THE EFFECTS OF HABITAT FRAGMENTATION ON   HABITAT USE BY   NATIVE SMALL
MAMMALS

by

Meredith Penthorn
A Thesis
Submitted to the
Graduate Faculty
of
George Mason University
in Partial Fulfillment of
The Requirements for the Degree
of
Master of Science
Environmental Science and Policy

Committee:

_____   Dr. Thomas Lovejoy, Thesis Director

_____   Dr. William McShea, Committee Member

_____   Dr. Larry Rockwood, Committee Member

_____   Dr. Albert P. Torzilli, Graduate
                                     Program Director

_____   Dr. Robert B. Jonas,
                                     Department Chairperson

_____   Dr. Richard Diecchio, Interim Associate Dean
                                     for Student and Academic Affairs,
                                     College of Science

_____   Dr. Peggy Agouris, Interim Dean, College of
                                     Science

Date: _____ Fall Semester 2013
                                     George Mason University
                                     Fairfax, VA

The Effects of Fragmentation on Habitat Usage in Native Small Mammals

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at George Mason University

by

Meredith Penthorn
Bachelor of Science
University of Wisconsin-Madison, 2010

Director: Thomas E. Lovejoy, Professor
Department of Environmental Science and Policy

Fall Semester 2013
George Mason University
Fairfax, VA

DEDICATION

To my family, both human and animal, especially to my parents, Cynthia Petzold and Lowell Inhorn, and in memory of Dr. Gerald L. Schertz

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

THE EFFECTS OF FRAGMENTATION ON HABITAT USAGE IN NATIVE SMALL MAMMALS

Meredith Penthorn, M.S.

George Mason University, 2014

Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at George Mason University

Director: Thomas E. Lovejoy, Professor

Habitat fragmentation removes original habitat and creates a matrix of new habitat with remnants of original habitat embedded within. Small mammals such as *Peromyscus leucopus*, *Blarina brevicauda*, *Microtus pennsylvanicus*, *Zapus hudsonius*, and *Tamias striatus* may not be able to cross the matrix habitat to access continuous forest habitat or other forest fragments if the amount of cover is insufficient, because the benefits of acquiring new resources do not justify the predation risk. A combination of sampling techniques, including live trapping, giving-up density (GUD) trials, plant surveys, and camera trapping were employed to assess the relative importance of habitat type (fragment, matrix, or continuous forest), vegetative composition and structure, demographic attributes, fragment size, and matrix distance in determining foraging behavior over two summers. Trapping and GUD indicate where animals are foraging, and

GUD gives a more specific measure of the relative amount of time spent in each habitat. Predator and plant surveys and camera trapping illuminate possible drivers of this behavior. Results indicated that habitat type most strongly affected animals; most species displayed some aversion to foraging in the matrix as opposed to the fragments and forest (p<0.0001). Plant diversity was significantly different between fragment and matrix habitat (p<0.0001). Removing matrix structure further delineates fragment, forest, and matrix (p<0.0001). Year also had a strong effect, with significantly fewer captures and higher GUD's in 2012 as opposed to 2013 (p<0.05). Fragment size and isolation did not have a significant effect on foraging behavior (p>0.1). These habitat attributes, along with the risk of predation, influenced the demographic profile of *P. leucopus* individuals that use fragment and matrix habitat. Results suggest that maintaining connectivity and structural complexity in fragmented habitats are most beneficial to small mammals.

1. INTRODUCTION AND LITERATURE REVIEW

Overview of Habitat Fragmentation

Habitat fragmentation is a landscape-level process with large-scale, long-term consequences for ecological communities. Fragmentation converts continuous habitat into smaller habitat patches of different sizes and configurations embedded in a matrix of disturbed habitat (Ewers and Didham 2006, Fahrig 2003). Unlike in continuous habitat, connectivity in fragmented habitat depends upon the distribution of patches across the landscape and the composition and conditions in the matrix surrounding them (Ewers and Didham 2006). Unlike simple habitat loss, fragmentation changes the characteristics of the remaining habitat, including amount of edge, fragment size, shape, and arrangement, and degree of isolation (Ewers and Didham 2006, Fahrig 2003). Fragmentation can affect individuals, populations, species, and communities across local and regional scales, and the outcomes for complex systems are often unpredictable (Bierregaard et al. 2001, Laurance 2008). The impacts of other disturbances, such as deforestation and wildfires, are also more profound in fragmented areas, because effects of such disturbances are able to penetrate farther into remnant interior habitat (Hoffmeister et al. 2005).

Island Biogeography and Fragmentation Reality

Habitat fragmentation research is conceptually rooted in island biogeography theory, first proposed by MacArthur and Wilson (1967). According to the basic island biogeography model, the rates of species colonization and extinction on an island vary until

11

an equilibrium number of species is attained (Schoener 2010). The distance and size properties of an island contribute to these rates (Laurance 2008). Islands that are closer to the mainland or to other islands have a higher immigration rate than those with a greater degree of separation, and therefore have more species (Laurance 2008 and Schoener 2010). Smaller islands have fewer species because they contain fewer habitats and are more vulnerable to intense interspecific competition and the demographic, genetic, and stochastic effects of small population size (Laurance 2008, Schoener 2010). Thus, according to the tenants of island biogeography theory, larger, more connected landmasses are preferable for conserving species diversity (Laurance 2008).

While island biogeography theory provided a theoretical foundation for habitat fragmentation studies, its implications for species and community composition do not always perfectly describe reality (Laurance 2008, Bierregaard et al. 2001). Low species turnover rates, or, in other words, low rates of colonization and extinction, should distinguish these landscapes; however, fragments will initially exhibit a higher extinction rate than immigration rate (Bierregaard et al. 2001). Also, immigration and emigration rates can change over time and with degrees of fragmentation (Hanski 2010). Another departure from island biogeography theory is that certain species can incorporate matrix habitat into their range, and individuals can migrate into the islands from the matrix surrounding them, thus affecting species diversity and distribution (Bierregaard et al. 2001, Laurance 2008). Additionally, species can survive the fragmentation event, thereby comprising the suite of species already present on an island before the island biogeography model goes into effect (Bierregaard et al. 2001). Moreover, real species have different

12

habitat requirements and life histories, and therefore behave and interact differently than theoretical island species. Habitat fragmentation also affects ecological processes in fragments and the matrix (Bierregaard et al. 2001). Edge effects further complicate island biogeography theory because they add the dimension of fragment shape to the overall equation of the effects of fragmentation on biodiversity (Laurance 2008).

