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Habitat selection in four sympatric small mammal species and the effects of potential predators  
on *Peromyscus leucopus*.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science  
at Virginia Commonwealth University

By

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## Abstract

### HABITAT SELECTION IN FOUR SYMPATRIC SMALL MAMMAL SPECIES AND THE EFFECTS OF POTENTIAL PREDATORS ON *PEROMYSCUS LEUCOPUS*

Adam D. Chupp, B.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

Virginia Commonwealth University, 2005

Thesis Director: Dr. John F. Pagels, Professor, Department of Biology

I examined the effects of potential predators in relation to habitat selection in *Peromyscus leucopus*. I also examined habitat selection in three other sympatric species (*Blarina brevicauda*, *Blarina carolinensis*, *Sorex longirostris*). I utilized data from 49 sampling sites on National Park Service land; Petersburg National Battlefield Eastern Front Unit (15), Five-forks Unit (17), Appomattox Court House National Historical Park (15) and Booker T. Washington National Monument (12). Sites were categorized by location (park unit) and habitat type (i.e. bottom-land hardwood), and the microhabitat within each sampling site was characterized by four variables (% cover of grasses, herbs, shrubs, and volume of downed wood). Importance values of tree species within each sampling site were also measured.

*Peromyscus leucopus*, *B. brevicauda*, *B. carolinensis*, and *S. longirostris* were captured in all habitat types. Low capture rates for shrew species and high variability in the abundance of shrew species among all sampling sites were likely responsible for the lack of differences in

abundance among habitats ( $p > 0.05$ ). *Peromyscus leucopus* represented 76% of the captures among prey species and was the only species to demonstrate differences in relative abundance among habitat types. The relative abundance of *P. leucopus* was higher in bottom-land hardwood habitat when compared to pine forest plantation habitat (ANOVA,  $p < 0.05$ ). Although microhabitat components and importance values of tree species failed to explain this variation, my results suggest that differences in the relative abundance of *P. leucopus* among these habitat types may be explained by differences in understory structural diversity. Furthermore, the corresponding increase in the relative abundance of *Procyon lotor* (the most abundant predator during the study) in structurally heterogeneous habitat (bottom-land hardwood) suggests the importance of anti-predator behaviors within these habitat types. Ultimately, this may suggest that prey cannot escape the presence or calculate the abundance of predators and instead simply avoid dangerous habitats.

Although the relative abundance of the most abundant predator (*P. lotor*) and prey (*P. leucopus*) species were positively associated within certain habitat types, a negative association between predator and prey species abundance was evident within parks. In the Eastern Front unit the relative abundance of prey (*P. leucopus*, *S. longirostris*) was lower in comparison to the Five-forks unit while the abundance of *P. lotor* was higher (ANOVA,  $p < 0.05$ ). Although statistical tests indicated no difference in captures of other predator species among these parks, the trends in captures and night photographs suggest otherwise. Captures and night photographs indicated that the abundance of *P. lotor*, *Didelphis virginiana*, and *Urocyon cinereoargenteus* were higher in the Eastern Front unit when compared to the Five-forks unit. It appeared that the lethal effects of predators are evident at larger scales (within parks) despite the anti-predator behaviors of prey at smaller scales (within microhabitats). My results indicate that at larger

scales (within parks) the lethal effects (removal of prey) of abundant predators may overwhelm the non-lethal effects (anti-predator behaviors) exhibited by prey at smaller scales, especially in areas where structurally heterogeneous habitats are lacking.

## Introduction

Several recent studies indicated that there are relationships between the abundance and/or survival of small mammals and the presence of certain microhabitat characteristics (Bellows et al. 2001b, Bowman et al. 2000, Butts and McComb 2000, Carey and Johnson 1995, Kotler et al. 1991, Manning and Edge 2004). It has also been suggested that microhabitat partitioning is responsible for sympatry among small mammals (i.e. Price and Kramer 1984). The continued focus on the use of microhabitat by small mammals, including its effects on survival and the coexistence of closely related species, emphasizes the perceived importance of microhabitat selection in the biology of small mammals. Although microhabitat partitioning among closely related species (resulting in sympatry) may not explain larger spatial scale (i.e. macrohabitat) variation in small mammal assemblages (Jorgensen 2004), the survival of individuals (Manning and Edge 2004) and the dynamics of populations (Bowman et al. 2000, Bellows et al. 2001b) may be influenced by microhabitat conditions.

Much is known about rodent habitat selection and there is considerable literature that suggests predation risk may play a role in selection and use of microhabitats by rodents (Kotler and Brown 1988, Kotler et al. 1991, Holbrook and Schmitt 1988, Lima et al. 1985, Manning and Edge 2004, Morris and Davidson 2000, Roche 1999, Stokes and Slade 1994, Thorson et al. 1998). For example, rodents may avoid foraging in unsheltered microhabitats and forest edges where they are more likely to be detected by avian (Kotler et al. 1991) and other vertebrate predators (Morris and Davidson 2000). In addition, Roche (1999) suggests that deer mice

*Peromyscus maniculatus*) may restrict their movements to quieter routes by traveling on downed wood rather than on noisy leaf litter. In managed forests on the central Oregon Coast, Manning and Edge (2004) found that survival rates of deer mice (*P. maniculatus*) were highest when downed wood volume reached 2.0 m<sup>3</sup> per 0.01 hectare, however, they also found that creeping voles (*Microtus oregoni*) had the highest survival rates in home ranges with no downed wood. Based on these results, Manning and Edge (2004) suggested that rather than being habitat generalists, as previously suspected, the deer mouse and creeping vole are habitat specialists linked to specific amounts of particular habitat components within home ranges. The findings of Manning and Edge (2004) provide the most recent support for the idea that the distribution of rodent species within home ranges is a result of the availability and abundance of certain microhabitat components. Moreover, based on other studies (see Sullivan and Sullivan 1980) and on the frequent capture of ermine during their own study, Manning and Edge (2004) speculated that the effects of predation on the survival of small mammals may have contributed to the complexity of their survival response curves.

Predators influence prey populations by not only removing prey from the system (lethal effects) but by altering the behavior of prey individuals as well. Although the lethal effects of many predator-prey relationships are well understood, much less is known about how the presence of predators affects the behavior of prey individuals and the dynamics of prey populations (non-lethal effects) (Lima 1998). As a result of predator pressure, prey demonstrate anti-predator behaviors which have been associated with the use of sheltered microhabitats (i.e. under vegetative cover) (i.e. Kotler et al. 1991). Prey may implement anti-predator behaviors in response to direct or indirect cues of predator pressure. Prey may smell or hear a predator (direct cue) or they may simply avoid dangerous situations (indirect cue) such as exposed microhabitats

or brightly moonlit nights (Orrock et al. 2004). Among small mammal species anti-predator behaviors may promote coexistence (Kotler and Brown 1988) or cause competitive exclusion (Stokes and Slade 1994). Although anti-predator behaviors may explain variation in the distribution of prey among microhabitats, it is poorly understood how interactions between predators and prey may translate into larger scale patterns of predator-mediated habitat selection (Lima 1998). Furthermore, it is not known how the non-lethal effects of predators (anti-predator behavior) interact with the lethal effects (prey removal) of predation. However, large scale increases in predator species diversity and abundance will likely be detrimental to prey species populations, especially across areas with poor microhabitat structure and diversity. This could have cascading effects on community structure. For example, variation in abundant prey species, such as *Peromyscus spp.*, may result in variable predator pressure on other species such as migratory birds (McShea 2000). Understanding predator-prey interactions at multiple scales may give rise to emergent ecological patterns in the survival and/or abundance of organisms whose distributions span physiographic ranges.

The genus *Peromyscus* (Order: Rodentia) is one of the most intensively studied genera of North American mammals (Kirkland and Layne 1989) and observations on the ecology of *Peromyscus spp.* may have widespread applicability. At least one or more species of *Peromyscus* can be found in almost any region of North America (Kirkland and Layne 1989) and most species of *Peromyscus* are abundant and relatively easy to capture. *Peromyscus leucopus* (Rafinesque 1818) occurs along the eastern coast of Mexico and in all of the eastern United States except Florida (Osgood 1909). In Virginia, *Peromyscus leucopus* occurs in all physiographic regions from the Coastal Plain to the Ridge and Valley and Cumberland Plateau provinces (Webster et al. 1985). *Peromyscus leucopus* is an important prey species for many

predators (Knable 1970, Phillips and Hubert 1980, Swengel and Swengel 1992) as well as an important consumer of seeds, insects, and bird eggs (Whittaker 1966, McShea 2000). Although *Peromyscus* species have many generalized biological characteristics (i.e. dietary, reproductive and metabolic patterns) and the ability to occupy a wide range of macrohabitats (MacMillen and Garland 1989), certain microhabitat components may be important to species of this genus (i.e. Manning and Edge 2004, Roche 1999). As was mentioned earlier, *Peromyscus* species may also exhibit antipredator behaviors that link them to certain microhabitats (Orrock et al. 2004, Roche 1999).

Data for this study were collected as part of a much larger mammal survey conducted for the National Park Service Inventory and Monitoring Program. The goal of that survey was to establish a baseline inventory of non-volant mammalian species that exist within four National Park Units in Virginia. The four locations represent a geographic transect that covers a latitudinal distance of 190 km (115 mi) from the Coastal Plain to the upper Piedmont. Thirty-nine species are thought to occur within these areas combined and 15 of those are small mammal species (Handley and Patton 1947, Linzey 1998, Webster et al. 1985). Although *P. leucopus* was expected to be one of the more abundant species during this survey, other generalist species including the northern short-tailed shrew (*Blarina brevicauda*), southern short-tailed shrew (*Blarina carolinensis*), and southeastern shrew (*Sorex longirostris*) are also sometimes abundant (Handley and Patton 1947, Linzey 1998, Webster et al, 1985). Potential predators of small mammal species include, but are not limited to, omnivorous opportunistic species such as the common raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*) and striped skunk (*Mephitis mephitis*). These species are common in Virginia and are relatively easy to capture (Handley and Patton 1947, Linzey 1998, Webster et al, 1985).

My study investigates possible ecological interactions among microhabitat features, the abundance of *P. leucopus*, and potential predators. The objectives were to determine: 1) if the abundance of *P. leucopus* and other sympatric species is related to measures of microhabitat components across all sites; 2) whether variation in the abundance of *P. leucopus* and other sympatric species is evident among habitat types and parks, and if so, what habitat characteristics best describe that variation; 3) whether geographic variation in predator abundance mediates any relationships among *P. leucopus* abundance, microhabitat components, habitat types and parks that span roughly 190 km (115mi).

## Materials and Methods

### *Study areas*

The Eastern Front Unit of Petersburg National Battlefield (EF) is primarily located within the city limits of Petersburg, VA, and is bounded on the east by Fort Lee, a U.S. military installation. The unit lies within the Coastal Plain physiographic region immediately east of the Fall Line (the juncture of the Coastal Plain and Piedmont physiographic regions). The average elevation at EF is approximately 30.5 m (100 ft). The Eastern Front covers an area of 585 ha (1,445 acre) that includes fields of fescue grasses (*Festuca spp*) and a mosaic of forested successional habitat types ranging from pine forests to hardwood forests. A one-way tour road, numerous recreational trails, and a highway bisect portions of the unit. Earthen remnants of Civil War activity as well as remnants from more recent training sites for World War I are evident in many areas. Roughly 90% of the unit is forested and contains a relatively even mix of deciduous and coniferous species. The western edge of the unit contains the only fields, and those are maintained (mowed) to preserve the cultural landscape. In addition, there are several creeks that meander through the park. Areas surrounding EF are somewhat rural only on the eastern boundary where it abuts Fort Lee. Otherwise, as a result of the park's popularity (~150,000 visitors/yr.) and surrounding commercial and residential development, mammal species within the park may be strongly influenced by human activities.

