (*Juglans spp.)* and oak (*Quercus spp.)* trees. These trees do not occur in large continuous stands, but are widely distributed accross the single-family homes that dominate this park's matrix.

Statistically, model *D1* was the most supported model. However, when comparing models *D1* and *D2* the statistical differences were small, even though model *D2* incorporated more parameters (Table 3.3). Additionally, model *D2* incorporated park canopy cover, which has been shown to be a key habitat feature for squirrel abundance in urban areas (Flyger, 1955; Thompson and Thompson, 1980; Williamson, 1983). I acknowledge the rule of parsimony and the need for constructing the most parsimonious model possible; however, when considering the ecological interpretations of the models, *D2* seems to be the stronger model. The presence of trees is clearly important to gray squirrel abundance (Williamson, 1983; Steele and Koprowski, 2001); therefore, a model that excludes this attribute would seem inappropriate. Fewer trees, along with more building cover, in the landscape adjacent to the park increased squirrel density in the park. This would explain the high densities in Federal Hill and Lakeland Park, which both have small amounts of tree cover in the surrounding landscapes.

All models were strongly influenced by the amount of buildings and trees in the matrix. Patch size, because it provides area to forage, and canopy cover, which provides shelter, are important characteristics for squirrels in urban parks. Although slight statistical differences were evident between models *D1* and *D2*, ecologically they were similar in that they showed that the amount of urbanization outside the parks influenced squirrel density within the parks. Building cover or the numbers of buildings, combined with the number of trees or tree cover in the matrix, may increase squirrel density within the park by limiting available resources in the area adjacent to the park.

Startle distances were comparable to those reported in previous studies (Manski *et al.*, 1980; Gustafson and VanDruff, 1990). Federal Hill, which exhibited high squirrel densities throughout the study, also had low startle distances among parks. This lower degree of wariness, which is reflected in the reduced startle distance, may signal that gray squirrels in urban areas are less wary when in greater numbers.

Model *W1* used less canopy cover and increased squirrel population density as predictors of squirrel wariness. Canopy cover has been shown to be an important habitat component for gray squirrels because of the food resources certain tree species may make available (Williamson, 1983; McPherson and Nilon, 1987) and tree cavities for raising their young (Robinson and Cowan, 1954). Although predation pressure is reduced for gray squirrels in urban areas, trees with large canopies do provide protection from predators (Powell, 1982). Dogs (*Canis familiaris*), cats (*Felis catus*), and birds of prey are the primary predators of squirrels in urban areas (Powell, 1982). Parks with greater canopy cover may allow squirrels to become less wary by providing protection from an aerial attack from birds of prey, and an area to flee from terrestrial predators.

Humans and human activity often surround gray squirrels in urban areas. Because of this, squirrels may become skillful in determining distances in which individual humans become a threat. In the social system of gray squirrels, auditory cues are used to warn of predators and other threats (Schwartz and Schwartz, 1981; Koprowski, 1994). In areas of high density, squirrels may be bolder because of more individuals present to observe and warn of threats. Model *W3*, which used density as the only predictor, was a weaker model than *W1*; however, when density was combined with canopy cover, model *W1*, it proved to be a more efficient model. Initially, I was concerned that density may confound the effectiveness of the variables used to predict squirrel density (size, building cover, tree cover); however, when evaluating these variables ability to predict wariness they were less effective than model *W3*.

The best approximating model, *A1*, for squirrel aggression used variables associated with food resources, increased park basal area and matrix tree cover, and increased squirrel density. Tree basal area within the park provides food and space for leaf nests (Williamson, 1983; Steele and Koprowski, 2001). The matrix tree cover provides these same resources. Since densities are high in these urban parks, competition for resources are apt to be increased and, as in the case of wariness, squirrels may have to be more aggressive to secure resources. Conversely, areas having lower squirrel population densities and substantial levels of park tree basal area and matrix tree cover would likely elicit less competition for resources and squirrels may not have to be more aggressive. This would also explain why density was the best predictor of squirrel activity levels, as was seen in model *P1*. If population densities are elevated, squirrels may have to be more active to secure resources.

Gray squirrels, because of their ability to move between habitats, are not confined within the margins of small urban parks. Based on the results of my study and previous research, squirrels may utilize resources across the entire landscape. As urban areas continue to expand, the use of landscape scale studies will become more important in the studying of urban systems. Thus, studies on urban species should not only look at the habitat, but also the adjacent landscape.

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Table 3.1. Park and matrix characteristics of six urban parks located in Baltimore, Maryland.

	Patch Characteristics				Matrix Characteristics			
Location	Size (ha)	Canopy cover (%)	Total number trees	Total basal area (m^2)	Tree cover (%)	Total number trees	Building cover (%)	Total number buildings
Federal Hill	3.9	60	68	46.2	< 0.01	158	19.59	565
Irvin Luckman	2.2	65	160	89.9	56.60	1229	11.90	1346
Stoney Run	2.7	45	76	55.9	63.36	3369	12.96	2056
Lakeland	4.9	50	105	203.1	6.43	1139	12.80	502
Burdick	4.2	45	125	121.1	14.53	2464	12.07	1928
Carroll	6.9	40	123	103.0	4.37	1967	23.38	1287

Table 3.2. Results of correlation analysis used to evaluate relationships between patch and matrix characteristics, squirrel density, and behavior (wariness, aggression, and activity). A significant correlation at the $P < 0.05$ level is indicated by a single asterisk (*); a significant correlation at the $P < 0.01$ level is indicated by two asterisks (**).

	Park Characteristics				Matrix Characteristics					Behaviors		
	Size	Canopy	Basal area	Tree number	Building cover	Building number	Tree cover	Matrix trees	Squirrel Density	Wariness	Aggression	Activity
Size	1											
Canopy	-0.640**	1										
Basal area	0.388	-0.227	1									
Tree number	-0.017	0.179	0.321	1								
Building cover	0.717**	-0.263	-0.291	-0.243	1							
Building number	-0.292	-0.420*	-0.340	0.185	-0.328	1						
Tree cover	-0.770**	0.214	-0.358	0.204	-0.571**	0.621*	1					
Matrix trees	-0.081	-0.684**	-0.085	0.012	-0.287	0.894**	0.534**	1				
Density	0.036	0.383	0.065	-0.305	0.115	-0.615**	-0.524**	-0.668**	1			
Wariness	0.199	-0.595**	0.115	0.149	-0.034	0.517**	0.259	0.664**	-0.854**	1		
Aggression	-0.006	0.234	0.407*	-0.056	-0.222	-0.437*	-0.343	-0.405*	0.787**	-0.662**	1	
Activity	-0.019	0.081	0.064	0.260	-0.033	0.011	0.111	-0.013	0.159	-0.252	0.453*	1

Table 3.3. Summary of *a priori* models to predict density, wariness, aggression, and activity patterns of gray squirrels in urban parks. Models are shown, including the number of parameters (*K*), AIC values, Δ_i = AIC – AIC$_{min}$ values, Akaike weights (W_i), from lowest to highest Δ_I, adjusted R^2 (R^2_{adj}), and P-values.

Model	Variables	K	AIC	Δ_i	W_i	R^2_{adj}	*P-value*
Density							
D1	17.30 – (size) + (building cover) – (tree cover)	3	57.40	0	0.237	0.56	0.000
D2	4.58 – (size) – (canopy) + (building number) – (matrix trees)	4	57.59	0.19	0.215	0.60	0.000
D3	18.29 – (size) + (building number) – (tree cover)	3	57.65	0.24	0.209	0.55	0.000
D4	18.19 – (size) – (basal area) – (tree cover)	3	57.66	0.26	0.208	0.55	0.000
matrix	13.21 – (building cover) – (building number) – (tree cover) – (matrix trees)	4	61.77	4.37	0.026	0.43	0.004
park	-9.30 + (size) + (canopy) +(basal area) – (tree number)	4	62.37	4.97	0.019	0.41	0.007
null	6.15	0	62.90	5.50	0.015	0.51	0.032
global	-22.16 + (size) + (canopy) – (basal area) – (tree number) – (building cover) + (building number) + (tree cover) + (matrix trees)	8	64.99	7.59	0.006	0.58	0.001
Wariness							
W1	20.84 – (canopy) – (density)	2	48.42	0	0.500	0.80	0.000
W2	23.21 – (canopy) – (matrix trees) – (density)	3	50.09	1.67	0.216	0.79	0.000
W3	15.21 – (density)	1	50.89	2.47	0.145	0.72	0.000
W4	23.68 – (canopy) – (building number) – (matrix trees) – (density)	4	51.01	2.59	0.137	0.80	0.000
park	27.29 – (size) – (canopy) – (basal area) + (tree number)	4	64.32	15.90	0.000	0.39	0.000
null	9.56	0	64.60	16.18	0.000	0.02	0.050
matrix	3.24 + (building cover) – (building number) – (tree cover) + (matrix trees)	4	64.88	16.46	0.000	0.36	0.012
global	21.64 + (size) – (canopy) – (basal area) – (tree number) – (building cover) - (building number) + (tree cover) + (matrix trees) – (density)	9	71.13	22.71	0.000	0.77	0.000

Table 3.3. (Continued).