Characteristics of a Fragmented Landscape

As knowledge of habitat fragmentation has evolved, the focus of inquiry has shifted from individual islands to the network of fragments and matrix (Bierregaard et al. 2001). Since they emerge from anthropogenic processes, fragment characteristics and locations reflect human landscape conditions and represent only those species tolerant of those conditions (Bierregaard et al. 2001, Laurance 2008). Fragments are more often found in less desirable habitat, such as slopes and poorer quality land, and near human structures (Bierregaard et al. 2001, Laurance 2008).

Size of fragments and arrangement within the matrix exert a notable effect on populations, species, and communities. Species-specific patch size requirements result in a lower number of species in any given remnant than in the continuous habitat (Fahrig 2003). Sensibly, then, larger fragments are more biologically diverse; in the Amazon rainforests, for instance, larger fragments harbored more species than smaller fragments (Bierregaard et al. 2001). Use of a size-area relationship (SAR) model can predict the number of species that can coexist on a fragment of a given size (Hanski et al. 2013). However, in extremely fragmented areas, using the SAR model can actually underestimate the extinction rate in fragments (Hanski et al. 2013). Similarly, the distribution-abundance relationship model

predicts that organisms with higher carrying capacities will be more widely distributed (Hanski 2010). Both models suggest that smaller patch sizes are more detrimental to species diversity. Species extinctions are more likely to occur as the size of the fragment decreases, especially for larger, specialist species that occupy higher trophic levels (Hanski et al. 2013 and Ewers and Didham 2006). The smaller patch size excludes larger populations, and sometimes even larger individual territories; in this manner, fragment size can be prohibitive to species that require a large area of continuous habitat (Bierregaard et al. 2001, Fahrig 2003). In limiting the size of populations, smaller fragments increase vulnerability to random fluctuations, mortality from natural disasters, skewed age and sex ratios, and reduced genetic diversity; thus, inbreeding and genetic drift are common, and can render a population susceptible to parasitism and predation (Ewers and Didham 2006, Hoffmeister et al. 2005). Reduction in fragment size, and the accompanying isolation, has a less profound impact on species with better dispersal ability (Ewers and Didham 2006). However, metapopulations of strong dispersers, consisting of several interrelated patches of local populations, can persist in habitats with small and isolated patches if colonization exceeds extinction within the network (Ewers and Didham 2006, Rockwood 2009). Thus, even if a patch goes extinct, the metapopulation can persist as long as other patches can supply emigrants (Rockwood 2009). Fragmentation events also present unique arrangements of fragments across the landscape, so that population movements and species diversity vary between cases (Fahrig and Merriam 1994). Configuration of patches may transcend number of patches in terms of the ability of populations to cope with

fragmentation; those closer together provide a better opportunity for dispersal (Fahrig and Merriam 1994).

Additionally, fragment and matrix quality affect species and metapopulation occupancy in a fragmented area. According to Mortelliti et al. (2010), patch use results from an animal's assessment of whether the benefits of higher quality and quantity outweigh the risks of smaller size or isolation. Greater resource abundance promotes a larger population, while better resource quality enhances an individual's probability of survival and reproduction, and a metapopulation's chance of long-term survival (Fahrig and Merriam 1994, Johnson 2007). Varying degrees of quality within a single patch also influence a population's probability of extinction, with more homogenous patches more prone to extinction (Mortelliti et al. 2010). Hanski et al. (2013) reported that species richness was related not only to fragment size, but to habitat type within the fragment. Similar to fragments, matrix habitability depends on structure of the matrix and tolerance of the organisms (Hoffmeister et al. 2005). The matrix can act as either a route of dispersal into fragments, or as an obstacle to dispersal to other fragments. Species abundance is positively correlated with presence in the matrix as well as the fragments (Bierregaard et al. 2001, Ewers and Didham 2006). Jules and Shahani (2003) suggest that predators with a tolerance for certain types of matrix can increase in prevalence, thus applying a greater predation pressure to small mammal herbivores within the matrix. The quality of the matrix can affect dispersal between fragments, and good quality matrices may supplement food resources that are sparse in fragments (Jules and Shahani 2003, Ewers and Didham 2006). The habitat potential of the matrix sets it apart from true islands, as matrix-tolerant species can

15

utilize it as habitat (Laurance 2008). Creating corridors of appropriate habitat and dimensions can facilitate dispersal across the matrix. Corridor establishment between patches augments the area of available habitat, potentially alleviating area-induced population pressures (Tewksbury et al. 2002). More importantly, it increases animal movement and seed and pollen dispersal between patches, allowing plants to colonize other fragments (Tewksbury et al. 2002). Levey et al. (2005) demonstrated that bluebirds (*Sialia sialis*) traveled alongside corridors rather than through them; this indicates that the functional value of corridors may exceed the structural value, and that the presence of corridors can positively affect seed dispersal between fragments as well as in the matrix.

Edge effects present characteristics and species of both the fragments and the matrix, and occur due to environmental changes on the edge of fragments (Bierregaard et al. 2001, Fahrig 2003, Jones and Lindquist 2012). Edge allows sunlight penetration further into the fragments, restructuring vegetation and temperature, hydrologic, and soil regimes deeper in the fragment interiors. For instance, Rankin-De Merona and Hutchings (2001) found that the proportion of dead and damaged trees was concentrated near the edge. Laurance (2001) demonstrated that plant biodiversity decreases in fragments and around the edges due to modified environmental conditions, species invasions, and other disturbances. The shape of a patch can contribute to the proportion of edge and interior habitats as well (Ewers and Didham 2006). The composition of the matrix can also shape edge effects in patches. A matrix of pastureland or bare ground modifies the amount of sunlight and nutrients that reaches the fragment (Bierregaard et al. 2001).

Species composition on the edge often differs from the interior of the fragment (Ewers and Didham 2006). If species preferring the matrix and those preferring the fragments occupy the edge, the total number of species is higher than either habitat type (Ewers and Didham 2006). On the other hand, if species avoid the edge, richness is lower, because the sharp and distinct transition between habitat and edge may discourage dispersal (Ewers and Didham 2006, Yahner 1988). Edge effects around patches increase the chance that an animal will leave the fragment and enter the matrix, which presents a higher rate of mortality (Fahrig 2003). This leads to population decreases and species extinctions when animals are stranded within the fragments (Ewers and Didham 2006). Even if the fragment edge appears attractive to certain individuals, the higher mortality rate, coupled with the altered community composition and interactions on the edge, can lead to reduced reproductive success (Fahrig 2003, Ewers and Didham 2006). Edge may be used seasonally, on an individual basis, or by certain foraging guilds such as predators and parasites, and edge habitat can occur around a fragment or on one side (Fahrig 2003, Yahner 1988). Thus, edge habitat creates varying degrees of diversity in a landscape (Ewers and Didham 2006). Studies of *P. leucopus* demonstrate the variability in edge habitat use, with some populations ignoring the edge and others using it seasonally (Jones and Lindquist 2012). Based on Jones and Lindquist's (2012) trapping results, white-footed mice are found in greater densities on the edges of smaller, highly disturbed fragments than larger, more secluded ones.