The Five-forks Unit of Petersburg National Battlefield (FF) is located in Dinwiddie County 32 km (20 mi) southwest of the EF unit. Five-forks is located in the eastern portion of

the Piedmont physiographic region just west of the Fall Line and has an average elevation of roughly 69 m (225 ft). The unit covers 452 ha (1,118 acre) and similar to EF it includes fields of fescue grasses and a mosaic of successional habitat types ranging from pine forests to hardwood forests. Nearly 90% of FF is wooded with young coniferous stands dominating the forested landscape. Hatchers Run, located in the north-eastern section of the unit, is the source of a small lake, associated wetlands, and a beaver pond. Agricultural and otherwise maintained (mowed) fields comprise only a small portion of the park. However, natural old field habitat does not exist within the unit. Five-forks, unlike EF, is surrounded by a rural setting that includes agricultural activity, forests of various ages, and scattered residences that are characteristic of much of present day south-central Virginia.

Appomattox Court House National Historical Park (APCO) is located in Appomattox County, Virginia, roughly 110 km (65 mi) west of the Fall Line. The park is located in the Piedmont physiographic region of south-central Virginia, 148 km (92 mi) west of Richmond and 29 km (18 mi) east of Lynchburg. The average elevation at APCO is approximately 229 m (750 ft), and covers an area of 718 ha (1,774 acre) that includes a mosaic of successional habitat types ranging from fescue fields to hardwood forests. The park has nearly 469 ha (1,160 acres) of wooded land with 30% of the woodlands being deciduous and the remainder coniferous. The site also contains 13 km (8 mi) of bottom-land hardwood (BLHWD) habitat along the Appomattox River and its tributaries. Within APCO there are 243 ha (600 acres) of open fields, most of which are maintained (mowed) once or twice a year. Although most of these fields consist of fescue grass (*Festuca spp.*), 26 ha (64 acres) are being chemically treated and planted with the intention of bringing back warm season (native) grasses. In addition to natural colonization by broomsedge (*Andropogon virginicus*), the mixed grass seed that is being planted

includes Indian grass (*Sorghastrum nutans*), little blue stem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), purple top (*Tridans flavus*), and gamma grass (*Tripsacum dactyloides*).

Booker T. Washington National Monument (BOWA) is located in the upper Piedmont physiographic region, 35 km (22 mi) southeast of Roanoke, in Franklin County, Virginia. The park lies within view of the Blue Ridge Mountains. The average elevation at BOWA is approximately 274 m (900 ft). The park covers an area of 91 ha (224 acres) that includes a mosaic of habitat types including fescue (*Festuca spp.*) fields and successional habitat types that range from pine forests to hardwood forests. Forests comprise most of the park except for roughly 26 hectares (65 acres) of pasture and hay fields. Non-pasture fields are maintained (mowed) once or twice a year. Two small streams run through the park: Jack O' Lantern Branch that runs along the eastern edge, and Gills Creek which runs along the western edge of the park.

### ***Site selection***

To select sampling sites within each of the four areas (park units), I first determined the major habitat types within each area. With the initial help of natural resource managers and aerial photographs I determined the available habitat types and scouted possible sampling sites within each habitat type. In all, six major habitat types were identified at FF, including field forest edge (FFE), pine forest plantation (PFP), mixed pine-hardwood (MPH), hardwood (HWD), bottom-land hardwood (BLHWD) and wetland (WD). Not all habitat types were present at each park. The WD habitat type was present only at FF, and BOWA lacked the PFP habitat type. Once all habitats within each area were identified, three sampling sites per habitat type were set up. Sample locations were randomly selected using a grid and random numbers

system, but in most cases required re-location in the field to ensure that the samples were located in an area representative of the selected habitat type. Due to limited habitat, only two replicates of BLHWD were set up at FF. Boundaries of all sites were at least 300 m apart and at least 30 m from the edge of the given habitat. Therefore, buffer zones were created between and among habitat types being sampled. In this way, the total area of the park was more effectively sampled. The following is a brief description of each habitat type sampled.

Field-forest edge (FFE) - In nearly all situations field maintenance or mowing created very abrupt or narrow contact areas along the field and forest edges. In most areas the edge habitat type was only 1-5 m wide. Vegetation along field-forest edges was typically a mix of field and forest vegetation and much more heterogeneous than in the field or forest. This habitat type often contained both coniferous and deciduous species in the overstory. The understory was comprised of saplings of overstory species. However, the understory was often dominated by shade-intolerant pioneer species such as eastern red cedar (*Juniperus virginiana*). Herbs, grasses, (i.e. non-native fescue), and shrubs were more common here than in other habitats. Native broomsedge (*Andropogon virginicus*) and bramble (*Rubus spp.*) were abundant at one site within APCO.

Pine forest plantation (PFP) - Among EF and FF sites the overstory of pine plantations was dominated by stands of loblolly pine (*Pinus taeda*) estimated to be 20 to 25 years in age (based on clear cutting records). Among APCO sites loblolly and Virginia pine (*Pinus virginiana*) collectively dominated the overstory of this habitat. When young, these stands can be very thick, but the stands we sampled had begun a natural thinning process and at most sites the understory

was beginning to open. Pine forest plantations were also characterized by a thick layer of pine needle litter. The understory was dominated by saplings of deciduous tree species and nearly all understory trees in this habitat type were small (dbh [diameter at breast height] < 10cm). In all parks, grasses, herbs and shrubs were relatively uncommon.

Mixed pine hardwood (MPH) - This habitat type included both deciduous and coniferous species in the overstory. Mixed pine hardwood forest is considered to be an intermediate successional stage between pine and hardwood forest. Loblolly pine (*Pinus taeda*) was the dominant coniferous species among EF and FF sites. Loblolly and Virginia pine (*Pinus virginiana*) were both present at APCO and Virginia pine was the dominant conifer at BOWA. Although deciduous trees were more abundant than conifers in the overstory, the DBH of the conifers was usually larger (i.e. there were fewer coniferous trees than deciduous trees but the conifers were larger). Understory tree species were mostly saplings of overstory species. However, as expected in this successional stage, deciduous saplings were more common than coniferous saplings. At BOWA club moss (*Lycopodium sp.*) was extremely common ground cover in this habitat type.

Hardwood (HWD) - This habitat type was characterized by various deciduous species in the overstory and understory. Overstory species common to all parks included red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), blackgum (*Nyssa sylvatica*), white oak (*Quercus alba*), red oak (*Quercus rubra*), and hickories (*Carya sp.*). Sweetgum was only present at EF and FF. Subcanopy species included sassafras (*Sassafras albidum*), ironwood (*Carpinus caroliniana*) American holly (*Illex opaca*), dogwood (*Cornus florida*) and eastern red cedar (*Juniperus*

*virginiana*). Understory tree species were mostly saplings of overstory species. Ground cover consisted primarily of deciduous leaf litter. Herbs, grasses, and shrubs were relatively sparse in the HWD habitat types.

Bottomland hardwood (BLHWD) - The BLHWD habitat type was largely restricted to floodplain situations near streams or rivers (APCO). At all parks overstory trees were primarily deciduous species. Overstory species indicative of this habitat type were American sycamore (*Platanus occidentalis*), ash (*Fraxinus spp*) and birch (*Betula spp*). The understory was comprised of saplings of overstory species. Alder (*Alnus spp.*), common greenbrier (*Smilax rotundifolia*), and the fragrant shrub spicebush (*Lindera benzoin*) were frequently observed in the understory. Paw paw (*Asimina triloba*) was an abundant component at sites within APCO and BOWA. Among all parks, a variety of grasses and herbs were observed in much greater abundance here than in any other habitat type. Switch cane grass (*Arundinaria gigantean*) was abundant at one site within EF. Ferns were also common in this habitat type at all parks. With locations so close to water sources, BLHWD sampling sites had very moist substrates. Washouts from flooding were not unusual at most of our BLHWD sampling sites.

Wetland (WD) – This habitat occurred only at FF. Two of these sampling sites were located along the fringe of Hatchers Run and one site was located south of Hatchers Run adjacent to a beaver pond. In each case, the substrate was very moist and standing water was always at least 20% of the ground cover. Birch (*Betula spp*) and red maple (*Acer rubrum*) were the most abundant overstory tree species. The understory was dominated by shrub species including

spicebush, common greenbrier, and alder. Abundance of grass and herbaceous growth was similar to that of BLHWD.

Japanese stiltgrass (*Arundinaria gigantea*) was an obvious herbaceous component at a couple of our sampling sites at EF. However, Japanese stiltgrass was evident in many areas of EF and stands of the grass either encroached into our sampling sites or were evident nearby. Sites where the grass was observed included one PFP site, two FFE sites, two MPH sites, and all three BLHWD sampling sites. Japanese stiltgrass was not recorded in the HWD sites.

### ***Survey and collection methodology***

The circular-plot sampling scheme used at most sampling sites was modified from other studies. The scheme has been successfully used in studies on mammal population dynamics (Orrock et al. 2000), mammal communities (Bellows et al. 2001b, McShea et al. 2003), documenting presence of endangered species (Orrock et al. 2000), and determining new records of occurrence (Bellows et al. 1999). Each sampling site consisted of a 30 m diameter circle with markers in the center and 15 m from the center in each cardinal direction (Figure 1). In this way, the site was divided into four equal quadrants. Three 7.6 x 8.9 x 22.9 cm (3" x 3.5" x 9") Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida) were placed at likely capture spots within a 2 m radius extending toward the center from each cardinal direction. Two 40.6 x 12.7 x 12.7 cm (16" x 5" x 5") Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were placed in opposite quadrants from each other, and one 81.3 x 25.4 x 30.5 cm (32" x 10" x 12") Tomahawk live trap was placed at or near the center of the site. Sherman live traps were baited with an oatmeal-peanut butter mixture that was wrapped in wax paper and

hung from the back door of the trap. Small dabs of peanut butter were also placed on the open front door. Small Tomahawk traps were baited with apples covered in peanut butter. The large Tomahawk live traps were baited with apples and sardines. Live traps typically underestimate the abundance of shrews, whereas pitfall traps are very efficient in capturing shrews, especially the smallest species (Mitchell et al. 1993, Kirkland and Sheppard 1994). In order to more effectively sample smaller mammals such as shrews, two pitfall traps were placed in each of the sites' four quadrants. Natural drift fences (i.e., fallen logs and stumps) and 533 ml (16 oz) beverage cups filled with approximately five centimeters of water were used for all initial pitfall traps. Plastic mesh lids (15 cm x 15 cm) elevated by nails were used to shield the pitfall traps from falling leaves and other debris. Pitfall traps larger than those that I used are more effective for many small mammals (Mitchell et al. 1993). However, in initial discussions with NPS personnel I was encouraged to keep soil disturbance to a minimum at historical sites. Because of poor capture success of shrews, two larger pitfall traps were added to each site for sampling in spring 2004. The larger pitfall traps were made from 2L plastic soda bottles with the tops cut off (after Handley and Varn 1994). Two or three drift fences made of steel mesh 0.6 cm (1/4") hardware cloth (two drift fences if a natural barrier was present) were used for these larger pitfall traps. All traps were placed at the most likely capture spots (i.e., near coarse woody debris) whenever possible. The mesh was lowered over the pitfall traps to close them between sampling sessions.