Model	Variables	K	AIC	Δ_i	W_i	R^2_{adj}	*P-value*
Aggression							
A1	2.29 + (basal area) + (tree cover) + (density)	3	39.54	0	0.567	0.77	0.000
A2	0.21 – (size) + (basal area) + (density)	3	40.72	1.18	0.314	0.75	0.000
A3	0.84 + (density)	1	43.38	3.83	0.083	0.60	0.000
A4	1.70 – (canopy) + (density)	2	45.21	5.67	0.033	0.59	0.000
null	4.04	0	52.97	13.43	0.000	0.41	0.024
matrix	11.21 – (building cover) + (building number) – (tree cover) - (matrix trees)	4	53.71	14.17	0.000	0.34	0.017
park	-2.18 + (size) + (canopy) + (basal area) – (tree number)	4	55.44	15.89	0.000	0.24	0.056
global	0.29 – (size) – (canopy) + (basal area) – (tree number) + (building cover) + (building number) + (tree cover) + (matrix trees) + (density)	9	61.35	21.80	0.000	0.76	0.000
Activity							
P1	6.94 + (density)	1	34.02	0	0.253	0.25	0.457
P2	5.34 – (size) + (building number) + (density)	3	34.91	0.89	0.162	0.14	0.120
P3	3.96 + (size) + (canopy) + (building number) – (tree cover)	4	35.85	1.82	0.101	0.15	0.502
P4	6.83 + (canopy) + (density)	2	36.02	1.99	0.093	0.02	0.760
null	7.22	0	37.33	3.30	0.048	0.00	0.982
matrix	7.44 – (building cover) + (building number) – (tree cover) – (matrix trees)	4	37.81	3.79	0.038	0.02	0.381
park	6.12 + (size) – (canopy) + (basal area) + (tree number)	4	39.47	5.44	0.016	0.06	0.839
global	4.98 – (size) – (canopy) + (basal area) + (tree number) + (building cover) + (building number) + (tree cover) + (matrix trees) + (density)	9	47.00	12.97	0.000	0.08	0.319

Table 3.4. Summer and fall index of abundance (individuals/ha) for gray squirrels located in six urban parks located in Baltimore, MD.

	2003		2004	
Location	Summer	Fall	Summer	Fall
Federal Hill	13.1	11.9	8.5	10.4
Irvin Luckman	2.9	2.7	5.2	8.9
Stoney Run	3.7	2.9	2.2	3.0
Lakeland	3.2	7.2	9.5	11.6
Burdick	5.6	5.2	6.1	7.9
Carroll	2.4	2.0	4.8	6.7

Table 3.5. Results of gray squirrel wariness, aggression, and activity in six urban parks of Baltimore, MD. Wariness (= startle distance) expressed in meters, followed by the SE, and the number of animals sampled. Aggression data is expressed in number of aggressive acts per hour, followed by the SE, and (n) which represents the total number of daylight hours observed. Activity is expressed as the index of activity followed by SE, and the number of animals sampled.

	2003		2004		
Location	Summer	Fall	Summer	Fall	Location Total
Federal Hill					
Wariness	5.05 ± 0.34 (n = 32)	4.96 ± 0.31 (n = 38)	4.55 ± 0.39 (n = 35)	4.00 ± 0.35 (n = 30)	4.64 ± 0.17 (n = 135)
Aggression	7.10 ± 1.06 (n = 28)	5.30 ± 0.87 (n = 24)	3.20 ± 0.52 (n = 30)	5.40 ± 0.83 (n = 25)	5.25 ± 0.80 (n = 107)
Activity	0.28 ± 0.02 (n = 21)	0.20 ± 0.00 (n = 21)	0.20 ± 0.02 (n = 21)	0.19 ± 0.02 (n = 21)	0.22 ± 0.02 (n = 84)
Irvin Luckman					
Wariness	10.08 ± 0.82 (n = 30)	11.14 ± 0.64 (n = 37)	7.03 ± 0.40 (n = 37)	5.42 ± 0.24 (n = 31)	8.40 ± 0.36 (n = 135)
Aggression	2.30 ± 0.25 (n = 27)	2.10 ± 0.21 (n = 22)	5.40 ± 0.90 (n = 29)	4.90 ± 0.88 (n = 23)	3.70 ± 0.86 (n = 101)
Activity	0.24 ± 0.02 (n = 21)	0.23 ± 0.04 (n = 21)	0.29 ± 0.00 (n = 21)	0.23 ± 0.02 (n = 21)	0.25 ± 0.01 (n = 84)
Stoney Run					
Wariness	14.48 ± 0.88 (n = 34)	10.05 ± 0.21 (n = 39)	12.84 ± 0.33 (n = 37)	12.66 ± 0.22 (n = 32)	12.50 ± 0.44 (n = 142)
Aggression	2.50 ± 0.20 (n = 28)	1.80 ± 0.19 (n = 23)	2.10 ± 0.34 (n = 27)	2.70 ± 0.12 (n = 22)	2.30 ± 0.20 (n = 100)
Activity	0.23 ± 0.00 (n = 21)	0.24 ± 0.00 (n = 21)	0.20 ± 0.00 (n = 21)	0.23 ± 0.01 (n = 21)	0.22 ± 0.00 (n = 84)
Lakeland					
Wariness	13.94 ± 0.65 (n = 35)	11.36 ± 0.52 (n = 36)	6.79 ± 0.64 (n = 37)	4.40 ± 0.20 (n = 30)	9.12 ± 0.43 (n = 138)
Aggression	3.50 ± 0.47 (n = 27)	5.00 ± 0.62 (n = 20)	7.20 ± 1.01 (n = 26)	9.70 ± 1.23 (n = 21)	6.40 ± 1.35 (n = 94)
Activity	0.21 ± 0.04 (n = 21)	0.24 ± 0.02 (n = 21)	0.21 ± 0.00 (n = 21)	0.26 ± 0.00 (n = 21)	0.23 ± 0.01 (n = 84)

Table 3.5. (Continued)

	2003		2004		
Location	Summer	Fall	Summer	Fall	Location Total
Burdick					
Wariness	12.35 ± 1.21 (n = 35)	11.89 ± 0.92 (n = 34)	9.01 ± 0.84 (n = 38)	8.25 ± 0.66 (n = 30)	10.37 ± 0.48 (n = 137)
Aggression	6.00 ± 1.02 (n = 29)	4.00 ± 0.79 (n = 22)	5.30 ± 0.98 (n = 27)	3.60 ± 0.82 (n = 22)	4.70 ± 0.56 (n = 100)
Activity	0.22 ± 0.02 (n = 21)	0.20 ± 0.01 (n = 21)	0.26 ± 0.01 (n = 21)	0.21 ± 0.00 (n = 21)	0.22 ± 0.01 (n = 84)
Carroll					
Wariness	16.65 ± 1.18 (n = 35)	13.10 ± 0.71 (n = 38)	10.95 ± 0.57 (n = 33)	8.63 ± 0.45 (n = 31)	12.33 ± 0.46 (n = 137)
Aggression	0.00 ± 0.00 (n = 28)	0.00 ± 0.00 (n = 24)	4.20 ± 0.90 (n = 29)	4.80 ± 0.92 (n = 20)	2.20 ± 1.30 (n = 101)
Activity	0.18 ± 0.00 (n = 21)	0.21 ± 0.01 (n = 21)	0.27 ± 0.03 (n = 21)	0.28 ± 0.01 (n = 21)	0.23 ± 0.02 (n = 84)
Season Totals					
Wariness	12.10 ± 0.44 (n = 201)	10.37 ± 0.32 (n = 222)	8.53 ± 0.35 (n = 217)	7.31 ± 0.29 (n = 184)	8.54 ± 0.19 (n = 824)
Aggression	3.60 ± 1.06 (n = 167)	3.00 ± 0.85 (n = 135)	4.60 ± 0.74 (n = 168)	5.20 ± 0.99 (n = 133)	3.85 ± 0.47 (n = 608)
Activity	0.23 ± 0.00 (n = 126)	0.22 ± 0.00 (n = 126)	0.24 ± 0.00 (n = 126)	0.24 ± 0.00 (n = 126)	0.23 ± 0.00 (n = 504)