Species Interactions in Patchy Habitats

The combined effects of habitat loss, degradation of remaining habitat, and reduced connectivity necessarily alter species interactions in multiple manners. Population size and density fluctuations can have either a positive or negative effect on the system. Decrease in population size can adversely affect mutualisms, leading to reduced reproductive output for either party (Bierregaard et al. 2001). Decrease in population density of predators can allow prey abundance to increase, but may also increase competition among prey (Bierregaard et al. 2001). Altered interactions can open fragments to species invasions. Invasive species can either outcompete weaker competitors, or annex vulnerable niches, further decreasing populations of resident species (Bierregaard et al. 2001). The frequency of encounters between predators, prey, pollinators, seed dispersers, plants, and disease organisms most often decreases in fragmented habitats; this can drive change on a genetic level as organisms adapt to the altered ratios of other species (Hoffmeister et al. 2005). For example, plants may evolve lower resistance to diseases and herbivores (Hoffmeister et al. 2005). Fragmented communities are also volatile; population fluctuations in predators and prey can disturb entire communities in small fragments (Laurance 2008). When the matrix is a hostile environment to certain species, they may be unable to access vital resources in other patches, or, conversely, may lose their route of dispersal (as in plants requiring seed dispersers) (Hoffmeister et al. 2005). Alterations in foraging behavior, especially when animals sacrifice food-rich habitats for safer habitats, modify predator and parasite attack rates in addition to the survival or reproduction of dependent species (Ewers and Didham 2006). Ewers and Didham (2006) describe several examples in which altered pollinator behavior had a noticeable impact on flowering plant reproduction. Trophic cascades can

originate when prey experience predator release (stemming from the local extinction of

natural predators) and multiply (Hoffmeister et al. 2005). This dramatically affects the

abundance of smaller animal prey and plants, and can reduce overall species richness.

Fragmentation may cause trophic cascades from prey as well, if prey microhabitat is

disrupted. In this case, a basic prey item vanishes, causing disintegration higher up the food

chain (Hoffmeister et al. 2005). Trophic cascades eventually favor habitat generalists and

herbivores (Laurance 2008).

On the other hand, some effects of fragmentation may be positive for certain species

(Fahrig et al. 2003). Some species are quite tolerant of habitat fragmentation, and can persist

both in the fragments and the matrix (Ewers and Didham 2006). Depending on the

circumstances, fragmentation can increase the abundance of herbivores or increase the

abundance of predators (Hoffmeister et al. 2005). The mosaic of habitat types can enhance

habitability for species that require several types (Fahrig 2003). Species occupancy may

focus on only a few edges of a fragment, so that interactions center on those points. The

more stochastic conditions on the edge of fragments, such as shifts in environmental

conditions and species arrivals, can change the frequencies and types of interactions (Ewers

and Didham 2006).

Temporal Implications of Fragmentation
The ramifications of habitat fragmentation on individuals, species, populations, and

communities progress over time and landscape scales. Changes on local, intermediate, and

regional levels can lead to increase, maintenance, or decrease in species richness. Locally,

individuals and habitats may disappear, causing populations or species to be obliterated if

they are composed of only a few individuals, or if the habitat is a species requirement (Bierregaard et al. 2001). The most immediate effects include increase in population densities and species richness in the fragments, and loss of species in the matrix (Ewers and Didham 2006). For fragmented populations, immigration has more of an impact on population persistence than population dynamics (Fahrig and Merriam 1994). A greater rate of change in size and configuration of habitat over time causes a decrease in population survival probability (Fahrig and Merriam 1994). Within a metapopulation, dispersal ability may be adversely affected and thus prevent an individual's movement between patches (Bierregaard et al. 2001). Thus, behavioral changes in dispersal ability must occur more quickly than landscape-level changes for survival of a metapopulation (Fahrig and Merriam 1994). Opdam and Wascher (2004) write that metapopulations that have evolved in the presence of some degree of fragmentation are less dramatically affected by fragmentation than those that have evolved in stable habitats.

Over time, fragment species richness decreases because weaker competitors cede to more dominant species (Ewers and Didham 2006, Bierregaard et al. 2001). Competition has genetic consequences, and can drive species evolution in a different direction after the initial fragmentation event (Hoffmeister et al. 2005). Genetic response to fragmentation will favor the extremes of fecundity and dispersal ability, with moderate fecundity and moderate dispersal selected against (Hoffmeister et al. 2005). Species that have evolved in low disturbance habitats are more likely to be specialists, while those that have developed with the pressure of higher disturbance levels tend to be generalists. Thus, generalists will increase in abundance in response to fragmentation, and are more likely to evolve defensive

20

strategies similar to those of invasive species (Hoffmeister et al. 2005). Ultimately, the shift in species composition restructures community interactions, leading to a new community regime (Ewers and Didham 2006).

Habitat fragmentation restructures other ecosystem functions as well. In forests, it predisposes trees to mortality, especially along the edge. This causes the release of greenhouse gases previously sequestered in the trees, elevating atmospheric carbon levels (Laurance 2008). Fragmentation also magnifies the effects of other human disturbances, such as poaching and species invasions, since accessibility to habitat fragments is improved (Ewers and Didham 2006). While habitat fragmentation is largely regarded as imparting a more severe impact on tropical ecosystems, this can be attributed to varying temporal differences in different parts of the world. Ewers and Didham (2006) suggest that the apparent sensitivity to fragmentation in certain locations around the world, such as tropical rainforests, reflects the short time period over which these landscapes have been degraded. In temperate regions, habitat fragmentation occurred long before scientists began to recognize and measure its effects. So, these habitats may have lost their most sensitive species, thus appearing to contain species more tolerant of fragmentation (Ewers and Didham 2006).

Climate change is likely to exacerbate the consequences of fragmentation, especially hindering dispersal ability. It is predicted to raise global temperatures, increase extreme weather events, and raise sea level. Even apart from future human disturbances, ecosystems are expected to undergo change in range of occurrence and species composition (Opdam and Wascher 2004). Climate change can lead to northward range shifts for many

species that require certain climactic conditions for survival and reproduction. However, habitat fragmentation may curtail range limits when extinction exceeds colonization at the edge of a population's range. The movement ability of metapopulations and species will then be based on the ease of dispersal between patches. On the other hand, increased temperatures and the resulting increase in productivity could instigate the development of new vegetative patches, which could increase connectivity within the landscape. Temperatures may also enhance an organism's speed of northward dispersal (Opdam and Wascher 2004).