Transects were used in place of circular plots to improve sampling efficiency at a few sites. Transects were used at all FFE and at three BLHWD sampling sites at BOWA because the habitat at these particular sites was narrow and use of the circular arrangement would have overlapped other habitat types. The sampling effort, as based on trap types and trap numbers,

was equivalent to those of the circular plots, but traps were arranged in a linear fashion (Figure 2) at most likely capture spots, generally within 2-4 m of the transect line.

Mammals smaller or equal to the size of a hispid cotton rat (*Sigmodon hispidus*) were tagged with Monel ear tags (National Band and Tag Co., Newport, Kentucky), weighed to the nearest gram, and examined for reproductive status and life history stage. Mammals larger or equal to the size of an eastern gray squirrel (*Sciurus carolinensis*) were marked with non-toxic spray paint and examined for distinguishable features and approximate age. The unique, but temporary paint marking allowed us to identify recaptures within a single trapping session only. All animals were released at the site of capture. Deceased animals, including pitfall trap captures, were stored in 70% propanol, placed on ice in the field, and later frozen to serve as museum voucher specimens and as resources for additional studies. For all captures, I recorded the site of capture (i.e. HWD 1), trap type, and trap location. In circular plots, the quadrant (i.e. NW) was recorded for pitfall and small Tomahawk captures and for Sherman trap captures the cardinal direction was recorded.

Night-camera photography was used as an additional method for documenting medium to large nocturnal species and was implemented with TrailMaster's Active Infrared Trail Monitor (Model # TM1550) and Camera Kit (Model # TM35-1) (TrailMaster Infrared Trail Monitors, Lenexa, Kansas). This method is appropriate for use in mammal inventories where larger mammals need to be surveyed (Silveira et al. 2003). Three cameras were used simultaneously within different portions of the park units. During each seasonal trapping session, cameras were active for the same number of nights as the trapping sites. Cameras were placed in areas most likely to be frequented by medium to large nocturnal mammals (i.e. game trails and small dirt roads or walking paths) and where vegetation and topography would not trigger the trail

monitors. Camera traps were not located near sampling sites, and camera location, most often in wooded areas, was varied among sampling sessions. Cameras were active from approximately dusk to dawn and were baited with sardines, peanut butter, apples and chicken.

Trapping sessions were partitioned into seasons and occurred between June 2003 and August 2004. All sampling sites within a park unit were sampled at the same time, and all parks were sampled during each of the four calendar seasons. Trapping effort was greatest during the summer due to time constraints in fall, winter, and spring. Trapping effort per trap type within each park and habitat type is given in Tables 1 and 2. Sometimes traps were sprung and had been moved about, likely the result of raccoon activity, and on these occasions a trap night was subtracted from the effort (modified from Nelson and Clark 1973).

### ***Site analysis***

Within trapping sites, the diameter at breast height (dbh ~ 1m) was recorded for all trees, defined as woody plants with a dbh > 5 cm. For transect sites, any tree less than 5 m from the transect line was considered to be within the site. All trees with a dbh > 5 cm were measured and identified to genus, and most trees were identified to species. Ground cover was determined using the line-transect method of Canfield (1941). For circular sites, two 40 m transects were established that divided the sampling site into four equal quarters, bisecting in the center. For transect plots, the same 60 m transect line established for mammal sampling was used. Using the line-transect method, we recorded observations in the following categories: herbaceous, grass, shrub, and downed wood. Downed wood was considered to be any portion of a woody stem or trunk that was greater than 1 m in length. The diameter was recorded for any intercepted piece of downed wood that had a dbh > 4 cm.

### ***Data treatment and statistical analyses***

Abundance was measured by the number of unique (excludes recaptures) individuals captured ( $M_{t+1}$ ; Slade and Blair 2000). Relative abundance was calculated as the number of individuals captured ( $M_{t+1}$ ) divided by the number of trap nights, for traps in which a species could be captured. For example, trap nights for *P. leucopus* were calculated using the number of Sherman traps because nearly all individuals of this species were captured by this trap type. Relative abundance of small mammals and predators was expressed per 100 trap nights. Differences in relative abundance of prey and predator species among parks and habitat types were detected using one-way ANOVA (Zar 1999). Significant differences ( $p < 0.05$ ) were detected using Tukey HSD *post hoc* comparisons. Prior to analysis, relative abundance data were arc-sine transformed to more approximate normality and examined for homogeneity among variances (Zar 1999). Arc-sine transformations, tests of variance homogeneity, one-way ANOVA, and *post hoc* comparisons were completed using SPSS 12.0 for Windows software.

Predator species (i.e. the Virginia opossum [*Didelphis virginiana*] and the common raccoon [*Procyon lotor*]), were marked to distinguish them in a given trapping session only so counts may not represent individuals. Therefore, abundance of the larger predator species was determined by the number of total captures, including recaptures, at each site. This metric was then used to calculate relative abundance for these species. Abundance of larger predator species within each park was also determined by the number of night photographs. However, since camera traps were not set up near sampling sites or within definable habitats (located on dirt roads or trails) they were used to estimate abundance within the park unit only. Furthermore,

since individuals could not be discerned among night-camera photographs, they could only be used as a vague measure of abundance within each park.

Abundance estimated using  $M_{t+1}$  is an index of population size because the number of individuals captured is a function of population size as well as the likelihood that an individual will be captured (Slade and Blair 2000, Pollock et al. 2002).  $M_{t+1}$  was used because it performs as well as estimators that incorporate capture probability (i.e., the Lincoln-Petersen estimator) when captures are low (Slade and Blair 2000), as was the case in my study. My estimates of relative abundance assume that capture probability does not differ among habitat types, trapping sessions, or types of traps where animals were captured. Capture probability for a single species may vary depending upon these factors (Pollock et al. 2002), but estimates of habitat-, season-, and trap-specific capture probabilities were not performed due to the limited data (Pollock et al. 2002).

Percent cover of herbs, grasses, and shrubs within each sampling site was calculated from line intercept data. The volume of downed wood was also calculated for each sampling site (Warren and Olsen 1964, Van Wagner 1968). Volume was calculated from the sum of the dbh of all intercepted pieces of woody debris for a sampling site. Volume of downed wood in each sampling site was expressed as  $\text{m}^3/\text{hectare}$ . Density and basal area were calculated for tree species found within each sampling site. Relative basal area and relative density were then used to calculate the importance values for each species (Barbour et al. 1999).

Multiple regression analysis (Zar 1999) was used to relate variation in microhabitat components (herb, grass, shrub, and downed wood) with the variation in relative abundance of *P. leucopus*. Variation in microhabitat components was also related to variation in the relative abundance of other generalist species, which are found to occur in all habitat types, and are

sympatric to *P. leucopus* (likely candidates include *B. brevicauda* and *B. carolinensis*). For each dependent variable (relative abundance) we analyzed data across all sampling sites, across sampling sites within each park, and across sampling sites within each habitat type.

Subsequently, all comparisons using multiple regression analysis were made with the addition of predator captures as a microhabitat (independent) variable. Prior to regression analyses, all independent variables were examined for linear responses with the dependent variable (i.e. curve estimation). Multicollinearity among independent variables was also tested where strong relationships between independent and dependent variables were observed. Homogeneity of variances for each dependent variable was tested among all sampling sites. All multiple regression analyses, curve estimations, and tests of homogeneity and multicollinearity were completed using SPSS Version 12.0 for Windows software. Results were deemed statistically significant if  $P \leq 0.05$ .

Principal components analysis (PCA, McCune and Grace 2002) was used to ordinate all sampling sites based on microhabitat. The distribution of microhabitat variables including percent cover of herb, grass, shrub, volume of downed wood, and abundance of potential predators among all sites was used as the primary matrix. This primary matrix was then overlaid with secondary matrices. The relative abundance of *P. leucopus* at each site was used as a secondary matrix. Relative abundance of generalist species such as *B. brevicauda* and *B. carolinensis*, which were captured in all habitat types, were also used as secondary matrices. Within park units and habitat types, only the strongest relationships between relative abundance and microhabitat (as determined by the multiple regression analyses) were ordinated. All sampling sites were also ordinated by the importance values of each tree species that occurred within each sampling site. This primary matrix was then overlaid with secondary matrices of

relative abundance of *P. leucopus* and *Blarina spp* at all sites. Percent of variance explained by axes, as well as Pearson correlation coefficients were used to determine the significance of each comparison. The variance/covariance (centered) cross-products matrix was used for all principal components analyses. Principal components analyses were performed using PC-Ord Version 4 for Windows software.

## Results

### *Mammal trapping*

A total of 847 individual (excluding recaptures) mammals representing 19 species was captured over 28,157 trap nights at the four park units. Fifteen species were small prey species and the remaining five were larger predator species. Predators were marked to distinguish them within a given trapping session only and due to probable recaptures in later trapping sessions the number of individuals is likely overestimated. Due to the sampling design, the number of trap nights among parks and habitat types was similar. The wetland habitat type occurred only in FF thereby increasing trap nights within FF. Conversely, WD habitat was represented by only three sampling sites and had the lowest number of trap nights among habitat types (Table 1, Table 2).

Of the small mammal species, 696 individuals were captured in the four park units. *Peromyscus leucopus* (432 individuals) was the most abundant mammal species captured all four park units and within each of the habitat types (Tables 1, Table 2). *Blarina brevicauda* and *B. carolinensis* followed *P. leucopus* in abundance and the three species represented 78% of all small mammal species captured. Among prey species, *P. leucopus*, *B. brevicauda*, *B. carolinensis*, and *S. longirostris* were captured in all habitat types (Table 1, Table 2). Although *S. longirostris* was captured in all habitat types, this species was excluded from multiple regression and principal components analyses due to low capture rates.

*Peromyscus leucopus* had the highest relative abundance among small mammal species within each park unit and habitat type. In some cases, the relative abundance of *P. leucopus*, *B.*

*brevicauda*, and *S. longirostris* differed among parks. The relative abundance of *P. leucopus* was lower in EF than in all other parks (ANOVA,  $p < 0.01$ ) (Table 1). The relative abundance of *B. brevicauda* was higher in BOWA than APCO (ANOVA,  $p < 0.05$ ) and the relative abundance of *S. longirostris* was higher in APCO when compared to EF (ANOVA,  $p < 0.05$ ). Among habitat types, *P. leucopus* was the only prey species to demonstrate a difference in relative abundance. The relative abundance of *P. leucopus* was higher in BLHWD when compared to PFP (ANOVA,  $p < 0.05$ ) (Table 2). Among parks, and habitat types *S. longirostris* and *B. carolinensis* were the only species to have unequal variances respectively (Levene's statistic,  $p < 0.05$ ).

Predator species (149 individuals) represented 18% of all mammal species captured. However, large Tomahawk traps, which captured most predators, represented only 4% of the total effort in trap nights. Five juvenile individuals were captured in small Tomahawk traps, and two juvenile *D. virginiana* and a long-tailed weasel (*Mustela frenata*) were captured in Sherman traps. *Procyon lotor* and *D. virginiana* were the two most abundant predator species captured, comprising 95% of predator individuals. *Procyon lotor* was most abundant at all parks except FF where *D. virginiana* was most abundant. Among parks, the number of night photographs reveal the same pattern for these species (Table 3). In some cases, night photographs suggest a greater abundance and diversity of predator species that trapping did not document such as the gray fox (*Urocyon cinereoargenteus*) at EF and the coyote (*Canis latrans*) and bobcat (*Felis rufus*) at FF. However, the number of animals in these photographs could not be quantified.