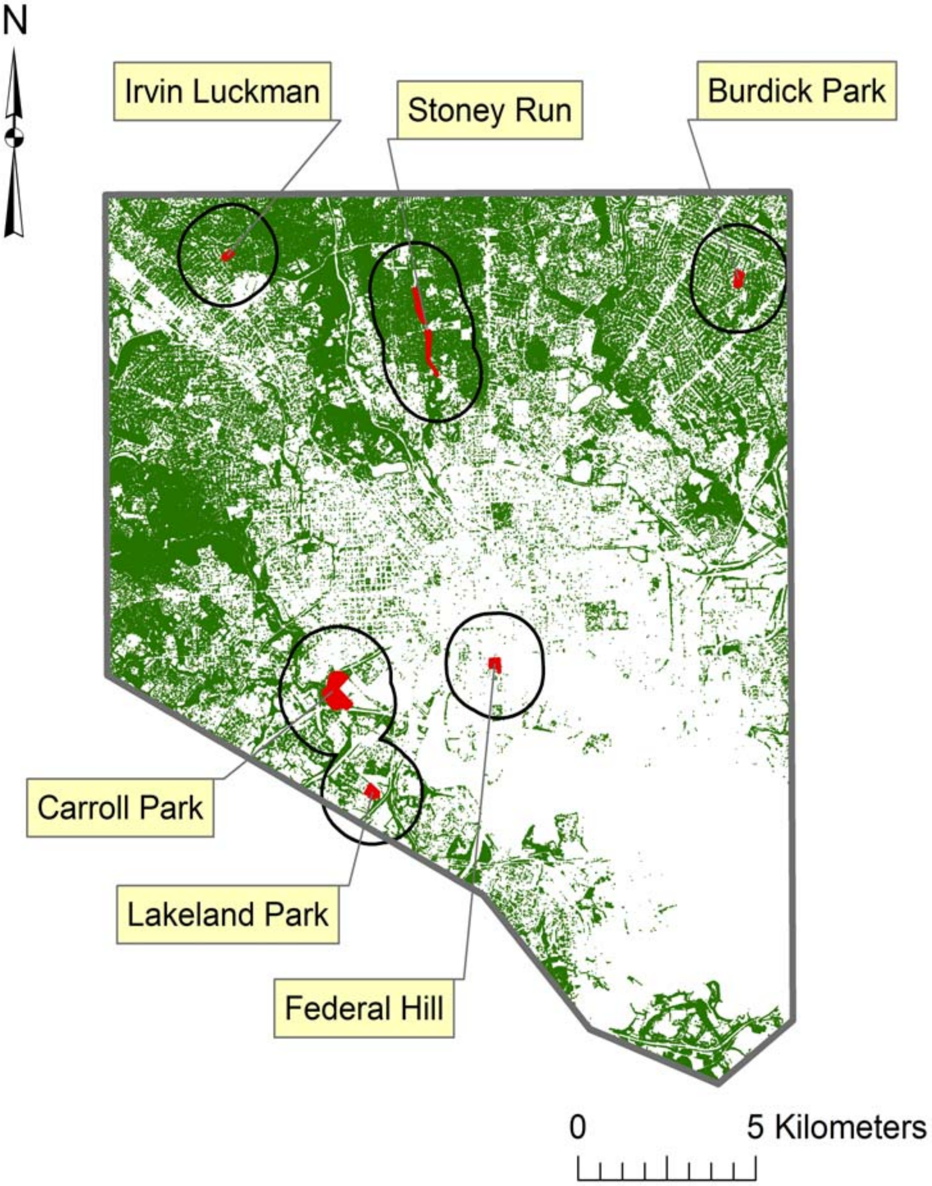

Figure 3.1. Map of study sites located in Baltimore, MD. Map contains, study sites (red), 2 km matrix surrounding each study site (black), and city tree cover (green).

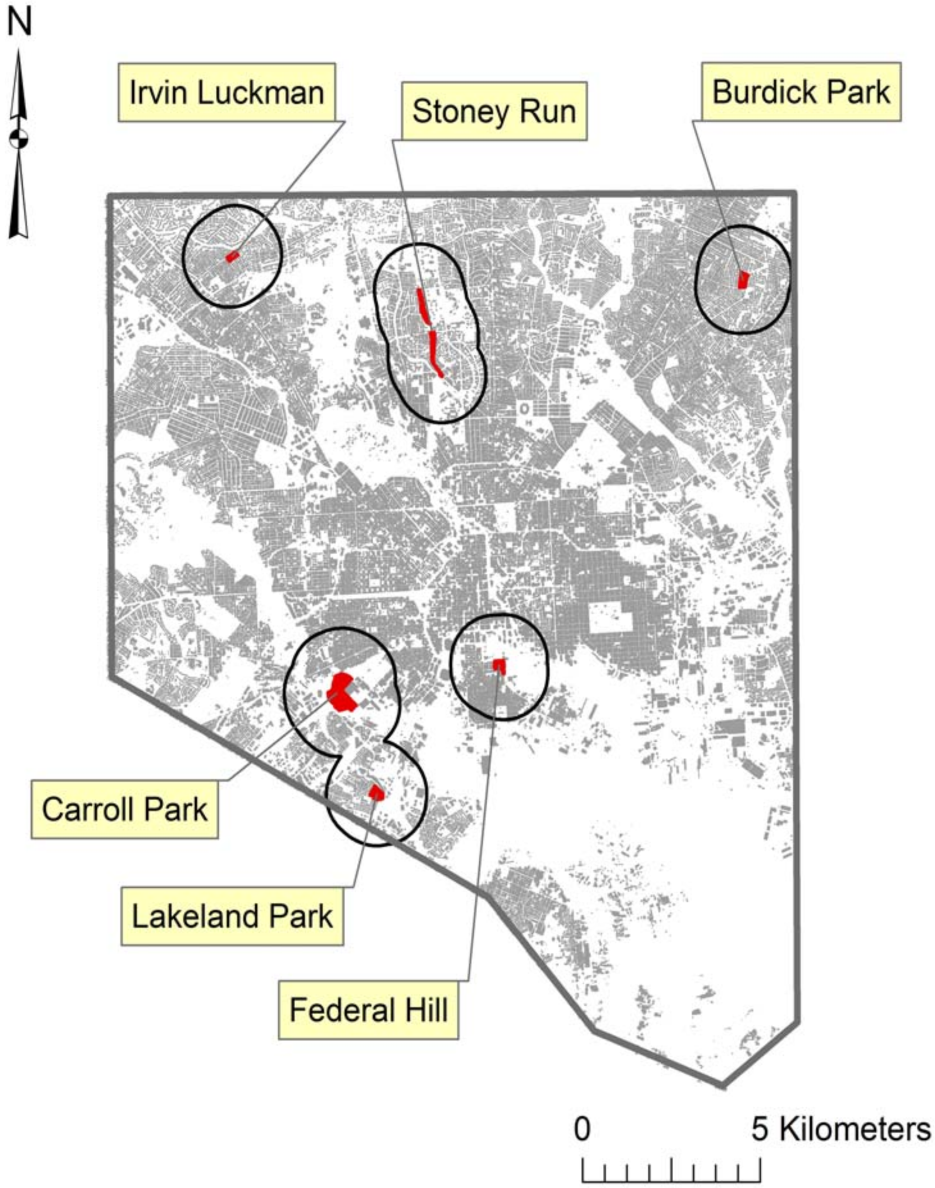

Figure 3. 2. Map of study sites located in Baltimore, MD. Map contains, study sites (red), 2 km matrix surrounding each study site (black), and city building cover (gray).

CHAPTER FOUR

Conclusions

Recent trends in ecological studies show increases in the studying of urban areas. Previous studies of gray squirrel population density and behavior provided the techniques and framework for this study. In these studies, the investigators have often described the habitat attributes that are important for gray squirrels in urban settings. Many of these investigations were limited to the individual parks or the habitats they were investigating. However, based on the results of my research, I contend that it is the interactions between the habitat and the adjacent landscape that may provide more insights regarding how urban ecosystems function.

The models I developed in this study to predict squirrel population density, wariness, aggression, and activity used combinations of park and landscape attributes. Models that included park or landscape attributes only were not as effective as models that included combinations of these attributes. Although, there was varying levels of predictive ability in the models, it demonstrates that the interactions between these attributes provide insights that may not be available if only using the attributes from one.

This study should serve as a tool for ecologist and managers in the prediction of squirrel densities, wariness, intraspecific aggression, and activity. The models developed in this study would prove helpful in urban areas where squirrels are overpopulated or are a nuisance species. In many cases, managers in urban systems use traditional methods to manage by altering the microhabitat of the species of concern. However, the results in this study suggest that altering the habitat and its adjacent landscape may prove more successful. Also, the approach used in this study may be beneficial for the studying of other urban species. Logically, any such study should take into account the ecology of the species, their ability to navigate through urban areas, and their resource requirements. These factors, of course, would greatly alter the scale in which the study should be conducted. However, landscape scale studies should be employed in the studying of urban systems.

Specific Findings

1. Gray squirrel population densities are not correlated with the habitat suitability of urban parks.
2. Gray squirrel population density is negatively correlated with gray squirrel wariness in urban parks.
3. Gray squirrel population density is positively correlated with intraspecific aggression in gray squirrels in urban parks.
4. Gray squirrels in urban parks display the activity patterns of a species that has undergone synurbization.
5. No differences were found between summer and fall activity of gray squirrels in urban parks.
6. The number of buildings and trees in the area surrounding an urban park may be used to approximate squirrel abundance inside the park. Parks situated in a landscape with many buildings and few trees will have increased gray squirrel population densities.
7. Park canopy cover and squirrel population density are the best predictors of gray squirrel wariness. Gray squirrels in urban parks with less canopy cover and low population densities will be more wary.

8. The average basal area of park trees, the amount of tree cover in the area adjacent to the park, and gray squirrel population density are the best predictors of gray squirrel intraspecific aggression. Squirrels will be more aggressive in urban parks with larger trees, high population densities, and those that have a landscape with substantial tree cover.
9. The best predictors of gray squirrel activity was population density. Gray squirrels in urban parks are more active with higher population densities.

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Appendix

Table 1. Summary of models and coefficients to predict density, wariness, aggression, and activity patterns of gray squirrels in urban parks.