The emerging field of terragenetics, proposed by Ewers et al. (2013) facilitates the study of a landscape over time. Terragenetic trees, analogous to phylogenetic trees, treat fragments as related entities derived from a common ancestor of continuous habitat. This allows study of the evolution of fragmented landscapes (Ewers et al. 2013). Similar to the species descendants in phylogeny, new fragments descended from older fragments can only inherit traits from the ancestral fragments. Hence, as fragments diverge terragenetically, the communities within the fragments also diverge (Ewers et al. 2013). Consistent with the size-area relationship, larger fragments will host more similar communities than smaller fragments. Furthermore, fragments closer together will be more similar in terms of community structure than those more widely spaced, because they evolved from a common habitat. However, to best apply this model to fragmented landscapes, species tolerances to fragmentation and dispersal ability through matrix habitat need to be assessed and incorporated (Ewers et al. 2013)

2. FRAGMENTATION AND SMALL MAMMALS

Small Mammals and their Responses to Fragmentation

For the purposes of this study, the term "small mammal" encapsulates animals in the orders Rodentia and Insectivora. These animals range in habit from diurnal to nocturnal, social to solitary, and herbivorous to omnivorous. Several aspects of these small mammals' life histories and population ecologies shape their responses to the conditions of a fragmented habitat, but in general several patterns of use emerge. These in turn have broader implications for potential prey, predators, mutualistic partners, and competitors.

Study Species

White-footed mice (*Peromyscus leucopus,* family Cricetidae, order Rodentia) are among the most common mammals trapped in forest or edge habitats of the eastern United States. They occur throughout Virginia and range from Canada south to Georgia and Mexico, and west to Arizona (Rappole 2007). They are active year-round (Burt and Grossenheider 1976). They average 14 – 31 g in weight, and live 2 – 3 years in the wild (Burt and Grossenheider 1976). While *P. leucopus* favors woodlands, it will inhabit fields and open areas as well. Omnivorous, these mice consume insects, seeds, and fruit, and will cache seeds (Rappole 2007). *Peromyscus leucopus* is a nocturnal mammal that takes refuge during the day (Kays and Wilson 2009, Wolff and Hurlbutt 1982). These mice prefer nesting in cavities, under logs and other debris, and beneath trees and shrubs (Wolff and Hurlbutt 1982). They reside in populations of 4 – 12 per acre, breeding from March until

December and producing multiple litters of 2 – 6 offspring per year (Burt and Grossenheider 1976, Rappole 2007). *P. leucopus* may be subject to cyclic population patterns that can lower abundance and density in certain areas. Elias et al. (2004) observed population cycling in these mice over 20 years of study. The authors noted a 4-year periodicity between population lows and highs for *Peromyscus leucopus.*

The meadow vole (*Microtus pennsylvanicus*, family Cricetidae, order Rodentia) is strongly associated with grassy cover (Kays and Wilson 2009). It is found from Canada to Georgia, and in the northwest United States. It is widespread in Virginia. These voles range in weight from 33 - 65 g, and occupy dense grassy habitats in meadows, forests, fields, and marshes (Kays and Wilson 2009, Rappole 2007). They create runways underneath the grasses, and are active day and night and throughout the year (Rappole 2007). Meadow voles consume plant products almost exclusively, and store food as well (Rappole 2007). They are promiscuous, breeding from April to October and producing several litters a year (Burt and Grossenheider 1976, Rappole 2007). They may also be territorial during the breeding season (Vlautin and Ferkin 2013). Meadow voles live 1 – 3 years, and are an important prey item for a variety of reptilian, mammalian, and avian predators (Burt and Grossenheider 1976).

Zapus hudsonius, the meadow jumping mouse (family Zapodidae, order Rodentia), possess elongated tails and feet compared to *P. leucopus*, which aid in locomotion (Kays and Wilson 2009). At 12 – 30 g, they are slightly smaller than the white-footed mouse (Kays and Wilson 2009). They range from northern Canada south to Colorado, and are found throughout Virginia. Habitats include grasslands, fields, and riparian areas (Kays and

Wilson 2009, Rappole 2007). These solitary mammals hibernate between October and May

(Rappole 2007). They favor arthropods during the first part of the summer, adding plant

material further into the season (Rappole 2007). Jumping mice live 1 – 2 years, but reach

sexual maturity during the second year (Burt and Grossenheider 1976, Rappole 2007).

Breeding takes place from May to September, and usually 2 litters are delivered per season,

producing 4 – 6 mice (Rappole 2007). Populations remain fairly low throughout the year

(Burt and Grossenheider 1976).

Eastern Chipmunks (*Tamias striatus,* family Sciuridae, order Rodentia) prefer

deciduous forest habitat, including secondary growth forests. Distributed in the entirety of

Virginia, *T. striatus* is a creature of the eastern United States and Canada (Rappole 2007).

They are solitary, and weigh 80 - 150 g (Kays and Wilson 2009). They are diurnal and

somewhat fossorial, and store food underground (Kays and Wilson 2009, Rappole 2007).

Diet consists of seeds, nuts, fruits, eggs, invertebrates, and meat. Two breeding cycles

occur, one in the spring and one in the summer (Rappole 2007). These produce 3 – 5

offspring each per female (Rappole 2007). Eastern chipmunks can live over 3 years, and

begin breeding after their first year. They also defend territories (Burt and Grossenheider

1976).

The northern short-tailed shrew, *Blarina brevicauda* (family Soricidae, order

Insectivora) is a common shrew of woodlands and grasslands in Virginia. In the

southernmost Coastal Plain region of the state, it is replaced by the closely related southern

short-tailed shrew (*Blarina carolinensis*), which was previously considered a subspecies

(Rappole 2007). Northern short-tailed shrews are found in eastern and central Canada and

the United States, and south through Colorado. They are smaller than mice, weighing 11 –

22 g (Burt and Grossenheider 1976). These shrews are most active nocturnally, but may

forage during the day for insects and soft-bodied invertebrates, as well as some plant

material (Rappole 2007). Short-tailed shrews are highly insectivorous, and must consume a

large quantity of food per day to fulfill their caloric requirements (Do et al. 2013). They may

also prey upon young cricetids (Burt and Grossenheider 1976). According to Lomolino

(1984), *B. brevicauda* can significantly decrease juvenile survivorship of meadow voles

(*Microtus pennsylvanicus*). Prey is subdued with potent neurotoxic venom (Lomolino

1984). These shrews have very short lifespans coupled with their high activity levels. In the

wild, they live to an age of about 18 months (Hindle et al. 2009). This species can achieve

population densities of 62 individuals per hectare, and is the most frequently observed

shrew species in its range (Burt and Grossenheider 1976, Rappole 2007). Breeding occurs

from March through November, producing 5 – 8 young that mature in 3 months (Rappole

2007).