The relative abundance of *P. lotor* was higher in EF when compared to FF (ANOVA,  $p < 0.01$ ) (Table 1). However, among parks and habitat types, no other significant differences in relative abundance were observed for any of the predator species (Table 1, Table 2). *Procyon*

*lotor* was the only predator species to have unequal variances in relative abundance among parks. (Levene's statistic,  $p < 0.05$ ). Conversely, among habitat types, all predator species except *P. lotor* had unequal variances in relative abundance (Levene's statistic,  $p < 0.05$ ).

### *Habitat and Relative Abundance*

Principal components analysis of tree species importance values revealed that 51% of the variation in tree species importance values among all sites was explained by the first two axes (axis 1 = 34%, axis 2 = 17%). Failure to explain variation in tree species importance values among the sites resulted in poor grouping (Figure 4). Importance values of loblolly pine showed the highest correlation with axis 1 ( $r = 0.99$ ), Virginia pine with axis 2 ( $r = -0.84$ ) and red maple with axis 3 ( $r = 0.69$ ). Among all sampling sites overlay of secondary matrices revealed low correlation to all axes. Relative abundances of *P. leucopus* and *Blarina spp.* were most correlated to axis 3 ( $r = 0.35$ ,  $r = 0.27$ ) (Figure 4). Variation in the relative abundance of these species was not explained by variation in tree species importance values among all sites.

Percent cover of herbs, grasses, and shrubs, as well as the volume of downed wood for habitat types within each park is shown in Table 4. Principal components analysis of the microhabitat data among all sites revealed that 80% of the variation in microhabitat components was explained by the first two axes (axis 1=55%, axis 2 = 25%). Percent cover of grasses and herbs was highly correlated with axis 1 ( $r = -0.90$ ,  $r = -0.83$ ). Volume of downed wood and percent cover of shrubs showed the highest correlation with axes 2 and 3, respectively ( $r = 0.83$ ,  $r = -0.78$ ). Overlay of secondary matrices describing relative abundance of *P. leucopus* and *Blarina spp.* showed no correlation to axes 1 and 2 of the primary matrix (Figure 5). Variation in

the relative abundance of these species was not explained by variation in microhabitat components among all sites.

Results of regression analyses comparing *P. leucopus* relative abundance to microhabitat variables, including the relative abundance of predators, revealed that comparisons among all data, within park data, and within habitat data had low correlation coefficients. In all cases curve estimation revealed the linear model as the best predictor. The strongest relationships occurred among APCO ( $p = 0.03$ ,  $R^2 = 0.71$ ) and BLHWD ( $p = 0.08$ ,  $R^2 = 0.75$ ) sampling sites when predator data was included (Table 5). Principal components analysis revealed that among APCO sites, axis 1 and 2 explained 74% and 20% of the variation in the microhabitat variables. Overlay of the *P. leucopus* relative abundance data revealed the greatest correlation to axis 1 ( $r = 0.39$ ) (Figure 6) Predator abundance alone was not significantly correlated to *P. leucopus* relative abundance on a microhabitat scale ( $p > 0.05$ ).

Regression analyses comparing the relative abundance of *B. brevicauda* and *B. carolinensis* to microhabitat variables, including the relative abundance of predators, were also found to be insignificant among all data and within park data. The only significant relationship was found among FFE sites. In all cases, curve estimation revealed the linear model as the best predictor. The strongest relationships occurred among FFE ( $p = 0.00$ ,  $R^2 = 0.92$ ) and APCO ( $p = 0.10$ ,  $R^2 = 0.59$ ) sampling sites when predator data was included (Table 5). Principal components analysis showed that among FFE sites, axis 1 and 2 explained 52% and 22% of the variation in microhabitat variables. However, overlay of *Blarina spp.* relative abundance revealed the greatest correlation to axis 3 ( $r = -0.81$ ) (Figure 7). Predator abundance alone demonstrated no significant correlation to *Blarina spp.* relative abundance on a microhabitat scale ( $p > 0.05$ ).

## Discussion

In a review of small mammal use of microhabitat, Jorgensen (2004) observed that microhabitat partitioning among small mammals does not explain variation in small mammal assemblages at larger spatial scales, that is, partitioning of microhabitat may enable species to coexist but it does not explain the distribution of species across macrohabitats. He emphasized concern for studies that broadly conclude rodent abundance and/or density is determined by the availability of preferred microhabitat and observed that there have been inconsistencies in the use of the term microhabitat that may have led to false beliefs regarding the amount of data that support such claims. For example, Jorgensen (2004) identified Rosenweig and Winakur (1969) as a commonly cited microhabitat study, but found that the smallest area they sampled (589 m<sup>2</sup>) was an inappropriately large scale at which to measure microhabitat. I used a sampling scheme that included suitable scales at which to measure microhabitat as well as other larger scales of measurement. My results suggest that although microhabitat partitioning may enable species to coexist, adaptive mechanisms such as the ability to use a variety of resources as well as predator-prey interactions may explain variation of small mammal assemblages at larger scales (Jorgensen 2004).

Many studies on microhabitat use reveal that certain microhabitat components may provide particular functions and are therefore attractive to small mammal species (Bowman et al. 2000, Barry and Francq 1980, Graves et al. 1988, Loeb 1999, Menzel et al. 1999, Roche 1999, Stokes and Slade 1994). In southeastern pine forests, Loeb (1999) demonstrated that increased

abundance of *Peromyscus gossypinus* was related to increases in coarse woody debris. In managed forests on the central Oregon coast, Manning and Edge (2004) revealed that survival of *Peromyscus maniculatus* and *Microtus oregoni* was dependent on specific volumes of downed wood. Preferences for certain microhabitat components exist even among generalist species (Barry and Francq 1980, Graves et al. 1988, and Menzel et al. 1999). For example, Barry and Francq (1980) found that the distribution of *P. leucopus* in New Hampshire woodlots was related to varying amounts of rocks and logs. In the piedmont physiographic province in Georgia, Menzel et al. (1999) suggested that the distribution of *P. leucopus* was influenced by the distribution of areas with a thick and diverse shrub layer. While I agree that preferences for certain microhabitat components may exist among many small mammals, microhabitat characteristics that I measured (grass, herb, shrub, downed wood) were not correlated with the relative abundance of *P. leucopus* or *Blarina spp.* (Table 5). These results provide further evidence of the habitat-generalist behavior of these species (Bellows et al. 2001a, 2001b, Clark et al. 1987, George et al. 1986, Pagels et al. 1992, Seamon and Adler 1996). The lack of significant correlations between microhabitat characteristics and the abundance of *P. leucopus* is consistent with other studies (Bellows et al. 2001b, Dueser and Shugart 1978, Yahner 1986). Although microhabitat components such as downed wood, rocks, shrubs, herbs and other vegetative structures may provide useful functions, I agree with Bellows et al. (2001a) that generalist species such as *P. leucopus* are capable of using a much larger variety of resources to meet their biological needs. It is difficult to link abundance and or survival of small mammals to specific microhabitat components, especially among generalist species. Heterogeneous habitat structure may be more important to these species than any one set of microhabitat components.

Low capture numbers prevented us from using more species in the analyses (i.e. *S. longirostris*). Low capture numbers for all species (excluding *P. leucopus*) was responsible for the large standard errors observed while estimating mean abundance for these species (Zar 1999). Furthermore, estimates of detection probability were also compromised because of low capture numbers. In studies that cover relatively large spatial scales such as this, detectability may be an important component of estimating abundance (Pollock et al. 2002). Although differences in capture rates were observed among species and sampling sites, which may be due to differences in detectability, total capture rates for all small mammal species were low (mean rate of 2.8 individuals per 100 trap nights). At Fort A. P. Hill in Caroline County, Virginia, Bellows et al. (2001a) captured a mean of 4.1 small mammals per 100 trap nights using Museum Special snap traps and pitfall traps. In the Appalachian forest of northwestern New Brunswick, Bowman et al. (2000) captured eight species of small mammals at the mean rate of 19.8 per 100 trap nights. The reason for differences in abundance that I recorded and those in other studies were most likely not related to trapping effort or the type of traps used. Jorgensen's (2004) review of 70 microhabitat studies found that > 50% of studies used  $\leq 5,000$  trap nights of effort. I utilized both Sherman live traps and pitfall traps because live traps are effective for catching small rodents and large shrews such as *Blarina spp.*, but not as effective as pitfalls for catching small shrews (Mitchell et al. 1993, Kirkland and Sheppard 1994). Although differences in detectability may have caused differences in capture rates among species and sampling sites, it is likely that other environmental factors were responsible for the low numbers of small mammals observed in my study.

The physiological stress of extreme weather conditions may have contributed to the low numbers of small mammals during my study. The year 2002, the year prior to my first sampling

year, was the last in a three year drought in Virginia. Based on Richmond records, which reflect the same weather patterns, the first sampling year (2003) was the second wettest on record. Precipitation in 2003 was 50 cm above a 109 yr average and was the largest recorded departure from the average (NOAA 2004). Shrews especially are impacted by humidity and precipitation extremes, but without long-term data for the parks, it is not possible to determine the impact of these extreme conditions on the mammal communities. However, the weather extremes are likely to have impacted the population densities of all mammal species. Decreases in the abundance and richness of small mammals captured during our study could also be due to the absence of old field habitat. In Virginia and other places, old field habitat is known to harbor both old field species (i.e. the meadow vole [*Microtus pennsylvanicus*] and hispid cotton rat [*Sigmodon hispidus*]), as well as generalist species that occur in both fields and forested habitats (Pagels et al. 1992). The early successional vegetation that characterizes old field habitat is structurally diverse and adds to the structural heterogeneity of field-forest edge habitat. The abundance of small mammals may have been higher in the field-forest edge habitat if true old fields were present. Furthermore, Bellows et al. (2001b) suggested that increased captures of small mammals that they observed in pine forest plantation habitat may have been due to abnormally high understory structural heterogeneity in that habitat as well as close proximity to other more structurally heterogeneous habitat types.

That *P. leucopus*, *B. brevicauda*, *B. carolinensis*, and *S. longirostris* were captured in all six habitat types that I sampled supports the well documented habitat-generalist behavior of these species (Bellows et al. 2001a, 2001b, Clark et al. 1987, George et al. 1986, Pagels et al. 1992, Seamon and Adler 1996), although *S. longirostris* has been more strongly associated with early successional habitats (Pagels et al. 1992, Pagels and Handley 1989). Despite not finding

differences in abundance on a microhabitat scale, *P. leucopus* was the only species to show a difference in relative abundance on a macrohabitat scale ( $p < 0.05$ ) (Table 2). Significant increases in the relative abundance of *P. leucopus* in bottom-land hardwood (BLHWD) when compared to within pine-forest plantations (PFP) could not be explained by differences in microhabitat components or by differences in the importance value of tree species (PCA). Several studies indicate that bottom-land hardwood (BLHWD) or riparian habitat is important to small mammals including habitat generalist species (Doyle 1990, Maisonneuve and Rioux 2001, Steel et al. 1999). Important structural components of this habitat include a complex vegetative structure (Maisonneuve and Rioux 2001) and woody debris piles deposited by flowing water in periods of high water (Steel et al. 1999). Within this habitat type, I observed on many occasions that mice would flee to river or stream banks upon release. These observations suggest that river or stream banks may provide an important structural component within this habitat type. In contrast, pine-forest plantation habitat is most often associated with less structural heterogeneity and therefore provides fewer resources than more structurally diverse habitats (Kirkland 1977). Trends in the microhabitat data (grass, herb, shrub, downed wood) (Table 4) reveal that all components were consistently more abundant within BLHWD habitat when compared to PFP habitat. The difference in the relative abundance of *P. leucopus* between these two habitat types may be due to these differences in understory heterogeneity and growth form diversity (Yahner 1986) between these two habitats.