Model	Intercept + Coefficient (Parameter)
Density	
D1	17.30 (intercept) - 2.16 (size) + 0.10 (building cover) - 1.56 (tree cover)
D2	4.58 (intercept) - 5.03 (size) - 1.22 (canopy) + 2.58 (building number) - 10.93 (matrix trees)
D3	18.29 (intercept) - 2.05 (size) + 0.26 (building number) - 1.64 (tree cover)
D4	18.19 (intercept) - 1.94 (size) - 0.16 (basal area) - 1.57 (tree cover)
matrix	13.21 (intercept) - 0.17 (building cover) - 0.33 (building number) - 0.46 (tree cover) -1.63 (matrix trees)
park	-9.30 (intercept) + 1.00 (size) + 0.31 (canopy) + 1.55 (basal area) - 5.58 (tree number)
null	6.15 (intercept)
global	-22.16 (intercept) + 8.97 (size) + 0.87 (canopy) - 8.84 (basal area) - 12.10 (tree number) - 2.20 (building cover) + 2.65 (building number) + 0.00 (tree cover) + 0.00 (matrix trees)
Wariness	
W1	20.84 (intercept) - 0.12 (canopy) - 0.78 (density)
W2	23.21 (intercept) - 0.15 (canopy) - 0.42 (matrix trees) - 0.85 (density)
W3	15.21 (intercept) - 0.91(density)
W4	23.68 (intercept) - 0.14 (canopy) - 1.00 (building number) - 0.08 (matrix trees) - 0.89 (density)
park	27.29 (intercept) - 0.78 (size) - 0.35 (canopy) - 0.38 (basal area) + 3.66 (tree number)
null	9.56 (intercept)
matrix	3.24 (intercept) + 0.15 (building cover) - 0.61 (building number) - 0.00 (tree cover) + 2.73 (matrix trees)
global	21.64 + 0.70 (size) - 0.08 (canopy) - 0.66 (basal area) - 0.29 (tree number) - 0.19 (building cover) - 0.87 (building number) + 0.00 (tree cover) + 0.00 (matrix trees) - 0.90 (density)

Table 1. (Continued).

Model	Intercept + Coefficient (Parameter)
Aggression	
A1	2.29 (intercept) + 1.93 (basal area) + 0.25 (tree cover) + 0.60 (density)
A2	0.21 (intercept) - 0.29 (size) + 1.85 (basal area) + 0.50 (density)
A3	0.84 (intercept) + 0.52 (density)
A4	1.70 (intercept) - 0.01(canopy) + 0.54 (density)
null	4.04 (intercept)
matrix	11.21(intercept) - 0.34 (building cover) +0.66 (building number) - 0.52 (tree cover) - 0.83 (matrix trees)
patch	-2.18 (intercept) + 0.07 (size) + 0.11(canopy) + 2.54 (basal area) - 2.32 (tree number)
global	0.29 (intercept) - 0.55 (size) - 0.03 (canopy) + 2.39 (basal area) - 0.24 (tree number) + 0.02 (building cover) + 0.96 (building number) + 0.00 (tree cover) + 0.00 (matrix trees) + 0.62 (density)
Activity	
P1	6.94 (intercept) + 0.04 (density)
P2	5.34 (intercept) - 0.02 (size) + 0.88 (building number) + 0.13 (density)
P3	3.96 (intercept) + 0.11(size) + 0.03 (canopy) + 0.68 (building number) - 0.01 (tree cover)
P4	6.83 (intercept) + 0.00 (canopy) + 0.04 (density)
null	7.22 (intercept)
matrix	7.44 (intercept) - 0.04 (building cover) + 0.95 (building number) - 0.03 (tree cover) - 0.38 (matrix trees)
park	6.12 (intercept) + 0.01 (size) +0.00 (canopy) - 0.03 (basal area) + 0.76 (tree number)
global	4.98 (intercept) -1.28 (size) - 0.06 (canopy) + 2.29 (basal area) + 0.72 (tree number) + 0.34 (building cover) + 0.94 (building number) + 0.00 (tree cover) + 0.00 (matrix trees) + 0.17 (density)

Table 2. Species, diameter at breast height, and basal area of trees located in urban parks of Baltimore, Maryland.

Location	**Common Name**	**Genus**	**Species**	**DBH**	**Basal Area**
Federal Hill	American Basswood	*Tilia*	*americana*	32	5.52
Federal Hill	American Basswood	*Tilia*	*americana*	30	5.04
Federal Hill	American Basswood	*Tilia*	*americana*	16	1.47
Federal Hill	Barberry Hawthorn	*Crataegus*	*berberifolia*	12	0.72
Federal Hill	Barberry Hawthorn	*Crataegus*	*berberifolia*	11	0.66
Federal Hill	Eastern Hophornbeam	*Ostrya*	*virginiana*	13	0.95
Federal Hill	English Elm	*Ulmus*	*procera*	110	66.47
Federal Hill	Gum Bumelia	*Bumelia*	*lanuginosa*	7	0.23
Federal Hill	Gum Bumelia	*Bumelia*	*lanuginosa*	6	0.20
Federal Hill	Ohio Buckeye	*Aesculus*	*glabra*	32	5.58
Federal Hill	Ohio Buckeye	*Aesculus*	*glabra*	30	4.88
Federal Hill	Ohio Buckeye	*Aesculus*	*glabra*	29	4.56
Federal Hill	Ohio Buckeye	*Aesculus*	*glabra*	22	2.54
Federal Hill	Ohio Buckeye	*Aesculus*	*glabra*	12	0.72
Federal Hill	Pin Oak	*Quercus*	*palustris*	47	11.89
Federal Hill	Pin Oak	*Quercus*	*palustris*	52	14.98
Federal Hill	Pin Oak	*Quercus*	*palustris*	24	3.22
Federal Hill	Red Bay	*Persea*	*borbonia*	25	3.41
Federal Hill	Red Maple	*Acer*	*rubrum*	33	5.98
Federal Hill	Red Maple	*Acer*	*rubrum*	20	2.26
Federal Hill	Red Maple	*Acer*	*rubrum*	17	1.61
Federal Hill	Red Maple	*Acer*	*rubrum*	14	1.12
Federal Hill	Red Maple	*Acer*	*rubrum*	14	1.04
Federal Hill	Red Maple	*Acer*	*rubrum*	13	0.95
Federal Hill	Red Maple	*Acer*	*rubrum*	13	0.92
Federal Hill	Red Maple	*Acer*	*rubrum*	12	0.79
Federal Hill	Red Maple	*Acer*	*rubrum*	7	0.29
Federal Hill	Red Maple	*Acer*	*rubrum*	6	0.20

Table 2. (Continued)

Federal Hill	Red Maple	*Acer*	*rubrum*	6	0.18
Federal Hill	Red Maple	*Acer*	*rubrum*	5	0.12
Federal Hill	Red Maple	*Acer*	*rubrum*	4	0.10
Federal Hill	Red Maple	*Acer*	*rubrum*	4	0.08
Federal Hill	Red Maple	*Acer*	*rubrum*	4	0.07
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	Red Maple	*Acer*	*rubrum*	2	0.02
Federal Hill	September Elm	*Ulmus*	*serotina*	23	2.94
Federal Hill	Sweetgum	*Liquidambar*	*styraciflua*	14	1.01
Federal Hill	Sycamore	*Platanus*	*occidentalis*	19	1.97
Federal Hill	White Oak	*Quercus*	*alba*	47	11.89

Table 2. (Continued)

Federal Hill	White Oak	*Quercus*	*alba*	37	7.51
Federal Hill	White Oak	*Quercus*	*alba*	33	6.05
Federal Hill	White Oak	*Quercus*	*alba*	25	3.33
Federal Hill	White Oak	*Quercus*	*alba*	25	3.27
Federal Hill	White Oak	*Quercus*	*alba*	24	3.01
Federal Hill	White Oak	*Quercus*	*alba*	23	2.94
Federal Hill	White Spruce	*Picea*	*glauca*	9	0.42
Federal Hill	Yellow Poplar	*Liriodendron*	*tulipifera*	31	5.38
Federal Hill	Yellow Poplar	*Liriodendron*	*tulipifera*	21	2.36
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	36	7.18
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	30	4.88
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	30	4.84
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	28	4.31
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	26	3.74
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	25	3.52
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	19	1.89
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	18	1.85
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	18	1.81
Irvin Luckman	American Beech	*Fagus*	*grandifolia*	14	1.08
Irvin Luckman	American Chestnut	*Castanea*	*dentata*	8	0.32
Irvin Luckman	American Chestnut	*Castanea*	*dentata*	7	0.28
Irvin Luckman	American Elm	*Ulmus*	*americana*	30	4.99
Irvin Luckman	American Elm	*Ulmus*	*americana*	22	2.56
Irvin Luckman	Eastern Hophornbeam	*Ostrya*	*virginiana*	17	1.54
Irvin Luckman	Eastern Hophornbeam	*Ostrya*	*virginiana*	13	0.96
Irvin Luckman	Eastern Redbud	*Cercis*	*candensis*	12	0.84
Irvin Luckman	Eastern Redbud	*Cercis*	*candensis*	11	0.68
Irvin Luckman	Flowering Dogwood	*Cornus*	*florida*	5	0.12
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	17	1.49
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	16	1.44
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	16	1.33