These mammal species are ecologically important herbivores, predators, seed

dispersers, and prey, and their behavior in fragmented habitats can influence community

interactions (Rappole 2007, Munshi-South 2012). Additionally, although these animals

can persist in habitats with small (< 1 ha) fragments, their abundance and distribution

may vary spatially (Diffendorfer et al. 2005, Brady et al. 2011). Predators, competitors,

and plants may therefore alter their distribution in response. Ticks and Lyme disease risk

have been reported to be elevated in fragmented landscapes, possibly because of high

mammal densities in fragments (Allen et al. 2003, McCallum and Dobson 2002, Ostfeld

and Keesing 2000). Understanding mammals' responses to fragmentation might therefore predict where other species interactions are likely to occur.

Study Overview

Previous fragmentation studies have encompassed experimentally modified landscapes, focused on either quantity or quality of matrix habitat, or examined the relationship between fragment size and species richness (Debinski and Holt 2000). This study examined fragmentation in relation to habitat use and foraging behavior by small mammals, through the use of pre-existing fragments of varying sizes, over the course of two summers. Both quantity and quality of habitat were evaluated and habitat types (fragment, matrix, and forest) were compared. For the purposes of this investigation, the matrix was considered any herbaceous habitat that differed in both structure and species composition from the fragment and forest habitats. The fragments and forests consisted of rock, herbaceous ground cover, shrubs, and trees, whereas the matrix was composed of grass and herbaceous ground cover with few shrubs or trees. Additionally, I used a standard feeding test to gauge the perception of predation pressure for small mammals feeding within each habitat type. The average height of the vegetation within the matrix was manipulated during the second year to provide greater or less connectivity between fragments and the nearby forest. Finally, small mammals' occurrence within fragments was examined relative to fragment size and distance from larger forest patches.

Habitat usage of the forest, matrix, and fragment

Small mammal populations are responsive to food availability and predation risk in fragmented habitats. Marcello et al. (2008) found that food availability increased white-

footed mouse (*Peromyscus leucopus*) reproductive success, and increased population densities in forest fragments. Fragments with a certain type of resource can affect population size and density as well; for example, *Peromyscus* and *Tamias* populations are correlated with abundance of acorns, a cyclical food (McShea 2000). During years following a small acorn crop, small mammals increase their predation on bird eggs, thereby negatively impacting other species (McShea 2000). However, years with large acorn crops also coincided with lower artificial nest predation rates by small mammals (McShea 2000). McShea (2000) determined that yearly acorn mast crops accounted for a significant portion of the small mammal population variability; therefore, fragments with this food source can augment rodent populations at a lower cost to other species.

Animals forage to maximize food intake while minimizing the costs of possible predation (Verdolin 2006). The risk of predation is tied directly to the amount of cover, and affects where animals will forage (Verdolin 2006, Hughes et al. 1994). *Peromyscus leucopus* tolerate some of the effects of habitat fragmentation (Allan et al. 2003). These mice can reach high population densities in small fragments possibly due to the elimination of larger predators and interspecific competitors (Allan et al. 2003).

According to Hughes et al. (1994), GUD tests utilizing seed trays assume that animals will forage in a certain area as long as the benefits of the food outweigh the costs of using that specific area. GUD tests require an animal to spend time at the seed tray, as seeds are interspersed with a substrate through which the animal must sort to access the food (Hughes et al. 1994). Predation risk was demonstrated to have a strong effect on GUD results for several studies, with higher GUD's (less bait removed) in areas with a

higher predation risk (Verdolin 2006). Verdolin (2006) further suggests that the type of

habitat may influence the degree of predation risk.

The Impacts of Matrix Structure and Quality

In the summer, when population density can be high, mice may use habitat types

other than woodland to avoid competition (Cummings and Vessey 1994). Deer mice (*P.

maniculatus*), for example, were observed to use the matrix surrounding experimental

fragments (Diffendorfer et al. 1995). However, the structural quality and complexity of the

matrix, as well as the distance between fragments and the forest, influences such behavior

(Barnum et al. 1992, Klein and Cameron 2012). *Peromyscus leucopus* prefers cover types

that provide the greatest degree of protection from predators (Barnum et al. 1992). In terms

of ground cover, mice choose to travel under forbs while avoiding grasses (Barnum et al.

1992). Forbs provide more cover than grasses, and mice can move through them more

silently (Barnum et al. 1992). Seasonal growth and senescence of vegetation can also alter

habitat use for mice, as the amount of cover shifts with the seasons (Barnum et al. 1992).

White-footed mice are tolerant of several habitat types, but thrive in areas with greater

vegetative complexity, and avoid crossing grass fields (Cummings and Vessey 1994).

Cummings and Vessey (1994) demonstrated that *Peromyscus leucopus* avoided shorter

matrices and bare ground, and foraged in more structurally complex matrices. Similarly,

Merriam and Lanoue (1990) determined that *P. leucopus* in agricultural fields preferred to

move along fencerows than in the fields, and selected fencerows with greater structural

complexity. Klein and Cameron (2012) found that female mice relied on vertical structure

when woody cover was less abundant. In contrast, Jones and Lindquist (2012) observed

that white-footed mice were not restricted to woody debris. Preference for cover is not restricted to mice. In voles (*Microtus* sp.), Getz and McGuire (2008) found that cover was more strongly correlated with animal movement than food availability.

Patch Size and Configuration

Larger patches are generally considered to harbor greater species richness (Fahrig 2003, Hanski et al. 2013). However, small patches may contain more animals per unit area than larger fragments (Allan et al. 2003, Anderson and Meikle 2010), possibly due to the absence of predators in the small fragments, or microhabitat characteristics that develop in small fragments as a result of increased edge (Anderson and Meikle 2010). Configuration of fragments also affects foraging behavior (Fahrig 2003, Diffendorfer et al. 1995). Fragment occupancy for *P. leucopus* increases when the fragments are closer to larger forested areas. Diffendorfer et al. (1995) reported that among deer mice (*Peromyscus maniculatus*) and prairie voles (*Microtus ochrogaster*), animals moved less frequently and for longer distances in response to increasing levels of fragmentation (larger blocks to smaller blocks in their experiment).

Demographic Attributes of a Fragmented Population

Individual foraging behavior can translate to population-level effects when dispersers are demographically distinct. According to Cummings and Vessey (1994) and Krohne et al. (1984), dispersing individual *P. leucopus* were more likely to be adult males than females. In contrast, Linzey et al. (2012) observed that juvenile male *P. leucopus* were more likely to colonize suboptimal habitat. While both studies indicated

that males were more likely to migrate, the age difference could be due to local and seasonal population fluctuations at each study site.