The edge hypothesis states that edge habitats will support higher densities of mice because of the higher quality of this habitat (Wolf and Batzli 2002). However, other studies report that the abundance and fitness of mice is lower in edge habitat. Morris (1989) revealed that fitness of *P. leucopus* was lower in edge habitat and argued that mice should prefer forested

habitat. He suggested that intraspecific competition was responsible for decreased fitness within the edge habitat. Morris and Davidson (2000) had similar results but suggested that mice avoided open forest edges because of predation risks. Although these studies indicate that field forest edge habitat should not be attractive to mice, they did not measure habitat quality in terms of vegetation and other structural features. Within field-forest edge habitat I found no difference in the relative abundance of *P. leucopus* when compared with other forested habitat types. As mentioned earlier, the lack of old fields may have contributed to the decreased heterogeneity of field-forest edge habitat and ultimately made this habitat less attractive to *P. leucopus*, especially when predators were present.

In response to predators, prey may implement anti-predator decision making so that they are more difficult to detect and capture (Lima 1998). Although studies provide links between mammalian prey behavior (habitat selection) and predator pressure, it is not clear which scales best predict these relationships. Some suggest specific microhabitat components are most important to predator avoidance strategies (Kotler et al. 1991, Roche 1999), while others suggest patch scale differences in habitat are most important (Brown et al. 1992, Morris and Davidson 2000). Lima (1998) noted that little is known about how non-lethal effects (i.e. antipredator behaviors) interact with lethal effects (i.e. removal of prey) of predators at these different scales. Because strong correlations did not exist between any of the microhabitat variables and the relative abundance of *P. leucopus* or *Blarina spp.* (multiple regression analyses, PCA) (Table 5), there was no reason to believe that anti-predator behaviors were linked to any microhabitat component (Kotler et al. 1991, Roche 1999). However, in some cases, my analyses revealed that the addition of predator abundance as a microhabitat variable added to the relationship between small mammals and microhabitat (Table 5). In cases where multiple regression analysis

predicted the strongest relationships (Table 5), PCA revealed that variation in the secondary matrix was strongly correlated with only one axis, and that axis explained only a small percent of total variation in the primary matrix. For example, among FFE sites, variation in the relative abundance of *Blarina spp.* was strongly correlated with the microhabitat characteristics including predator abundance ( $p = 0.00$ ,  $R^2 = 0.92$ ) (Table 5). However, PCA revealed that variation in *Blarina spp.* relative abundance was best predicted by axis 3 ( $r = -0.81$ ) which explained only 15% of variation in the microhabitat data (Figure 7). These results suggest that at the microhabitat scale, abundance of predators is a poor predictor of *P. leucopus* and *Blarina spp.* abundance.

Although the relative abundance of predator species did not explain variation in prey species at the microhabitat scale, I suggest that relationships between predator and prey abundance exist at larger scales. Most studies on the behavioral effects of predators have been completed at small spatial scales (Lima 1998), therefore little is known about the larger scale effects of anti-predator behavior. Within two habitat types, I found a positive relationship between prey and predator species abundance. The most abundant prey (*P. leucopus*) and predator (*P. lotor*) species showed corresponding increases in relative abundance within BLHWD habitat type when compared to PFP habitat (for *P. leucopus*,  $p < 0.05$ ) (Table 5). Differences in the relative abundance of *P. lotor* were not significant ( $p < 0.05$ ) but the trends suggest otherwise. Although certain microhabitat components may offer some degree of protection from predators (Kotler et al. 1991, Roche 1999), my results suggest that understory habitat heterogeneity (exemplified by BLHWD habitat) collectively provides the most useful resources for evading predators, and is therefore ideal habitat for generalist prey species such as *P. leucopus*. The corresponding increase in the abundance of *P. lotor* within BLHWD habitat

suggests that predator species such as *P. lotor* are attracted to increases in prey (*P. leucopus*) density (i.e. Fryxell et al. 1999) as well as other resources within this habitat type. My results suggest that *P. leucopus* does not assess predator abundance and the dangers associated with increased predator abundance. Instead, it appears *P. leucopus* simply selects safer habitats. Similarly, Orrock et al. (2004) showed that foraging mice avoid dangerous situations (i.e. open microhabitat) and do not assess predation risk based on direct cues (cues produced by predator such as urine or sound). I suggest that although mammalian prey can detect the presence of predators, it is doubtful that they assess and react to changes in predator abundance. Consequently, a positive relationship between predator and prey abundance at the macrohabitat scale is not surprising, especially where mice are effectively using anti-predator behaviors. However, predators remove prey individuals from the ecosystem (lethal effects) and at some scales these effects may overwhelm even strong non-lethal effects (anti-predator behavior) (Lima 1998).

Negative relationships between the most abundant prey species, *P. leucopus*, and predator species, *P. lotor*, were apparent at the park scale. Evidence for this relationship was most evident at EF (where relative abundance of *P. leucopus* was lower and relative abundance of *P. lotor* was higher) and FF (where relative abundance of *P. leucopus* was significantly higher and relative abundance of *P. lotor* was significantly lower (ANOVA,  $p < 0.05$ ) (Table 5). Furthermore, as determined by both captures and night-camera photography, abundance of other predator species, such as Virginia opossum, domestic cat and gray fox was higher in EF than in FF (Table 3, Table 5). Although non-lethal effects such as anti-predator decision making may lead prey to less dangerous macrohabitats, my results suggest that lethal effects of predators (prey removal) are evident at larger scales.

## Conclusions

The microhabitat components that I measured were poor predictors of the relative abundance of *Peromyscus leucopus* and *Blarina spp.* across all scales of measurement. However, significant variation in the relative abundance of *Peromyscus leucopus* was evident among certain habitat types. Although microhabitat components and importance values of tree species failed to explain this variation, my results suggest that differences in the relative abundance of *P. leucopus* among habitat types may be explained by differences in understory structural diversity. Although abiotic factors such as weather (which was extreme before and during our study) may have contributed to differential selection of habitats by *P. leucopus*, predator-prey interactions may have been more influential.

Abundance of a potential predator, *P. lotor*, was both positively associated (within habitat types) and negatively associated (within parks) with the relative abundance of *P. leucopus*. Increased relative abundance of both *P. leucopus* and *P. lotor* in structurally heterogeneous habitat suggest the importance of non-lethal effects (prey selecting safer habitat) among habitat types. Ultimately, prey cannot escape the presence or calculate the abundance of predators and therefore simply avoid dangerous habitats. Although more heterogeneous habitats may offer a greater variety of food and shelter from adverse weather conditions, I suggest that a safer habitat may be more or equally valuable to generalist species such as *P. leucopus*. However, at a larger scale, my results indicate that the lethal effects (removal of prey) of predators may overwhelm the non-lethal effects (anti-predator behaviors) exhibited by *P. leucopus* at smaller scales.

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Table 1. Relative abundance (per 100 trapnights) of small and predator mammals within each park; EF = Petersburg National Battlefield Eastern Front Unit, FF = Petersburg National Battlefield, APCO = Appomattox Court House National Historical Park, BOWA = Booker T. Washington National Monument Small mammals included are those that were captured in all habitat types. All predator species that were captured are included. Values represent means  $\pm$  standard error. The number of individuals (excludes recaptures) captured is in parentheses. Within each row, values followed by different letters indicate significant differences ( $p < 0.05$ ) based on Tukey HSD *post hoc* comparisons. Trapnights per trap type are also provided for each park. Numbers following species names and trap types indicate the trap types used in determining relative abundance for those species. NA is given for those species whose distributions do not include certain parks.

| Species                                      | EF                                  | FF                                   | APCO                                 | BOWA                                 |
|--|-------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|
| <b>Prey species</b>                          |                                     |                                      |                                      |                                      |
| <i>Peromyscus leucopus</i> <sup>2</sup>      | 1.3 $\pm$ 0.2 <sup>a</sup><br>(46)  | 3.5 $\pm$ 0.4 <sup>b</sup><br>(142)  | 3.5 $\pm$ 0.5 <sup>b</sup><br>(115)  | 5.0 $\pm$ 0.7 <sup>b</sup><br>(129)  |
| <i>Blarina carolinensis</i> <sup>1,2</sup>   | 0.4 $\pm$ 0.1 <sup>a</sup><br>(25)  | 0.3 $\pm$ 0.1 <sup>a</sup><br>(19)   | NA                                   | NA                                   |
| <i>Blarina brevicauda</i> <sup>1,2</sup>     | NA                                  | NA                                   | 0.4 $\pm$ 0.1 <sup>a</sup><br>(22)   | 0.8 $\pm$ 0.2 <sup>b</sup><br>(42)   |
| <i>Sorex longirostris</i> <sup>1</sup>       | 0 <sup>a</sup>                      | 0.4 $\pm$ 0.1 <sup>a,b</sup><br>(14) | 0.5 $\pm$ 0.2 <sup>b</sup><br>(13)   | 0.2 $\pm$ 0.1 <sup>a,b</sup><br>(4)  |
| <b>Predator species</b>                      |                                     |                                      |                                      |                                      |
| <i>Procyon lotor</i> <sup>4</sup>            | 12.1 $\pm$ 2.6 <sup>a</sup><br>(35) | 0.6 $\pm$ 0.4 <sup>b</sup><br>(2)    | 7.7 $\pm$ 2.5 <sup>a,b</sup><br>(22) | 7.6 $\pm$ 3.0 <sup>a,b</sup><br>(19) |
| <i>Didelphis virginiana</i> <sup>4</sup>     | 6.5 $\pm$ 1.7 <sup>a</sup><br>(19)  | 3.1 $\pm$ 1.1 <sup>a</sup><br>(11)   | 5.6 $\pm$ 0.9 <sup>a</sup><br>(17)   | 6.8 $\pm$ 1.5 <sup>a</sup><br>(17)   |
| <i>Mephitis mephitis</i> <sup>4</sup>        | 0 <sup>a</sup>                      | 0.6 $\pm$ 0.4 <sup>a</sup><br>(2)    | 0.7 $\pm$ 0.5 <sup>a</sup><br>(2)    | 0.4 $\pm$ 0.4 <sup>a</sup><br>(1)    |
| <i>Urocyon cinereoargenteus</i> <sup>4</sup> | 0 <sup>a</sup>                      | 0 <sup>a</sup>                       | 0 <sup>a</sup>                       | 0.4 $\pm$ 0.4 <sup>a</sup><br>(1)    |
| <i>Mustela frenata</i> <sup>2</sup>          | 0 <sup>a</sup>                      | 0 <sup>a</sup>                       | 0 <sup>a</sup>                       | 0.4 $\pm$ 0.4 <sup>a</sup><br>(1)    |
| <b>Trapnights/Trap type</b>                  |                                     |                                      |                                      |                                      |
| Pitfall <sup>1</sup>                         | 2933                                | 3434                                 | 2624                                 | 2255                                 |
| Sherman <sup>2</sup>                         | 3378                                | 4089                                 | 3327                                 | 2632                                 |
| Sm. Tomahawk <sup>3</sup>                    | 584                                 | 695                                  | 558                                  | 472                                  |
| Lg. Tomahawk <sup>4</sup>                    | 297                                 | 350                                  | 287                                  | 249                                  |
| <i>Total</i>                                 | 7192                                | 8568                                 | 6796                                 | 5608                                 |