Table 2. (Continued)

Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	15	1.27
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	15	1.17
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	15	1.17
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	13	0.97
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	13	0.93
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	12	0.80
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	12	0.72
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	11	0.72
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	11	0.65
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	11	0.64
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	11	0.60
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	11	0.60
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	10	0.50
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	10	0.50
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	9	0.46
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	8	0.37
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	8	0.36
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	8	0.36
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	8	0.35
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	8	0.35
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	8	0.31
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	7	0.30
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	7	0.25
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	6	0.21
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	5	0.12
Irvin Luckman	Loblolly Pine	*Pinus*	*taeda*	4	0.10
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	46	11.46
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	46	11.46
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	46	11.30
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	39	8.50
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	37	7.57

Table 2. (Continued)

Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	36	7.18
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	36	7.18
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	35	6.69
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	32	5.73
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	30	4.78
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	29	4.58
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	28	4.18
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	25	3.45
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	25	3.28
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	24	3.25
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	21	2.41
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	21	2.41
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	21	2.34
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	17	1.49
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	16	1.44
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	15	1.22
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	14	1.12
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	14	1.04
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	14	1.02
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	14	1.02
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	13	0.97
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	12	0.80
Irvin Luckman	Northern Pin Oak	*Quercus*	*palustris*	11	0.72
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	36	7.11
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	29	4.71
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	27	4.04
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	25	3.38
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	23	2.84
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	22	2.64
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	21	2.45
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	21	2.29

Table 2. (Continued)

Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	21	2.29
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	19	1.97
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	18	1.75
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	18	1.69
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	16	1.40
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	15	1.15
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	14	1.07
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	10	0.52
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	10	0.51
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	9	0.46
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	9	0.45
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	8	0.35
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	8	0.34
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	8	0.32
Irvin Luckman	Northern Red Oak	*Quercus*	*rubra*	6	0.18
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	40	8.91
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	35	6.81
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	32	5.75
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	29	4.71
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	25	3.45
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	24	3.01
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	21	2.34
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	20	2.26
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	20	2.26
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	20	2.10
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	19	1.99
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	16	1.33
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	15	1.27
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	11	0.72
Irvin Luckman	Persimmon	*Diospyros*	*virginiana*	11	0.60
Irvin Luckman	Persimmon	Diospyros	virginiana	10	0.50

Table 2. (Continued)

Irvin Luckman	September Elm	*Ulmus*	*serotina*	32	5.62
Irvin Luckman	September Elm	*Ulmus*	*serotina*	28	4.28
Irvin Luckman	September Elm	*Ulmus*	*serotina*	26	3.63
Irvin Luckman	September Elm	*Ulmus*	*serotina*	15	1.18
Irvin Luckman	September Elm	*Ulmus*	*serotina*	12	0.84
Irvin Luckman	September Elm	*Ulmus*	*serotina*	12	0.80
Irvin Luckman	September Elm	*Ulmus*	*serotina*	11	0.68
Irvin Luckman	September Elm	*Ulmus*	*serotina*	10	0.57
Irvin Luckman	September Elm	*Ulmus*	*serotina*	7	0.25
Irvin Luckman	September Elm	*Ulmus*	*serotina*	7	0.25
Irvin Luckman	September Elm	*Ulmus*	*serotina*	6	0.20
Irvin Luckman	September Elm	*Ulmus*	*serotina*	5	0.15
Irvin Luckman	Shagbark Hickory	*Carya*	*ovata*	13	0.91
Irvin Luckman	Shingle Oak	*Quercus*	*imbricaria*	14	1.08
Irvin Luckman	White Oak	*Quercus*	*alba*	45	10.90
Irvin Luckman	White Oak	*Quercus*	*alba*	36	7.07
Irvin Luckman	White Oak	*Quercus*	*alba*	34	6.27
Irvin Luckman	White Oak	*Quercus*	*alba*	33	6.08
Irvin Luckman	White Oak	*Quercus*	*alba*	32	5.69
Irvin Luckman	White Oak	*Quercus*	*alba*	31	5.09
Irvin Luckman	White Oak	*Quercus*	*alba*	28	4.40
Irvin Luckman	White Oak	*Quercus*	*alba*	28	4.28
Irvin Luckman	White Oak	*Quercus*	*alba*	28	4.22
Irvin Luckman	White Oak	*Quercus*	*alba*	28	4.18
Irvin Luckman	White Oak	*Quercus*	*alba*	27	3.83
Irvin Luckman	White Oak	*Quercus*	*alba*	22	2.74
Irvin Luckman	White Oak	*Quercus*	*alba*	18	1.83
Irvin Luckman	White Oak	*Quercus*	*alba*	17	1.61
Irvin Luckman	White Oak	*Quercus*	*alba*	13	0.94
Irvin Luckman	White Oak	*Quercus*	*alba*	11	0.64
Irvin Luckman	White Oak	*Quercus*	*alba*	11	0.60

Table 2. (Continued)

Irvin Luckman	White Oak	*Quercus*	*alba*	10	0.53
Irvin Luckman	White Oak	*Quercus*	*alba*	10	0.52
Irvin Luckman	White Oak	*Quercus*	*alba*	9	0.43
Irvin Luckman	White Oak	*Quercus*	*alba*	9	0.39
Irvin Luckman	White Oak	*Quercus*	*alba*	6	0.19
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	35	6.57
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	29	4.71
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	24	3.19
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	21	2.41
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	19	1.99
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	16	1.38
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	14	1.04
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	8	0.33
Irvin Luckman	Yellow Poplar	*Liriodendron*	*tulipifera*	7	0.27
Stoney Run	American Beech	*Fagus*	*grandifolia*	23	2.99
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	17	1.61
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	16	1.40
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	16	1.31
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	14	1.12
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	13	0.89
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	13	0.87
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	13	0.85
Stoney Run	Barberry Hawthorn	*Crataegus*	*berberifolia*	12	0.84
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	46	11.46
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	37	7.44
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	25	3.36
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	23	2.95
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	22	2.71
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	21	2.38
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	16	1.38
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	13	0.95

Table 2. (Continued)

Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	13	0.95
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	13	0.93
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	9	0.42
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	7	0.27
Stoney Run	Black Locust	*Robinia*	*pseudoacacia*	7	0.23
Stoney Run	Black Walnut	*Juglans*	*nigra*	25	3.38
Stoney Run	Black Walnut	*Juglans*	*nigra*	17	1.58
Stoney Run	Clammy Locust	*Robinia*	*viscosa*	36	6.93
Stoney Run	Clammy Locust	*Robinia*	*viscosa*	22	2.63
Stoney Run	Clammy Locust	*Robinia*	*viscosa*	14	1.07
Stoney Run	Clammy Locust	*Robinia*	*viscosa*	13	0.94
Stoney Run	Clammy Locust	*Robinia*	*viscosa*	13	0.93
Stoney Run	Clammy Locust	*Robinia*	*viscosa*	4	0.10
Stoney Run	Common Persimmon	*Diospyros*	*virginiana*	42	9.44
Stoney Run	Common Persimmon	*Diospyros*	*virginiana*	37	7.43
Stoney Run	Common Persimmon	*Diospyros*	*virginiana*	33	5.98
Stoney Run	Common Persimmon	*Diospyros*	*virginiana*	25	3.46
Stoney Run	Downy Serviceberry	*Amelanchier*	*arborea*	11	0.67
Stoney Run	European Beech	*Fagus*	*sylvatica*	30	4.88
Stoney Run	European Linden	*Tilia*	*cordata*	24	3.01
Stoney Run	Green Ash	*Fraxinus*	*pennsylvanica*	30	4.91
Stoney Run	Green Ash	*Fraxinus*	*pennsylvanica*	20	2.25
Stoney Run	Honey Locust	*Gleditsia*	*triacanthos*	28	4.28
Stoney Run	Northern Pin Oak	*Quercus*	*palustris*	10	0.55
Stoney Run	Northern Pin Oak	*Quercus*	*palustris*	10	0.55
Stoney Run	Nutmeg Hickory	*Carya*	*myristiciformis*	28	4.31
Stoney Run	September Elm	*Ulmus*	*serotina*	35	6.69
Stoney Run	September Elm	*Ulmus*	*serotina*	23	2.79
Stoney Run	September Elm	*Ulmus*	*serotina*	15	1.17
Stoney Run	September Elm	*Ulmus*	*serotina*	13	0.88
Stoney Run	September Elm	*Ulmus*	*serotina*	10	0.58

Table 2. (Continued)