I hypothesized that animals will forage longer on a standardized food tray in areas with more cover (habitat fragments or forest sites) as opposed to the matrix; that foraging behavior within the matrix will depend on the amount of cover (tall or short grass); that animals will occupy larger and less isolated fragments; and that mice (*P. leucopus*) occupying the fragments and matrix are more likely to be the sub-demographic most likely to disperse (i.e. adult scrotal males). My null hypothesis was that animals would not alter their habitat use based on degree of fragmentation or fragment or matrix quality. A combination of methods, including live trapping, giving-up density (GUD), plant surveys, and camera trapping were employed to test these hypotheses. Live trapping provides data on where animals reside, as well as their demographics and condition. GUD indicates the relative amount of time spent foraging under risk of predation, while plant surveys and camera trapping describe perceived cover and predation risk for these small mammals. The results were compared between summers, and were analyzed to determine which factors have the greatest influence on an animal's use of fragmented landscapes..

3. METHODS

Data was collected over the summers of 2012 and 2013 at the Smithsonian Conservation Biology Institute (SCBI) in Warren County, Virginia (38°53'15.6" N, 78°9'54.6" W). The area consisted of old pastureland (33%) bordered by deciduous forest (61%), as well as active hay fields (6%), covering an area of approximately 118 ha (ArcMap 10.1). The fields were created prior to 1948 to graze domestic livestock (McShea et al. 1993), creating fragments of secondary forest embedded in a matrix of new field habitat. I sampled in twenty wooded fragments located in four different fields (See Figure 8, Appendix). These fragments were situated in a grass matrix that separated them from continuous forest, which exceeded 1 ha in area and contained a greater proportion of woody vegetation than either the fragments or the matrix. The majority (18) of the patches were sampled both seasons, but two patches were replaced from 2012 to 2013. In one of these cases, multiple stems of autumn olive (*Elaeagnus umbellata*) had encroached on the matrix and connected the fragment to the larger forest. In the second case, the fragment was destroyed as part of a construction project. The replacement patches were located in the same study area, within 300 m of the originals. Management of the study area consisted of annual bush hogging of the matrix during the non-sampling season. In the summer of 2013, patch connectivity was manipulated by advancing the date of mowing into the middle of the trapping season. This acceleration resulted in trials

with a tall (>60 cm) matrix, followed by short (<40 cm) matrix trials. My intent was to

change the matrix structure but not the plant species composition (see Jacob and Brown

2000).

Experimental Design

The home range of *P. leucopus* was estimated to be 100 m^2 in fragmented habitats

(Diffendorfer et al.1995; Bowers et al. 1996), with a minimum size of 32 m^2

(Diffendorfer et al. 1995). My fragment sizes ranged from 100 m^2 to 756 m^2 . The

median fragment size for the current study was used to delineate small and large

fragments for size comparisons; fragments with an area <172 m^2 were considered small,

and those with an area >172 m^2 were classified as large. Fragments were separated by >

25 m from other fragments, and from continuous forest. Fragments varied in proportion

of different cover classes (bare soil, rock, woody debris, herb/vine/bush vegetation, and

trees) (see Table 1). The distance between the fragment and the closest continuous forest

was classified into two classes, with short distances considered 25 – 40 m and long

distances inclusive of 40 – 110 m; the median of the data was used to determine the

classification.

Table 1: Fragment characteristics, including size, cover class, matrix length (distance to forest), distance to nearest fragment, and average matrix height for the summer of 2013. Sampling included live trapping, GUD, and plant surveys for each fragment. Fragments 2 and 15 not sampled in 2013; fragments 21 and 22 were replacements for 2 and 15, and were sampled in 2013 only. Small (S) and large (L) fragment sizes and near (N) and far (F) distances from forest were determined relative to the median of the area and isolation measures. Fragments 16, 17, 19, and 20 were tall matrix controls throughout 2013; plants remained tall (>60 cm) throughout the summer.

Name	Fragment Size (m^2)	% Bare Soil and Rock	% Woody Debris	% Herbs	% Trees (>3 m tall)	Matrix Length (m)	Distance to Nearest Fragment (m)	Small/ Large Near/ Far	Avg Tall Matrix Height (cm)	Avg Short Matrix Height (cm)
1	100	0	5	55	40	25	47	S, N	90	30 - 40
9	100	20	20	30	30	25	39	S, N	120	30 - 40
18	104	10	25	50	15	90	195	S, F	120	30 - 40
10	110	25	10	50	15	40	50	S, N	140	30 - 40
11	110	21	11	8	60	62	29	S, F	90	30 - 40
20	110	0	20	70	10	103	107	S, F	60	90
7	120	4	6	60	30	30	32	S, N	95	30 - 40
13	126	6	14	50	30	60	45	S, F	95	30 - 40
2	150	15	15	30	40	60	34	S, F	~60	~60
19	153	25	10	30	35	26	94	S, N	60	90
21	168	5	20	30	45	33	43	S, N	60	30 - 40
6	176	25	15	20	40	42	44	L, F	120	30 - 40
17	200	10	20	40	30	110	53	L, F	100	170
22	270	3	15	15	67	25	31	L, N	90	30 - 40
14	272	0	15	20	65	55	31	L, F	95	30 - 40
3	390	0	25	45	30	39	23	L, N	95	30 - 40
8	400	2	20	50	28	51	34	L, F	120	30 - 40
5	450	10	10	50	30	29	43	L, N	60	30 - 40
16	480	10	15	45	30	25	51	L, N	130	180
4	544	5	25	35	35	27	23	L, N	95	30 - 40
15	576	15	30	25	30	58	117	L, F	~90	~90
12	756	10	20	15	55	80	46	L, F	90	30 - 40

Twenty fragments and their corresponding transects were identified in six different fields. Transects ran along the most direct path from each fragment, through the matrix and into continuous forest. Continuous forest was distinguished from edge habitat

and the matrix by the presence of trees at least 10 cm in diameter (after Rankin-De

Merona and Hutchings 2001 and Laurance 2001), and all areas of continuous forest were

greater than 1 ha. Based on the assumption that an animal prefers not to forage more than

10 m into the matrix due to unsuitable habitat and increased predation risk (similar to