Table 2. Relative abundance (per 100 trap nights) of small and predator mammals within each habitat type; FFE = field-forest edge, PFP = pine forest plantation, MPH = mixed pine hardwood, HWD = hardwood, BLHWD = bottom-land hardwood, WD = wetland. Small mammals included are those that were captured in all habitat types. All predator species that were captured are included. Values represent means  $\pm$  standard error. The number of individuals (excludes recaptures) captured is in parentheses. Within each row, values followed by different letters indicate significant differences ( $p < 0.05$ ) based on Tukey HSD *post hoc* comparisons. Trapnights per trap type are also provided for each park. Numbers following species names and trap types indicate the trap types used in determining relative abundance for those species. WD was found only at FF and is an area that is not included in the geographic range of *Blarina brevicauda* (NA)

| Species                                      | FFE                                 | PFP                                | MPH                                  | HWD                                 | BLHWD                               | WD                                  |
|--|-------------------------------------|------------------------------------|--------------------------------------|-------------------------------------|-------------------------------------|-------------------------------------|
| <b>Prey species</b>                          |                                     |                                    |                                      |                                     |                                     |                                     |
| <i>Peromyscus leucopus</i> <sup>2</sup>      | 3.4 $\pm$ 0.7 <sup>ab</sup><br>(89) | 1.4 $\pm$ 0.4 <sup>a</sup><br>(30) | 3.5 $\pm$ 0.5 <sup>ab</sup><br>(103) | 3.0 $\pm$ 0.5 <sup>ab</sup><br>(82) | 4.5 $\pm$ 0.8 <sup>b</sup><br>(113) | 3.4 $\pm$ 0.5 <sup>ab</sup><br>(25) |
| <i>Blarina carolinensis</i> <sup>1,2</sup>   | 0.3 $\pm$ 0.2 <sup>a</sup><br>(8)   | 0.1 $\pm$ 0.0 <sup>a</sup><br>(2)  | 0.7 $\pm$ 0.3 <sup>a</sup><br>(17)   | 0.1 $\pm$ 0.1 <sup>a</sup><br>(3)   | 0.4 $\pm$ 0.1 <sup>a</sup><br>(9)   | 0.4 $\pm$ 0.3 <sup>a</sup><br>(5)   |
| <i>Blarina brevicauda</i> <sup>1,2</sup>     | 0.6 $\pm$ 0.2 <sup>a</sup><br>(14)  | 0.1 $\pm$ 0.1 <sup>a</sup><br>(1)  | 0.7 $\pm$ 0.2 <sup>a</sup><br>(16)   | 0.3 $\pm$ 0.2 <sup>a</sup><br>(7)   | 1.1 $\pm$ 0.3 <sup>a</sup><br>(26)  | NA                                  |
| <i>Sorex longirostris</i> <sup>1</sup>       | 0.7 $\pm$ 0.3 <sup>a</sup><br>(11)  | 0.2 $\pm$ 0.2 <sup>a</sup><br>(3)  | 0.6 $\pm$ 0.2 <sup>a</sup><br>(11)   | 0.1 $\pm$ 0.1 <sup>a</sup><br>(1)   | 0.3 $\pm$ 0.3 <sup>a</sup><br>(4)   | 0.2 $\pm$ 0.2 <sup>a</sup><br>(1)   |
| <b>Predator species</b>                      |                                     |                                    |                                      |                                     |                                     |                                     |
| <i>Procyon lotor</i> <sup>4</sup>            | 10.3 $\pm$ 3.8 <sup>a</sup><br>(23) | 2.8 $\pm$ 1.2 <sup>a</sup><br>(5)  | 3.6 $\pm$ 1.6 <sup>a</sup><br>(9)    | 7.4 $\pm$ 2.5 <sup>a</sup><br>(18)  | 10.7 $\pm$ 3.4 <sup>a</sup><br>(23) | 0 <sup>a</sup>                      |
| <i>Didelphis virginiana</i> <sup>4</sup>     | 6.3 $\pm$ 1.3 <sup>a</sup><br>(16)  | 5.6 $\pm$ 2.7 <sup>a</sup><br>(10) | 4.2 $\pm$ 1.0 <sup>a</sup><br>(10)   | 4.9 $\pm$ 1.5 <sup>a</sup><br>(12)  | 5.2 $\pm$ 1.3 <sup>a</sup><br>(11)  | 7.9 $\pm$ 4.2 <sup>a</sup><br>(5)   |
| <i>Mephitis mephitis</i> <sup>4</sup>        | 1.7 $\pm$ 0.8 <sup>a</sup><br>(3)   | 0 <sup>a</sup>                     | 0 <sup>a</sup>                       | 0.6 $\pm$ 0.6 <sup>a</sup><br>(1)   | 0.6 $\pm$ 0.6 <sup>a</sup><br>(1)   | 0 <sup>a</sup>                      |
| <i>Urocyon cinereoargenteus</i> <sup>4</sup> | 0 <sup>a</sup>                      | 0 <sup>a</sup>                     | 1.6 $\pm$ 1.6 <sup>a</sup><br>(1)    | 0 <sup>a</sup>                      | 0 <sup>a</sup>                      | 0 <sup>a</sup>                      |
| <i>Mustela frenata</i> <sup>2</sup>          | 0 <sup>a</sup>                      | 0 <sup>a</sup>                     | 0 <sup>a</sup>                       | 0 <sup>a</sup>                      | 1.6 $\pm$ 1.6 <sup>a</sup><br>(1)   | 0 <sup>a</sup>                      |
| <b>Trapnights/Trap type</b>                  |                                     |                                    |                                      |                                     |                                     |                                     |
| Pitfall <sup>1</sup>                         | 2232                                | 1749                               | 2313                                 | 2314                                | 1628                                | 606                                 |
| Sherman <sup>2</sup>                         | 2634                                | 2125                               | 2673                                 | 2757                                | 2506                                | 731                                 |
| Sm. Tomahawk <sup>3</sup>                    | 455                                 | 362                                | 472                                  | 475                                 | 422                                 | 123                                 |
| Lg. Tomahawk <sup>4</sup>                    | 234                                 | 180                                | 245                                  | 245                                 | 216                                 | 63                                  |
| <i>Total</i>                                 | 5555                                | 4416                               | 5703                                 | 5791                                | 4772                                | 1523                                |

Table 3. Total number of night photographs capturing each predator species with the four park units (see Table 1).

| Species                         | EF | FF | APCO | BOWA |
|---------------------------------|----|----|------|------|
| <i>Didelphis virginiana</i>     | 11 | 25 | 16   | 1    |
| <i>Canis latrans</i>            |    | 5  |      |      |
| <i>Vulpes vulpes</i>            |    |    | 1    |      |
| <i>Urocyon cinereoargenteus</i> | 89 |    | 1    | 34   |
| <i>Procyon lotor</i>            | 89 | 5  | 34   | 20   |
| <i>Mephitis mephitis</i>        |    |    |      | 17   |
| <i>Felis rufus</i>              |    | 1  |      |      |
| <i>Domestic cat</i>             | 1  |    |      |      |

Table 4. Microhabitat measurements for sampling sites summarized by park unit and habitat type (see Tables 1 and 2). Measurements calculated from line intercept data. Data are presented as mean  $\pm$  std. error

| Park/Habitat type | Grass<br>(% cover) | Herbaceous<br>(% cover) | Shrub<br>(% cover) | Downed Wood<br>(Volume (m <sup>3</sup> /hectare)) |
|-------------------|--------------------|-------------------------|--------------------|---|
| <b>EF</b>         |                    |                         |                    |   |
| FFE               | 93 $\pm$ 6.5       | 45 $\pm$ 6.1            | 3 $\pm$ 1.5        | 13 $\pm$ 6.4                                      |
| PFP               | 1 $\pm$ 0.8        | 13 $\pm$ 7.1            | 2 $\pm$ 1.1        | 42 $\pm$ 11.0                                     |
| MPH               | 31 $\pm$ 15.5      | 18 $\pm$ 8.3            | 6 $\pm$ 5.1        | 58 $\pm$ 34.8                                     |
| HWD               | 2 $\pm$ 1.1        | 6 $\pm$ 3.3             | 16 $\pm$ 4.7       | 107 $\pm$ 18.1                                    |
| BLHWD             | 70 $\pm$ 15.6      | 21 $\pm$ 17.8           | 3 $\pm$ 2.2        | 49 $\pm$ 11.0                                     |
| <i>Total</i>      | 39 $\pm$ 10.6      | 20 $\pm$ 5.1            | 6 $\pm$ 1.9        | 54 $\pm$ 10.9                                     |
| <b>FF</b>         |                    |                         |                    |   |
| FFE               | 61 $\pm$ 10.3      | 76 $\pm$ 7.0            | 35 $\pm$ 6.7       | 6 $\pm$ 3.3                                       |
| PFP               | 2 $\pm$ 1.1        | 9 $\pm$ 3.3             | 24 $\pm$ 6.2       | 5 $\pm$ 2.3                                       |
| MPH               | 2 $\pm$ 2.1        | 8 $\pm$ 4.4             | 31 $\pm$ 7.3       | 20 $\pm$ 4.1                                      |
| HWD               | 6 $\pm$ 3.1        | 16 $\pm$ 7.6            | 20 $\pm$ 5.9       | 6 $\pm$ 1.7                                       |
| BLHWD             | 26 $\pm$ 3.8       | 9 $\pm$ 7.6             | 49 $\pm$ 40.4      | 54 $\pm$ 28.6                                     |
| WD                | 58 $\pm$ 4.8       | 27 $\pm$ 15.5           | 58 $\pm$ 2.5       | 23 $\pm$ 8.5                                      |
| <i>Total</i>      | 26 $\pm$ 6.7       | 25 $\pm$ 6.8            | 35 $\pm$ 5.2       | 17 $\pm$ 4.8                                      |
| <b>APCO</b>       |                    |                         |                    |   |
| FFE               | 93 $\pm$ 4.4       | 88 $\pm$ 1.5            | 74 $\pm$ 7.3       | 17 $\pm$ 7.1                                      |
| PFP               | 1 $\pm$ 0.7        | 3 $\pm$ 1.1             | 8 $\pm$ 4.0        | 26 $\pm$ 11.2                                     |
| MPH               | 6 $\pm$ 5.2        | 20 $\pm$ 7.6            | 17 $\pm$ 4.4       | 85 $\pm$ 9.2                                      |
| HWD               | 3 $\pm$ 1.9        | 8 $\pm$ 7.5             | 13 $\pm$ 2.2       | 49 $\pm$ 24.6                                     |
| BLHWD             | 77 $\pm$ 10.7      | 76 $\pm$ 8.7            | 30 $\pm$ 5.8       | 51 $\pm$ 20.8                                     |
| <i>Total</i>      | 36 $\pm$ 11.0      | 39 $\pm$ 9.9            | 29 $\pm$ 6.8       | 46 $\pm$ 8.8                                      |
| <b>BOWA</b>       |                    |                         |                    |   |
| FFE               | 64 $\pm$ 10.6      | 61 $\pm$ 7.7            | 57 $\pm$ 4.4       | 26 $\pm$ 11.2                                     |
| MPH               | 1 $\pm$ 1.3        | 16 $\pm$ 8.0            | 13 $\pm$ 2.7       | 51 $\pm$ 14.4                                     |
| HWD               | 4 $\pm$ 4.2        | 17 $\pm$ 8.7            | 14 $\pm$ 10.0      | 28 $\pm$ 15.1                                     |
| BLHWD             | 26 $\pm$ 13.4      | 60 $\pm$ 6.6            | 30 $\pm$ 20.2      | 43 $\pm$ 2.3                                      |
| <i>Total</i>      | 24 $\pm$ 8.4       | 38 $\pm$ 7.4            | 29 $\pm$ 7.2       | 37 $\pm$ 6.0                                      |