Stoney Run	September Elm	*Ulmus*	*serotina*	9	0.43
Stoney Run	Silver Maple	*Acer*	*saccharinum*	62	20.63
Stoney Run	Silver Maple	*Acer*	*saccharinum*	16	1.45
Stoney Run	Silver Maple	*Acer*	*saccharinum*	6	0.22
Stoney Run	Sugar Maple	*Acer*	*saccharum*	19	2.06
Stoney Run	Sugar Maple	*Acer*	*saccharum*	10	0.59
Stoney Run	Sycamore	*Platanus*	*occidentalis*	44	10.66
Stoney Run	Sycamore	*Platanus*	*occidentalis*	41	8.95
Stoney Run	Sycamore	*Platanus*	*occidentalis*	37	7.57
Stoney Run	Sycamore	*Platanus*	*occidentalis*	37	7.35
Stoney Run	Sycamore	*Platanus*	*occidentalis*	34	6.21
Stoney Run	Sycamore	*Platanus*	*occidentalis*	31	5.09
Stoney Run	Sycamore	*Platanus*	*occidentalis*	30	4.81
Stoney Run	Sycamore	*Platanus*	*occidentalis*	26	3.81
Stoney Run	Sycamore	*Platanus*	*occidentalis*	21	2.48
Stoney Run	Sycamore	*Platanus*	*occidentalis*	18	1.67
Stoney Run	White Ash	*Fraxinus*	*americana*	22	2.52
Stoney Run	White Ash	*Fraxinus*	*americana*	21	2.34
Stoney Run	White Ash	*Fraxinus*	*americana*	20	2.18
Stoney Run	White Ash	*Fraxinus*	*americana*	17	1.65
Stoney Run	White Ash	*Fraxinus*	*americana*	12	0.72
Stoney Run	White Mulberry	*Morus*	*alba*	5	0.13
Stoney Run	White Mulberry	*Morus*	*alba*	4	0.07
Stoney Run	White Oak	*Quercus*	*alba*	45	10.95
Stoney Run	White Oak	*Quercus*	*alba*	31	5.34
Stoney Run	White Oak	*Quercus*	*alba*	27	3.98
Stoney Run	Yellow Poplar	*Liriodendron*	*tulipifera*	14	1.02
Stoney Run	Yellow Poplar	*Liriodendron*	*tulipifera*	6	0.22
Lakeland	Black Cherry	*Prunus*	*serotina*	52	14.92
Lakeland	Black Cherry	*Prunus*	*serotina*	49	13.26
Lakeland	Black Cherry	*Prunus*	*serotina*	47	12.05

Table 2. (Continued)

Lakeland	Black Cherry	*Prunus*	*serotina*	44	10.75
Lakeland	Black Cherry	*Prunus*	*serotina*	42	9.58
Lakeland	Black Cherry	*Prunus*	*serotina*	39	8.30
Lakeland	Black Cherry	*Prunus*	*serotina*	17	1.63
Lakeland	Black Locust	*Robinia*	*pseudoacacia*	77	32.00
Lakeland	European Linden	*Tilia*	*cordata*	26	3.77
Lakeland	European Linden	*Tilia*	*cordata*	25	3.49
Lakeland	Honey Locust	*Gleditsia*	*triacanthos*	16	1.41
Lakeland	Honey Locust	*Gleditsia*	*triacanthos*	14	1.01
Lakeland	Loblolly Pine	*Pinus*	*taeda*	14	1.04
Lakeland	Loblolly Pine	*Pinus*	*taeda*	13	0.96
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	79	34.38
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	78	32.76
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	71	27.73
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	70	26.72
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	68	25.22
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	62	20.63
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	39	8.09
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	28	4.18
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	28	4.12
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	27	3.86
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	27	3.86
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	26	3.77
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	25	3.52
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	25	3.41
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	25	3.41
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	25	3.41
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	24	3.09
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	23	2.99
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	22	2.59
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	22	2.52

Table 2. (Continued)

Lakeland	Northern Pin Oak	*Quercus*	*palustris*	20	2.18
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	20	2.18
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	20	2.07
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	19	2.03
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	19	1.99
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	19	1.97
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	19	1.95
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	18	1.69
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	18	1.69
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	17	1.65
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	17	1.61
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	17	1.48
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	16	1.41
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	16	1.33
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	16	1.33
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	15	1.28
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	15	1.15
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	14	1.02
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	13	0.87
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	12	0.76
Lakeland	Northern Pin Oak	*Quercus*	*palustris*	12	0.76
Lakeland	Persimmon	*Diospyros*	*virginiana*	14	1.07
Lakeland	Red Maple	*Acer*	*rubrum*	70	26.88
Lakeland	Red Maple	*Acer*	*rubrum*	68	25.44
Lakeland	Red Maple	*Acer*	*rubrum*	26	3.63
Lakeland	Red Maple	*Acer*	*rubrum*	17	1.63
Lakeland	Red Maple	*Acer*	*rubrum*	17	1.63
Lakeland	Red Maple	*Acer*	*rubrum*	17	1.59
Lakeland	Red Maple	*Acer*	*rubrum*	17	1.59
Lakeland	Red Maple	*Acer*	*rubrum*	16	1.43
Lakeland	Red Maple	*Acer*	*rubrum*	15	1.16

Table 2. (Continued)

Lakeland	Red Maple	*Acer*	*rubrum*	14	1.05
Lakeland	Red Maple	*Acer*	*rubrum*	14	1.05
Lakeland	Red Maple	*Acer*	*rubrum*	14	1.05
Lakeland	Red Maple	*Acer*	*rubrum*	12	0.84
Lakeland	Red Maple	*Acer*	*rubrum*	12	0.80
Lakeland	Red Maple	*Acer*	*rubrum*	11	0.65
Lakeland	Red Maple	*Acer*	*rubrum*	10	0.55
Lakeland	Red Oak	*Quercus*	*rubra*	31	5.07
Lakeland	Red Oak	*Quercus*	*rubra*	29	4.56
Lakeland	Red Oak	*Quercus*	*rubra*	23	2.91
Lakeland	Red Oak	*Quercus*	*rubra*	20	2.12
Lakeland	Red Oak	*Quercus*	*rubra*	17	1.50
Lakeland	Sycamore	*Plantanus*	*occidentalis*	62	21.17
Lakeland	Sycamore	*Plantanus*	*occidentalis*	30	5.01
Lakeland	Sycamore	*Plantanus*	*occidentalis*	29	4.68
Lakeland	Sycamore	*Plantanus*	*occidentalis*	25	3.46
Lakeland	Sycamore	*Plantanus*	*occidentalis*	17	1.48
Lakeland	White Oak	*Quercus*	*alba*	90	43.88
Lakeland	White Oak	*Quercus*	*alba*	83	37.12
Lakeland	White Oak	*Quercus*	*alba*	75	30.92
Lakeland	White Oak	*Quercus*	*alba*	75	30.92
Lakeland	White Oak	*Quercus*	*alba*	73	28.75
Lakeland	White Oak	*Quercus*	*alba*	58	18.16
Lakeland	White Oak	*Quercus*	*alba*	33	5.83
Lakeland	White Oak	*Quercus*	*alba*	25	3.52
Lakeland	White Oak	*Quercus*	*alba*	21	2.41
Lakeland	White Oak	*Quercus*	*alba*	19	2.01
Lakeland	White Oak	*Quercus*	*alba*	19	1.99
Lakeland	White Oak	*Quercus*	*alba*	19	1.95
Lakeland	White Oak	*Quercus*	*alba*	18	1.79
Lakeland	White Oak	*Quercus*	*alba*	18	1.71

Table 2. (Continued)

Lakeland	White Oak	*Quercus*	*alba*	15	1.18
Lakeland	White Oak	*Quercus*	*alba*	12	0.79
Lakeland	White Poplar	*Popular*	*alba*	92	46.36
Lakeland	White Poplar	*Popular*	*alba*	77	32.67
Lakeland	White Poplar	*Popular*	*alba*	73	28.83
Lakeland	White Poplar	*Popular*	*alba*	69	25.59
Lakeland	White Poplar	*Popular*	*alba*	65	23.04
Lakeland	White Poplar	*Popular*	*alba*	62	20.63
Lakeland	White Poplar	*Popular*	*alba*	27	3.92
Burdick	American Beech	*Fagus*	*grandifolia*	39	8.09
Burdick	American Beech	*Fagus*	*grandifolia*	32	5.42
Burdick	American Beech	*Fagus*	*grandifolia*	30	4.88
Burdick	American Beech	*Fagus*	*grandifolia*	26	3.63
Burdick	American Beech	*Fagus*	*grandifolia*	23	2.95
Burdick	American Beech	*Fagus*	*grandifolia*	23	2.95
Burdick	American Beech	*Fagus*	*grandifolia*	23	2.95
Burdick	American Beech	*Fagus*	*grandifolia*	21	2.34
Burdick	American Beech	*Fagus*	*grandifolia*	18	1.80
Burdick	American Beech	*Fagus*	*grandifolia*	13	0.97
Burdick	American Beech	*Fagus*	*grandifolia*	6	0.22
Burdick	American Beech	*Fagus*	*grandifolia*	3	0.05
Burdick	Common Persimmon	*Diospyros*	*virginiana*	32	5.42
Burdick	Common Persimmon	*Diospyros*	*virginiana*	29	4.48
Burdick	Common Persimmon	*Diospyros*	*virginiana*	24	3.14
Burdick	Common Persimmon	*Diospyros*	*virginiana*	13	0.96
Burdick	Common Persimmon	*Diospyros*	*virginiana*	6	0.20
Burdick	Eastern White Pine	*Pinus*	*strobus*	15	1.28
Burdick	Eastern White Pine	*Pinus*	*strobus*	14	1.07
Burdick	Eastern White Pine	*Pinus*	*strobus*	12	0.72
Burdick	Eastern White Pine	*Pinus*	*strobus*	10	0.55
Burdick	Loblolly Pine	*Pinus*	*taeda*	20	2.23