Klein and Cameron 2012), the minimum transect length was set at 25 m from fragment to

forest to accommodate four trapping stations in the matrix (See Figure 1).
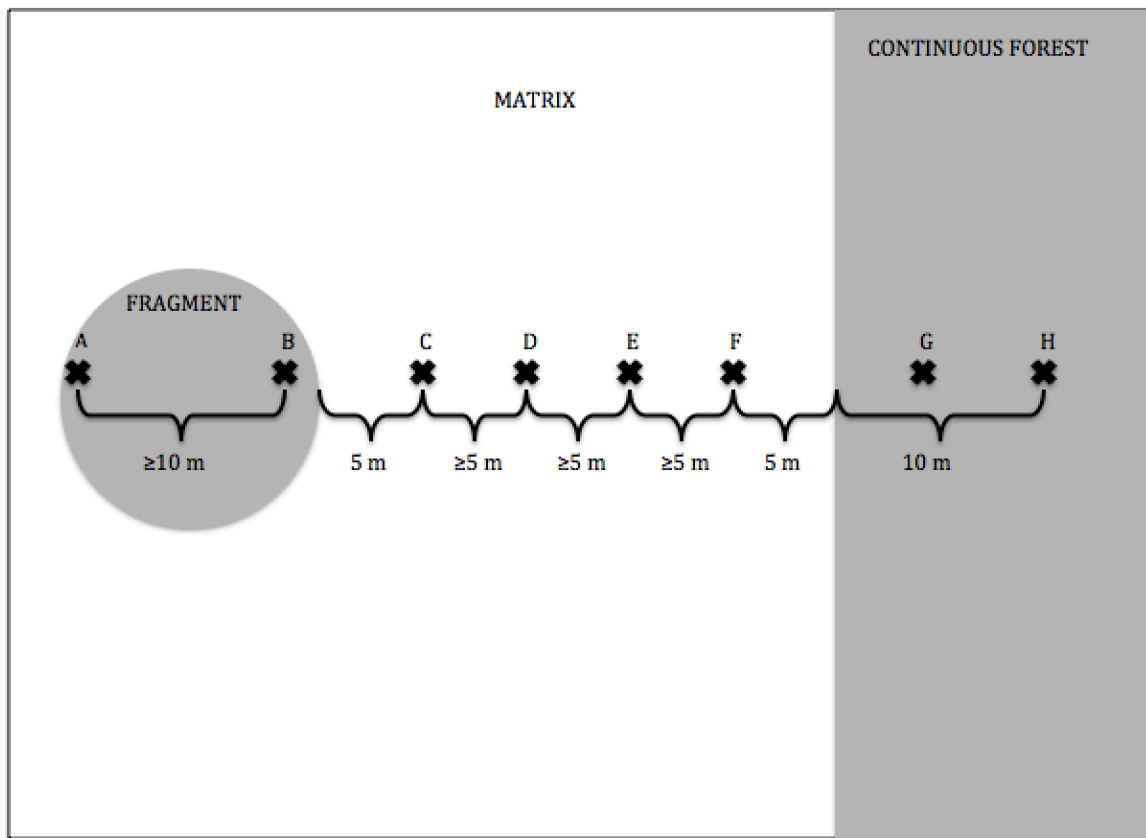
Figure 1: Trapping stations (black x) along a transect, from fragment to forest (shaded) through a grass matrix (unshaded). Each station consists of two traps. Matrix traps D and E were placed at least 10 m from fragment or forest; this distance varied based on matrix length.

For trapping, Sherman folding live traps (3.5 x 3.5 x 9 in, H. B. Sherman Traps Inc.,

Tallahassee FL) were set along each transect. Each transect consisted of eight trap

stations; two within the fragment, four within the matrix and two with the forest. For the

matrix one trap station was placed 5 m from the fragment, two in the matrix and

equidistant from fragment and forest, one trap station 5 m from the forest. Each trap

station consisted of two traps. Live trapping took place each week from June to August

(2012) and May to August (2013). Traps were baited with a mixture of whole oats and

black sunflower seeds, and were prebaited for one night prior to opening for two nights.

Traps were opened between 1500 and 1800 and checked between 0700 and 0900 (earlier

if high temperatures presented a serious risk of mortality). After checking and removing

animals, traps were closed to prevent captures during the day. Animals were removed

from traps in a plastic bag, and bags were discarded when soiled. Data on date, transect

number, trap location, species, age, sex, weight (Pesola® spring scale, Baar,

Switzerland), and reproductive status were noted for all animals except shrews (*Blarina*

brevicauda), and animals were marked with a unique numbered metal ear tag (Kent

Scientific Corporation, Torrington, CT) prior to release at the capture location. Shrews

were not marked or checked for gender, but were weighed before release. Animal

handling protocols followed the *Guidelines of the American Society of Mammalogists for*

the Use of Wild Mammals in Research (Sikes and Gannon 2011), and were approved by

the National Zoological Park Animal Care and Use Committee.

Giving up density (GUD) trials were conducted subsequent to the live trapping of

each transect. GUD trials consisted of an aluminum foil food tray within a mesh live

animal trap (mesh dimensions=2.54 x 2.54 cm) or conical chicken wire cage (mesh

diameter=5 cm). The cages over the trays were staked into the ground to deter predators

from uprooting them. Both cage types allowed mice and smaller mammals to access the

food through the mesh, but excluded larger animals. Three GUD cages (one in the

fragment, one in the middle of the matrix, and one in the forest) were placed on each

transect after the live trapping was complete. GUD trays were baited with a mixture of

whole oats and black sunflower seeds in a substrate of wood chips. Seeds were dried in a

drying oven overnight at 65°C prior to the trials. Each tray contained 4.0±0.004 g of

seeds and 8.0±0.004 g of wood chips. The remaining material was collected after one

night, and seeds were separated and dried for 48 hours before being reweighed.

To gauge habitat and cover for small mammals based on floristic diversity, plants

were sampled in the fragments, the matrix, and the forest at the end of the trapping

season. Plants were sampled within a 1 m^2 quadrat placed randomly within each

fragment. In the matrix, I used a random number generator to determine the distance from

the fragments (in meters); the maximum distance was 70 m. Herbaceous and woody

vegetation rooted in the quadrat, and any leaves within from the taller trees, were

identified to species if possible.

During the second summer, camera trapping was added to record small mammal

foraging behavior, as well as evidence of predators. Two adjacent camera trapping

transects were set; one included GUD trays baited with seeds and wood chips, and the

other control transect included trays with only wood chips. Spypoint HP-7 trail cameras

(G. G. Telecom, Vermont, USA) were attached to trees within 1 – 2 m of the GUD trays,

at a height of approximately 30 cm. Cameras were set for two nights; prior to the second

night, the trays were replenished with bait and wood chips as needed. Six sets of camera

lines were surveyed (six baited lines and six controls). Three cameras were placed on

each GUD and control line. Images of the same species appearing after a 30-minute time

interval were considered unique detections (Kelly and Holub 2008).

Matrix Treatments

During the 2013 season, the height of the matrix was manipulated to alter the

amount of cover between the fragments and forest. Trapping and GUD tests were

conducted twice for all transects within a tall matrix (plant height 60 – 180 cm tall).

Following mowing of the fields, the same trials were performed on 16 transects with a

short matrix (average plant height <40 cm tall). Four transects were not mown during the

interval and served as controls. At least three weeks elapsed between the tall and short

matrix treatments.