Table 5. Results of multiple regression analyses comparing microhabitat variables (G = % cover of grass, H = % cover of herbs, S = % cover of shrubs, DW = % cover of downed wood, P = relative abundance of predatory species) to the relative abundance of *Peromyscus leucopus* and *Blarina spp.* Only the two most significant results for each dependent variable are shown. \* denotes significant p-value  $\leq 0.05$

| Sampling Sites | Ind. Var.      | Dep. Var.                              | F-value | p-value | R <sup>2</sup> |
|----------------|----------------|--|---------|---------|----------------|
| APCO           | G, H, S, DW    | <i>P. leucopus</i> relative abundance  | 0.78    | 0.56    | 0.24           |
|                | G, H, S, DW, P | "                                      | 4.48    | 0.03*   | 0.71           |
| HWD            | G, H, S, DW    | "                                      | 2.40    | 0.15    | 0.58           |
|                | G, H, S, DW, P | "                                      | 3.60    | 0.08    | 0.75           |
| APCO           | G, H, S, DW    | <i>Blarina spp.</i> relative abundance | 2.51    | 0.11    | 0.50           |
|                | G, H, S, DW, P | "                                      | 2.56    | 0.10    | 0.59           |
| FFE            | G, H, S, DW    | "                                      | 1.89    | 0.22    | 0.52           |
|                | G, H, S, DW, P | "                                      | 14.40   | 0.00*   | 0.92           |

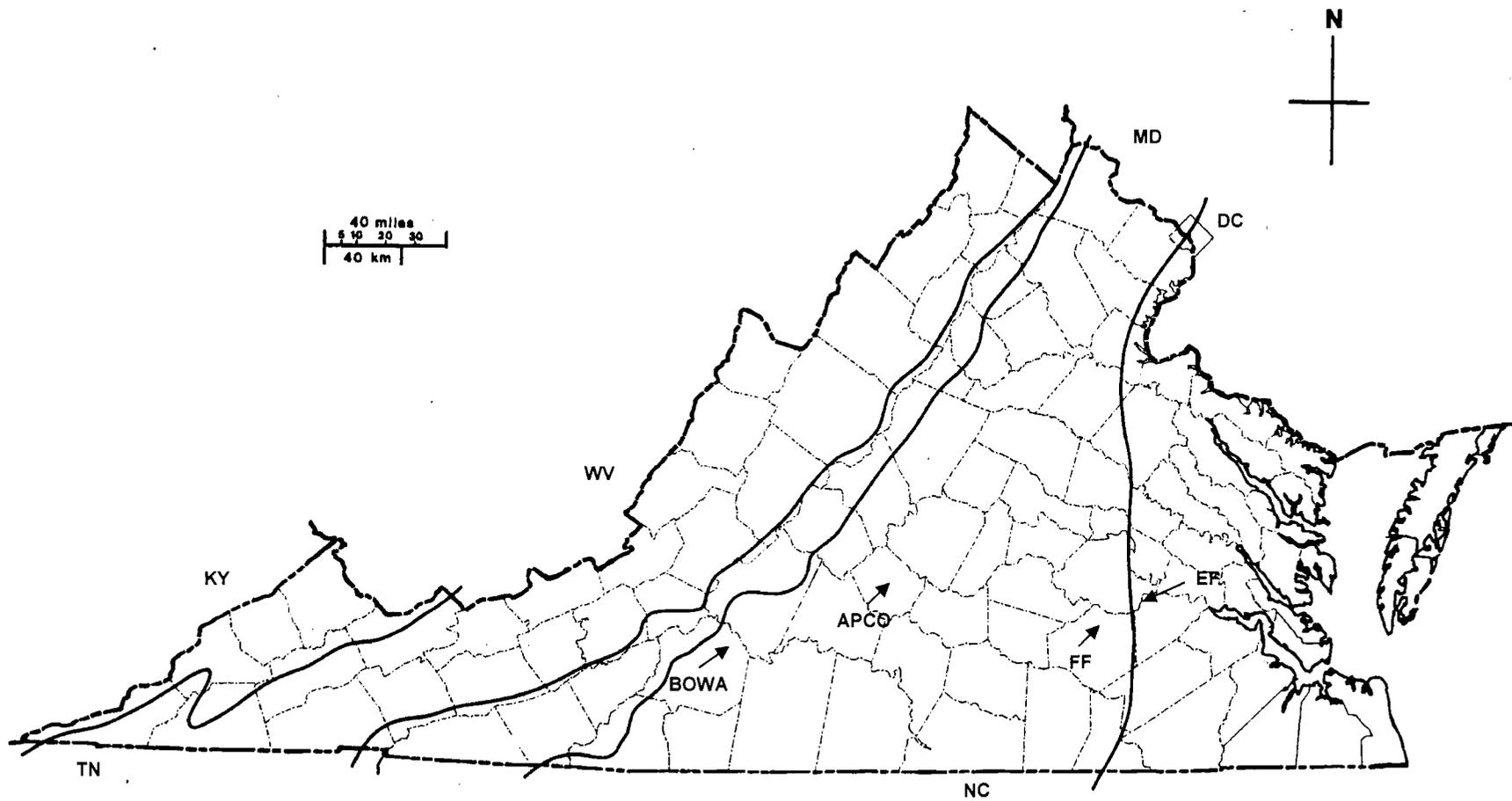


Figure 1. Map of Virginia depicting the location of our four study areas: Petersburg National Battlefield Eastern Front Unit (EF) and Five-forks Unit (FF), Appomattox Court House National Historical Park (APCO), and Booker T. Washington National Monument (BOWA).

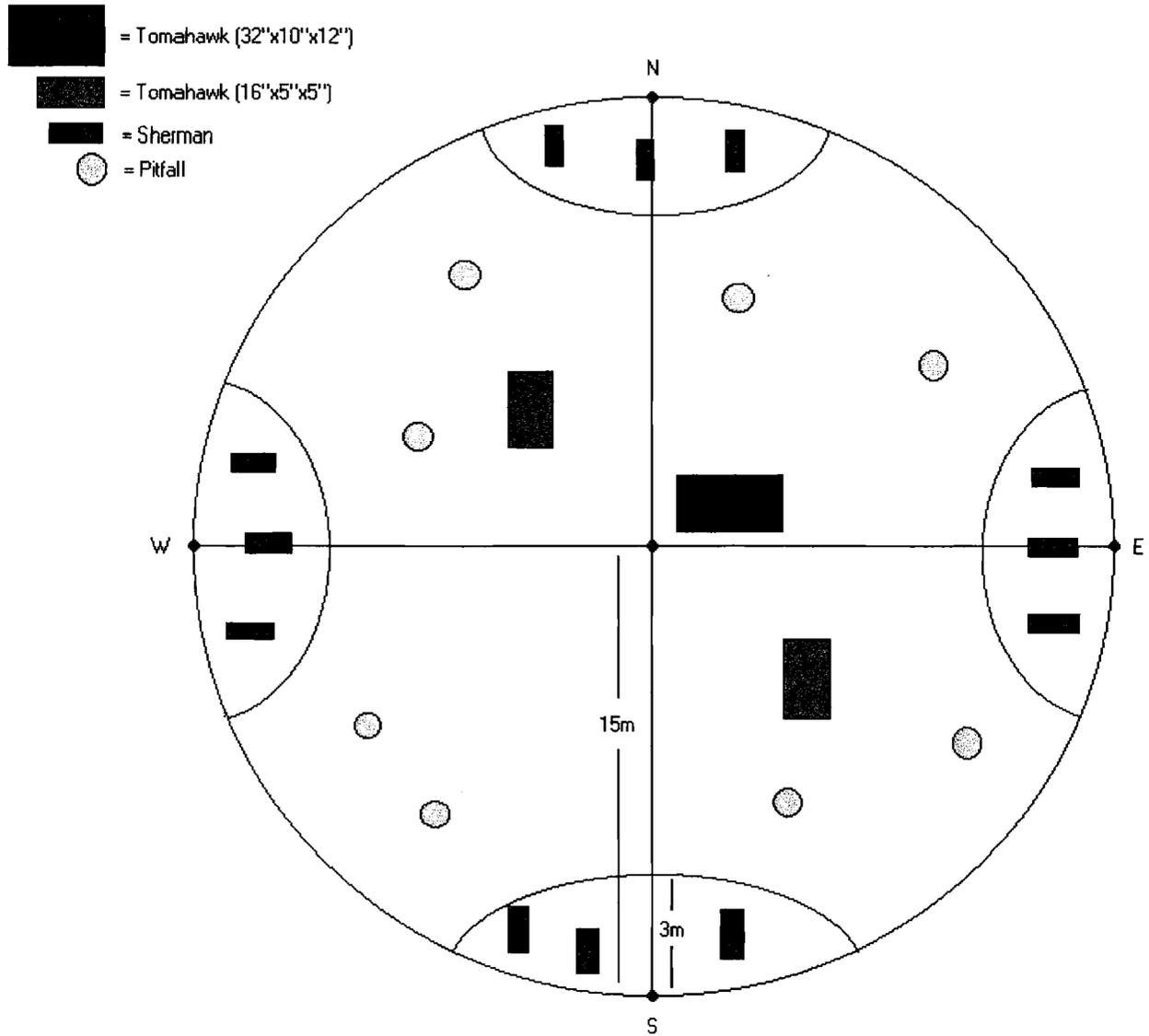


Figure 2. Mammal sampling configuration for circular sampling sites. This circular configuration was used at all sites excluding all FFE sites as well as BLHWD sites at Booker T. Washington National Monument.

-  = Tomahawk (32"x10"x12")
-  = Tomahawk (16"x5"x5")
-  = Sherman
-  = Pitfall

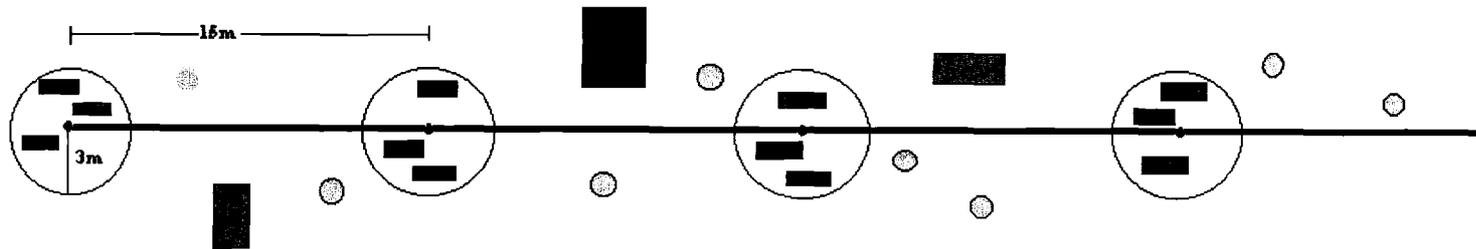


Figure 3. Mammal sampling configuration for transect plots. This configuration was used at all FFE sites as well as BLHWD sites at Booker T. Washington National Monument.