Table 2. (Continued)

Burdick	Loblolly Pine	*Pinus*	*taeda*	12	0.83
Burdick	Loblolly Pine	*Pinus*	*taeda*	10	0.49
Burdick	Northern Pin Oak	*Quercus*	*palustris*	51	14.15
Burdick	Northern Pin Oak	*Quercus*	*palustris*	49	13.28
Burdick	Northern Pin Oak	*Quercus*	*palustris*	39	8.36
Burdick	Northern Pin Oak	*Quercus*	*palustris*	39	8.36
Burdick	Northern Pin Oak	*Quercus*	*palustris*	38	7.83
Burdick	Northern Pin Oak	*Quercus*	*palustris*	31	5.24
Burdick	Northern Pin Oak	*Quercus*	*palustris*	27	4.09
Burdick	Northern Pin Oak	*Quercus*	*palustris*	26	3.63
Burdick	Northern Pin Oak	*Quercus*	*palustris*	22	2.71
Burdick	Northern Pin Oak	*Quercus*	*palustris*	17	1.61
Burdick	Northern Pin Oak	*Quercus*	*palustris*	16	1.38
Burdick	Northern Pin Oak	*Quercus*	*palustris*	16	1.33
Burdick	Northern Pin Oak	*Quercus*	*palustris*	14	1.02
Burdick	Northern Pin Oak	*Quercus*	*palustris*	14	1.02
Burdick	Northern Pin Oak	*Quercus*	*palustris*	13	0.97
Burdick	Northern Pin Oak	*Quercus*	*palustris*	11	0.68
Burdick	Red Maple	*Acer*	*rubrum*	28	4.22
Burdick	Red Maple	*Acer*	*rubrum*	28	4.18
Burdick	Red Maple	*Acer*	*rubrum*	23	2.95
Burdick	Red Maple	*Acer*	*rubrum*	14	1.01
Burdick	Red Maple	*Acer*	*rubrum*	12	0.84
Burdick	Red Maple	*Acer*	*rubrum*	7	0.24
Burdick	September Elm	*Ulmus*	*serotina*	25	3.54
Burdick	September Elm	*Ulmus*	*serotina*	24	3.03
Burdick	September Elm	*Ulmus*	*serotina*	21	2.34
Burdick	September Elm	*Ulmus*	*serotina*	15	1.27
Burdick	Sweetgum	*Liquidambar*	*styraciflua*	31	5.38
Burdick	White Oak	*Quercus*	*alba*	49	12.88
Burdick	White Oak	*Quercus*	*alba*	47	11.94

Table 2. (Continued)

Burdick	White Oak	*Quercus*	*alba*	47	11.84
Burdick	White Oak	*Quercus*	*alba*	47	11.84
Burdick	White Oak	*Quercus*	*alba*	47	11.79
Burdick	White Oak	*Quercus*	*alba*	46	11.78
Burdick	White Oak	*Quercus*	*alba*	41	9.35
Burdick	White Oak	*Quercus*	*alba*	40	8.73
Burdick	White Oak	*Quercus*	*alba*	39	8.23
Burdick	White Oak	*Quercus*	*alba*	38	7.88
Burdick	White Oak	*Quercus*	*alba*	37	7.55
Burdick	White Oak	*Quercus*	*alba*	37	7.43
Burdick	White Oak	*Quercus*	*alba*	36	7.15
Burdick	White Oak	*Quercus*	*alba*	36	7.15
Burdick	White Oak	*Quercus*	*alba*	36	7.07
Burdick	White Oak	*Quercus*	*alba*	36	6.99
Burdick	White Oak	*Quercus*	*alba*	36	6.93
Burdick	White Oak	*Quercus*	*alba*	34	6.45
Burdick	White Oak	*Quercus*	*alba*	33	6.09
Burdick	White Oak	*Quercus*	*alba*	33	5.83
Burdick	White Oak	*Quercus*	*alba*	32	5.65
Burdick	White Oak	*Quercus*	*alba*	32	5.58
Burdick	White Oak	*Quercus*	*alba*	32	5.42
Burdick	White Oak	*Quercus*	*alba*	31	5.31
Burdick	White Oak	*Quercus*	*alba*	31	5.20
Burdick	White Oak	*Quercus*	*alba*	30	4.97
Burdick	White Oak	*Quercus*	*alba*	30	4.94
Burdick	White Oak	*Quercus*	*alba*	30	4.91
Burdick	White Oak	*Quercus*	*alba*	30	4.78
Burdick	White Oak	*Quercus*	*alba*	29	4.68
Burdick	White Oak	*Quercus*	*alba*	29	4.59
Burdick	White Oak	*Quercus*	*alba*	29	4.56
Burdick	White Oak	*Quercus*	*alba*	29	4.49

Table 2. (Continued)

Burdick	White Oak	*Quercus*	*alba*	29	4.49
Burdick	White Oak	*Quercus*	*alba*	29	4.49
Burdick	White Oak	*Quercus*	*alba*	29	4.46
Burdick	White Oak	*Quercus*	*alba*	29	4.43
Burdick	White Oak	*Quercus*	*alba*	28	4.34
Burdick	White Oak	*Quercus*	*alba*	28	4.28
Burdick	White Oak	*Quercus*	*alba*	28	4.25
Burdick	White Oak	*Quercus*	*alba*	27	4.06
Burdick	White Oak	*Quercus*	*alba*	27	4.04
Burdick	White Oak	*Quercus*	*alba*	27	4.04
Burdick	White Oak	*Quercus*	*alba*	27	4.01
Burdick	White Oak	*Quercus*	*alba*	26	3.80
Burdick	White Oak	*Quercus*	*alba*	26	3.77
Burdick	White Oak	*Quercus*	*alba*	26	3.69
Burdick	White Oak	*Quercus*	*alba*	26	3.69
Burdick	White Oak	*Quercus*	*alba*	26	3.63
Burdick	White Oak	*Quercus*	*alba*	26	3.57
Burdick	White Oak	*Quercus*	*alba*	25	3.44
Burdick	White Oak	*Quercus*	*alba*	25	3.35
Burdick	White Oak	*Quercus*	*alba*	24	3.22
Burdick	White Oak	*Quercus*	*alba*	24	3.17
Burdick	White Oak	*Quercus*	*alba*	24	3.14
Burdick	White Oak	*Quercus*	*alba*	24	3.12
Burdick	White Oak	*Quercus*	*alba*	24	3.09
Burdick	White Oak	*Quercus*	*alba*	23	2.96
Burdick	White Oak	*Quercus*	*alba*	22	2.62
Burdick	White Oak	*Quercus*	*alba*	22	2.62
Burdick	White Oak	*Quercus*	*alba*	21	2.45
Burdick	White Oak	*Quercus*	*alba*	21	2.43
Burdick	White Oak	*Quercus*	*alba*	21	2.34
Burdick	White Oak	*Quercus*	*alba*	21	2.29

Table 2. (Continued)

Burdick	White Oak	*Quercus*	*alba*	20	2.07
Burdick	White Oak	*Quercus*	*alba*	19	2.05
Burdick	White Oak	*Quercus*	*alba*	19	2.05
Burdick	White Oak	*Quercus*	*alba*	19	2.05
Burdick	White Oak	*Quercus*	*alba*	19	1.99
Burdick	White Oak	*Quercus*	*alba*	19	1.99
Burdick	White Oak	*Quercus*	*alba*	17	1.61
Burdick	White Oak	*Quercus*	*alba*	13	0.88
Burdick	White Oak	*Quercus*	*alba*	12	0.76
Burdick	White Oak	*Quercus*	*alba*	11	0.65
Carroll	American Beech	*Fagus*	*grandifolia*	39	8.09
Carroll	American Beech	*Fagus*	*grandifolia*	20	2.14
Carroll	American Beech	*Fagus*	*grandifolia*	5	0.16
Carroll	Balsom Fir	*Abies*	*balsamea*	23	2.96
Carroll	Butternut	*Juglans*	*cinerea*	19	1.91
Carroll	European Linden	*Tilia*	*cordata*	37	7.57
Carroll	European Linden	*Tilia*	*cordata*	30	4.78
Carroll	European Linden	*Tilia*	*cordata*	27	4.09
Carroll	European Linden	*Tilia*	*cordata*	27	4.01
Carroll	European Linden	*Tilia*	*cordata*	25	3.36
Carroll	European Linden	*Tilia*	*cordata*	24	3.06
Carroll	European Linden	*Tilia*	*cordata*	23	2.87
Carroll	European Linden	*Tilia*	*cordata*	23	2.79
Carroll	European Linden	*Tilia*	*cordata*	23	2.79
Carroll	European Linden	*Tilia*	*cordata*	22	2.56
Carroll	European Linden	*Tilia*	*cordata*	21	2.48
Carroll	European Linden	*Tilia*	*cordata*	21	2.34
Carroll	European Linden	*Tilia*	*cordata*	20	2.12
Carroll	European Linden	*Tilia*	*cordata*	17	1.65
Carroll	European Linden	*Tilia*	*cordata*	15	1.22
Carroll	Ginkgo	*Ginkgo*	*biloba*	28	4.40

Table 2. (Continued)

Carroll	Ginkgo	*Ginkgo*	*biloba*	28	4.40
Carroll	Ginko	*Ginkgo*	*biloba*	27	3.99
Carroll	Ginko	*Ginkgo*	*biloba*	25	3.54
Carroll	Ginko	*Ginkgo*	*biloba*	24	3.11
Carroll	Ginko	*Ginkgo*	*biloba*	24	3.11
Carroll	Ginko	*Ginkgo*	*biloba*	23	2.87
Carroll	Ginko	*Ginkgo*	*biloba*	22	2.71
Carroll	Ginko	*Ginkgo*	*biloba*	20	2.19
Carroll	Ginko	*Ginkgo*	*biloba*	19	2.06
Carroll	Green Ash	*Fraxinus*	*pennsylvanica*	29	4.58
Carroll	Honey Locust	*Gleditsia*	*triacanthos*	36	7.18
Carroll	Horse Chestnut	*Aesculus*	*hippocastanum*	42	9.80
Carroll	Horse Chestnut	*Aesculus*	*hippocastanum*	30	4.75
Carroll	Horse Chestnut	*Aesculus*	*hippocastanum*	27	3.95
Carroll	Northern Catalpa	*Catalpa*	*speciosa*	35	6.61
Carroll	Northern Catalpa	*Catalpa*	*speciosa*	35	6.61
Carroll	Northern Catalpa	*Catalpa*	*speciosa*	31	5.31
Carroll	Northern Catalpa	*Catalpa*	*speciosa*	29	4.48
Carroll	Northern Catalpa	*Catalpa*	*speciosa*	24	3.03
Carroll	Northern Pin Oak	*Quercus*	*palustris*	38	7.70
Carroll	Northern Pin Oak	*Quercus*	*palustris*	35	6.69
Carroll	Northern Pin Oak	*Quercus*	*palustris*	33	5.98
Carroll	Northern Pin Oak	*Quercus*	*palustris*	27	3.99
Carroll	Northern Pin Oak	*Quercus*	*palustris*	24	3.04
Carroll	Northern Pin Oak	*Quercus*	*palustris*	23	2.89
Carroll	Northern Pin Oak	*Quercus*	*palustris*	21	2.47
Carroll	Northern Pin Oak	*Quercus*	*palustris*	20	2.14
Carroll	Northern Pin Oak	*Quercus*	*palustris*	18	1.81
Carroll	Northern Pin Oak	*Quercus*	*palustris*	17	1.61
Carroll	Northern Pin Oak	*Quercus*	*palustris*	15	1.21
Carroll	Northern Pin Oak	*Quercus*	*palustris*	14	1.05

Table 2. (Continued)

Carroll	Northern Pin Oak	*Quercus*	*palustris*	9	0.43
Carroll	Northern Pin Oak	*Quercus*	*palustris*	5	0.16
Carroll	Northern Pin Oak	*Quercus*	*palustris*	5	0.14
Carroll	Northern Pin Oak	*Quercus*	*palustris*	5	0.14
Carroll	Northern Pin Oak	*Quercus*	*palustris*	4	0.08
Carroll	Oriental Aborvitae	*Thuja*	*orientalis*	42	9.58
Carroll	Oriental Aborvitae	*Thuja*	*orientalis*	30	4.88
Carroll	Oriental Aborvitae	*Thuja*	*orientalis*	23	2.79
Carroll	Oriental Arborvitae	*Thuja*	*orientalis*	17	1.65
Carroll	Parsley Hawthorn	*Crataegus*	*marshallii*	24	3.19
Carroll	Parsley Hawthorn	*Crataegus*	*marshallii*	18	1.86
Carroll	Persimmon	*Diospyros*	*virginiana*	35	6.81
Carroll	Persimmon	*Diospyros*	*virginiana*	9	0.46
Carroll	Persimmon	*Diospyros*	*virginiana*	9	0.43
Carroll	Persimmon	*Diospyros*	*virginiana*	9	0.40
Carroll	Persimmon	*Diospyros*	*virginiana*	6	0.20
Carroll	Persimmon	*Diospyros*	*virginiana*	4	0.09
Carroll	Persimmon	*Diospyros*	*virginiana*	4	0.08
Carroll	Persimmon	*Diospyros*	*virginiana*	4	0.08
Carroll	Persimmon	*Diospyros*	*virginiana*	4	0.07
Carroll	Persimmon	*Diospyros*	*virginiana*	4	0.07
Carroll	Persimmon	*Diospyros*	*virginiana*	3	0.06
Carroll	Red Maple	*Acer*	*rubrum*	41	9.03
Carroll	Red Maple	*Acer*	*rubrum*	26	3.63
Carroll	Red Maple	*Acer*	*rubrum*	23	2.96
Carroll	Red Maple	*Acer*	*rubrum*	18	1.75
Carroll	Red Maple	*Acer*	*rubrum*	15	1.17
Carroll	Red Maple	*Acer*	*rubrum*	11	0.72
Carroll	Red Maple	*Acer*	*rubrum*	9	0.43
Carroll	Red Maple	*Acer*	*rubrum*	4	0.08
Carroll	Red Maple	*Acer*	*rubrum*	4	0.08

Table 2. (Continued)

Carroll	Red Maple	*Acer*	*rubrum*	4	0.08
Carroll	Red Maple	*Acer*	*rubrum*	4	0.08
Carroll	Red Maple	*Acer*	*rubrum*	4	0.08
Carroll	Red Mulberry	*Morus*	*rubra*	62	20.63
Carroll	Red Mulberry	*Morus*	*rubra*	38	7.92
Carroll	Red Mulberry	*Morus*	*rubra*	38	7.71
Carroll	Red Mulberry	*Morus*	*rubra*	26	3.74
Carroll	Red Mulberry	*Morus*	*rubra*	26	3.63
Carroll	Red Mulberry	*Morus*	*rubra*	23	2.87
Carroll	Red Oak	*Quercus*	*rubra*	24	3.19
Carroll	Red Oak	*Quercus*	*rubra*	20	2.19
Carroll	Red Oak	*Quercus*	*rubra*	18	1.80
Carroll	Red Oak	*Quercus*	*rubra*	18	1.73
Carroll	Red Oak	*Quercus*	*rubra*	14	1.12
Carroll	Red Oak	*Quercus*	*rubra*	14	1.12
Carroll	Red Oak	*Quercus*	*rubra*	7	0.24
Carroll	Red Oak	*Quercus*	*rubra*	6	0.20
Carroll	Red Oak	*Quercus*	*rubra*	6	0.20
Carroll	Red Oak	*Quercus*	*rubra*	6	0.20
Carroll	Red Oak	*Quercus*	*rubra*	3	0.06
Carroll	Silver Maple	*Acer*	*saccharinum*	48	12.60
Carroll	Silver Maple	*Acer*	*saccharinum*	41	9.08
Carroll	Silver Maple	*Acer*	*saccharinum*	24	3.19
Carroll	Silver Maple	*Acer*	*saccharinum*	24	3.19
Carroll	Silver Maple	*Acer*	*saccharinum*	10	0.50
Carroll	Sugar Maple	*Acer*	*saccharinum*	23	2.79
Carroll	Sugar Maple	*Acer*	*saccharinum*	17	1.52
Carroll	Sycamore	*Platanus*	*occidentalis*	70	26.75
Carroll	Sycamore	*Platanus*	*occidentalis*	51	14.30
Carroll	Sycamore	*Platanus*	*occidentalis*	46	11.62
Carroll	Sycamore	*Platanus*	*occidentalis*	45	10.95

Table 2. (Continued)

Carroll	Sycamore	*Platanus*	*occidentalis*	44	10.68
Carroll	Sycamore	*Platanus*	*occidentalis*	44	10.61
Carroll	Sycamore	*Platanus*	*occidentalis*	36	7.06
Carroll	Sycamore	*Platanus*	*occidentalis*	35	6.81
Carroll	Sycamore	*Platanus*	*occidentalis*	35	6.64
Carroll	Sycamore	*Platanus*	*occidentalis*	33	5.98
Carroll	Sycamore	*Platanus*	*occidentalis*	5	0.14
Carroll	Sycamore	*Platanus*	*occidentalis*	4	0.08
Carroll	Yellow Poplar	*Liriodendron*	*tulipifera*	3	0.06

VITA

Tommy Parker was born in Memphis, TN to John Etta and Charlie Edward Parker. In 1988, he completed high school in Memphis then attended Mississippi Valley State University (MVSU) on an athletic scholarship. After leaving MVSU in 1992, he returned to college attending The University of Memphis (UofM), where he earned a B.S. in Biology. He continued at UofM in graduate school and earned a M.S. in Ecology working under Dr. Michael Kennedy. His master's work was on the seasonal variation of food habits of coyotes in urban and suburban areas. After completing his M.S. degree he moved to Kansas City, Missouri. Prior to coming to University of Missouri for his doctorate, he worked as an urban ecologist/forester for the City of Kansas City Missouri. Since completed his Ph.D., Tommy has accepted a position with the USDA Forest Service as the Regional Endangered Species Biologist for the eastern region. He works out of the regional office in Milwaukee, WI.