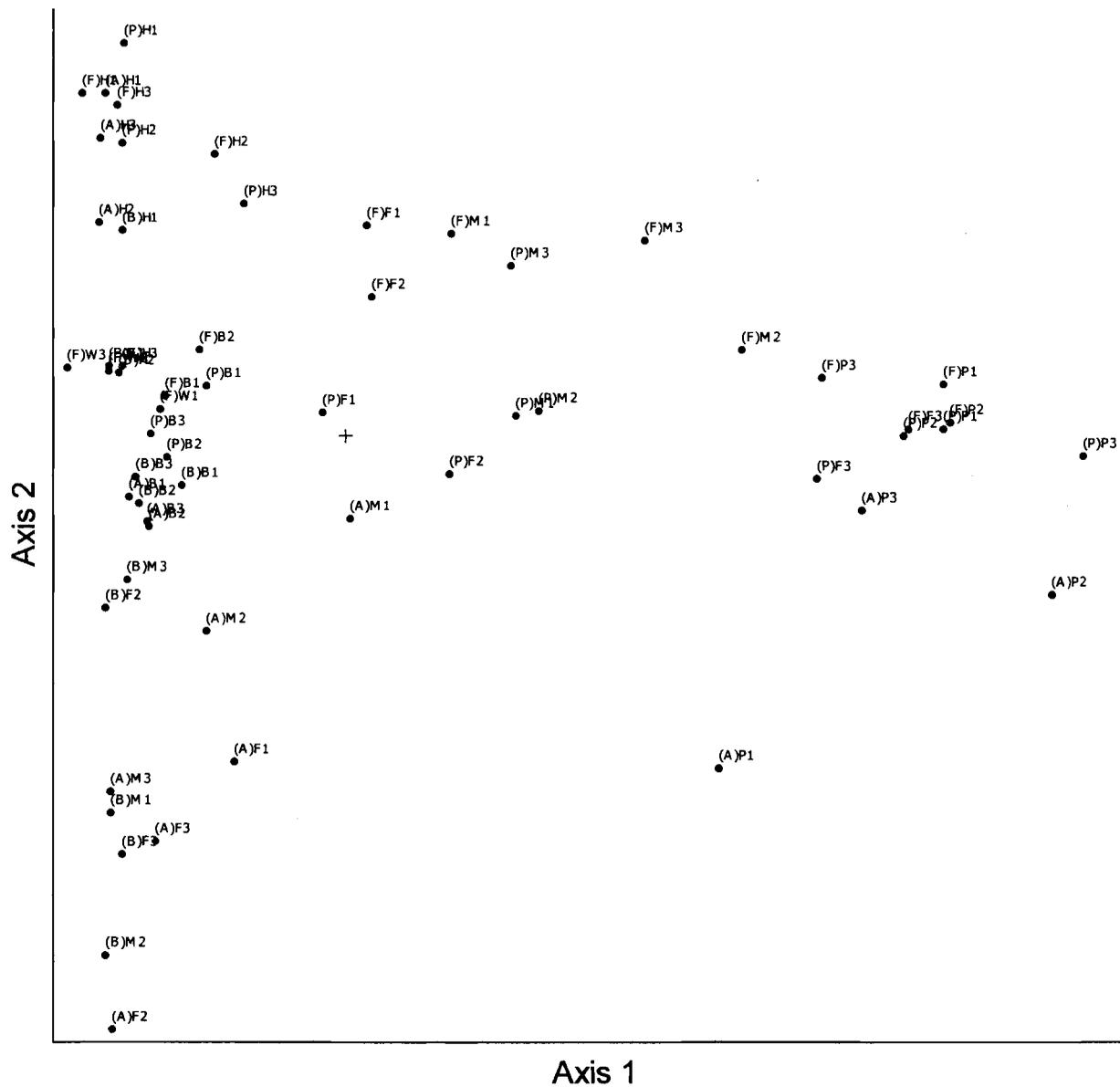


Figure 4. Principal components analysis of tree species importance values (primary matrix) and the relative abundance *P. leucopus* and *Blarina spp.* (secondary matrix) among all sites. Axes 1 and 2 explained 51% of the variation in tree species importance values among all sites and the relative abundance of *P. leucopus* and *Blarina spp.* was not correlated with this variation.



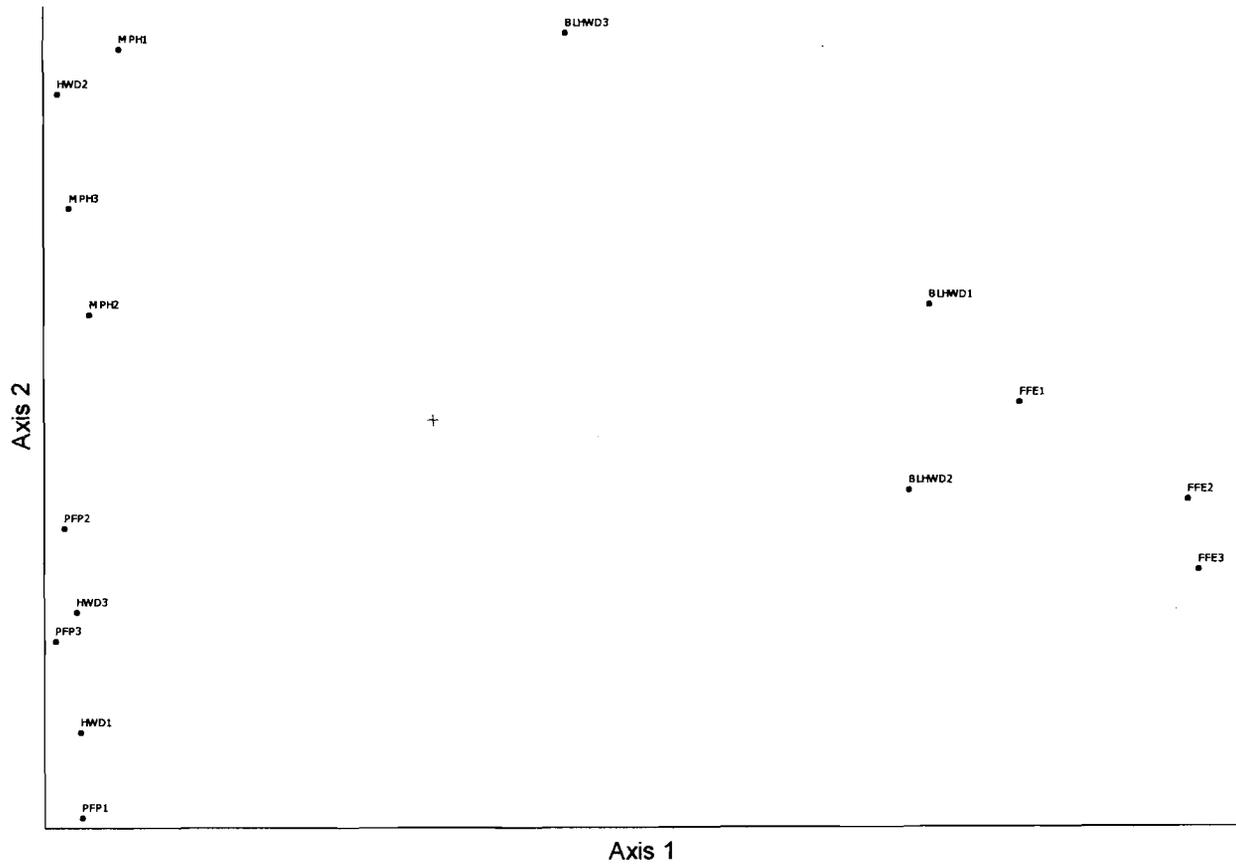


Figure 6. Principal components analysis of microhabitat variables (including predator abundance) (primary matrix) and the relative abundance of *P. leucopus* (secondary matrix) among the 15 sampling sites at APCO. Axes 1 and 2 explained 94% of the variation in microhabitat components among APCO sites and the relative abundance of *P. leucopus* was not correlated with this variation.

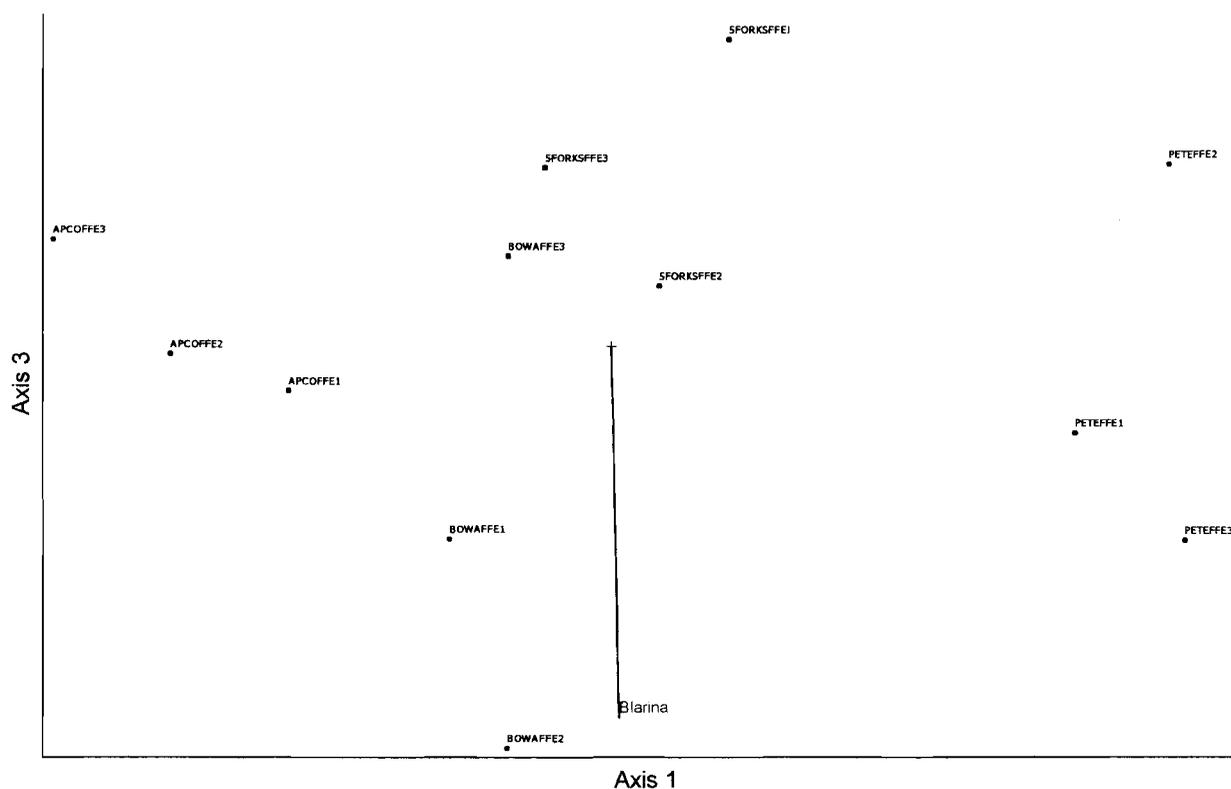


Figure 7. Principal components analysis of microhabitat variables (including predator abundance) (primary matrix) and the relative abundance of all *Blarina spp* (secondary matrix) among the 12 FFE sampling sites. Axes 1 and 2 explained 74% of the variation in microhabitat components among all sites and the relative abundance of *Blarina spp*. did not correlate with this variation. The relative abundance of *Blarina spp*. was highly correlated with axis 3 ( $r = -0.81$ )

## Vita

Adam Daniel Chupp was born on August 9, 1979 in Wooster, Ohio. He graduated from Triway High School in Wooster, Ohio in June 1998. Adam received his Bachelor of Science in Biology from Ohio University in June 2002. While attending Ohio University, he worked as an undergraduate assistant in the department of Biological Sciences under Dr. Donald B. Miles. As an undergraduate assistant, Adam was involved in field research documenting the effects of land management practices on southern flying squirrels and bat populations in Wayne National Forest. In the Fall of 2002, he was enrolled in the graduate program at VCU and under the supervision of Dr. John F. Pagels, he began work on a mammal survey for the National Park Service Inventory and Monitoring Program. While at VCU, Adam was also a teaching assistant for introductory biology laboratory courses.