Data Analysis
Live Trapping

Trapping results were analyzed with single-factor ANOVA to determine the

importance of habitat type in influencing habitat use. Only *Peromyscus leucopus* and

Blarina brevicauda captures were frequent enough to include in the analysis. Number of

captures in each habitat type per line was the dependent variable, reflecting frequency of

use in each habitat, and groups included the fragment, matrix, and forest. This test was

performed for each species, for both years combined. Capture probability of all individual

Peromyscus leucopus was calculated for each habitat type in 2012 and 2013 utilizing

Program MARK (White and Burnham 1999). Individuals recaptured in the same habitat

type at least two weeks apart were considered residents; those captured only once over the course of the sampling period and those moving between habitat types were considered transient animals. Demographic data on individual *P. leucopus* were aggregated for each habitat type, including the number of individuals per demographic attribute per transect. Demographic attributes included age (adult vs. juvenile), sex (male vs. female), weight class (<20 g (juveniles), 20 – 25 g, 26 – 30 g, >30 g), and reproductive status (non-reproductive, scrotal, or lactating). The weight classes were created so that weight could be more specifically defined as driving factors in the multivariate analyses. Paired t-tests and one-way ANOVA were conducted on demographic data categories (i.e., adult vs. juvenile, lactating vs. scrotal vs. non-reproductive) for each habitat type, in order to verify the significance of any differences. Any significant results from ANOVA tests were analyzed *post hoc* with the Tukey HSD test. Comparisons between small and large fragments and less and more isolated fragments, using capture frequency and individual demographic data organized by transect, were analyzed with one-way and two-way ANOVA and ordination. For the ANOVA tests, capture data was organized by habitat type and year, and analyzed with two-way ANOVA with replication. PC-ORD was used for multivariate data analyses, including tests for habitat, fragment size and isolation differences (McCune and Grace 2002). Non-metric multidimensional scaling (NMS) ordination and multi-response permutation procedure (MRPP) were employed to determine relatedness among transects, in which demographic data (age, sex, weight, and reproductive status) for *Peromyscus leucopus* individuals were the attributes of the data set. NMS identifies patterns and

driving factors, while MRPP assigns a significance value to the groups within the data.

For the habitat analyses, individuals in each habitat for each transect were tabulated, for a

total of 66 entities (3 habitats per 22 transects). For the size and isolation analyses,

demographic data for the fragment and matrix habitats were combined for each of the 22

transects. NMS employed Euclidean distance, and included 3 axes, a stability criterion of

0.00001, 250 maximum iterations, and a step length of 0.2. MRPP was conducted to

determine the significance of categorical groupings; MRPP tests were run using

Euclidean distance. Coding matrices corresponding with habitat type were generated for

this test.

Giving-up Density (GUD)

For both summers, GUD values were obtained for each trapping week, translating

to three values per transect per trapping week. For the summer of 2013, GUD trials were

replicated twice for each matrix treatment (tall vs. short), and data were included in

single-factor ANOVA tests for both location comparisons and matrix treatment

comparisons. GUD results for 2012 and 2013 were combined to determine the overall

significance of foraging behavior in each habitat. Since more GUD trials were performed

during 2013, values were averaged to make the numbers comparable to the 2012 trials.

Due to a noticeable yearly difference in the data, ANCOVA was utilized with grouping

by habitat type, and included year as a covariate to control for the effect of year on GUD

results.

Floristic Surveys

The differences in plant species richness were analyzed for both years between

the fragment, matrix, and forest with single-factor ANOVA. Number of species per line

(average between 2012 and 2013) was the dependent variable, and data were grouped by

habitat. Tukey HSD tests were performed on any significant results.

Matrix Treatments

       For the matrix treatments, one-way ANOVA was run for each treatment (tall vs.

short) to compare the habitat types. These were performed with abundance data for *P.*

leucopus and *B. brevicauda* individually. Similar one-way ANOVA tests were run for the

GUD trials in tall and short matrices. Subsequently, the control transects were analyzed

with one-way ANOVA between earlier and later sampling periods to determine if

seasonal movements could account for the capture results. A series of one-way ANOVA

tests between habitat types were employed to examine the differences between

demographic attributes of *Peromyscus leucopus* for the tall and short matrix treatments;

these tests were performed for each demographic category individually, and consisted of

the number of individuals from each habitat type grouped by matrix treatment. *Post hoc*

Tukey HSD tests were used to evaluate any significant results.

4. RESULTS

Live Trapping Success

For 2012, 52 captures occurred over 1216 trap nights, resulting in a 4.3% capture success. Five small mammal species were captured over the course of the study, including *Peromyscus leucopus*, *Blarina brevicauda, Microtus pennsylvanicus, Zapus hudsonius,* and *Tamias striatus*. Only *P. leucopus* and *Blarina brevicauda* were captured in all three habitat types. The overall mortality rate was 1.9%. For 2013, 433 captures occurred over 2528 trap nights, yielding a 17.1% capture success, and the mortality rate was 6% (See Table 2). Shrews accounted for most of the mortality, with a rate of 33.8%, and the white-footed mouse mortality rate was 0.83%. No vole or chipmunk deaths were observed.

Table 2: Capture success rates for each small mammal species. "Number of traps" reflects the total number of traps set for all nights when the species was captured.

Species	2012			2013		
	Number of Captures	Number of Traps	Capture Success (%)	Number of Captures	Number of Traps	Capture Success (%)
Peromyscus leucopus	44	1200	3.67	360	2480	14.5
Blarina brevicauda	6	800	0.75	68	1520	4.47
Microtus pennsylvanicus	0	0	0	3	240	1.25
Zapus hudsonius	2	240	0.83	0	0	0
Tamias striatus	0	0	0	2	160	1.25

Twenty-one of twenty-two fragments were occupied during 2012 and 2013 (See Figure 2). On average, each fragment hosted five individual mice over the two-year period, which encompassed 5 weeks of trapping per fragment. Thirteen animals were identified as fragment residents and ten as forest residents, while 233 were classified as transients. Fragment residents were mainly adult (9 adults, 4 juveniles) and non-reproductive (7 non-reproductive, 1 lactating, and 5 scrotal), but the number of male and female individuals was roughly equivalent (7 males and 6 females). Forest residents were also mainly adult (8 adults, 2 juveniles), but more residents were scrotal (4 non-reproductive, none lactating, 6 scrotal) and male (8 males and 2 females). Nine of the transients were recaptured in different lines during both years. All individuals that switched transects were male, and eight of nine were scrotal males. Four transect switches occurred through continuous forest, three through matrix habitat, and two to different fragments. In addition, 3 recaptured animals migrated between the forest and fragment habitats within the same transect. However, 70 of the 88 recaptures over both seasons occurred within 10 m of the original capture site.
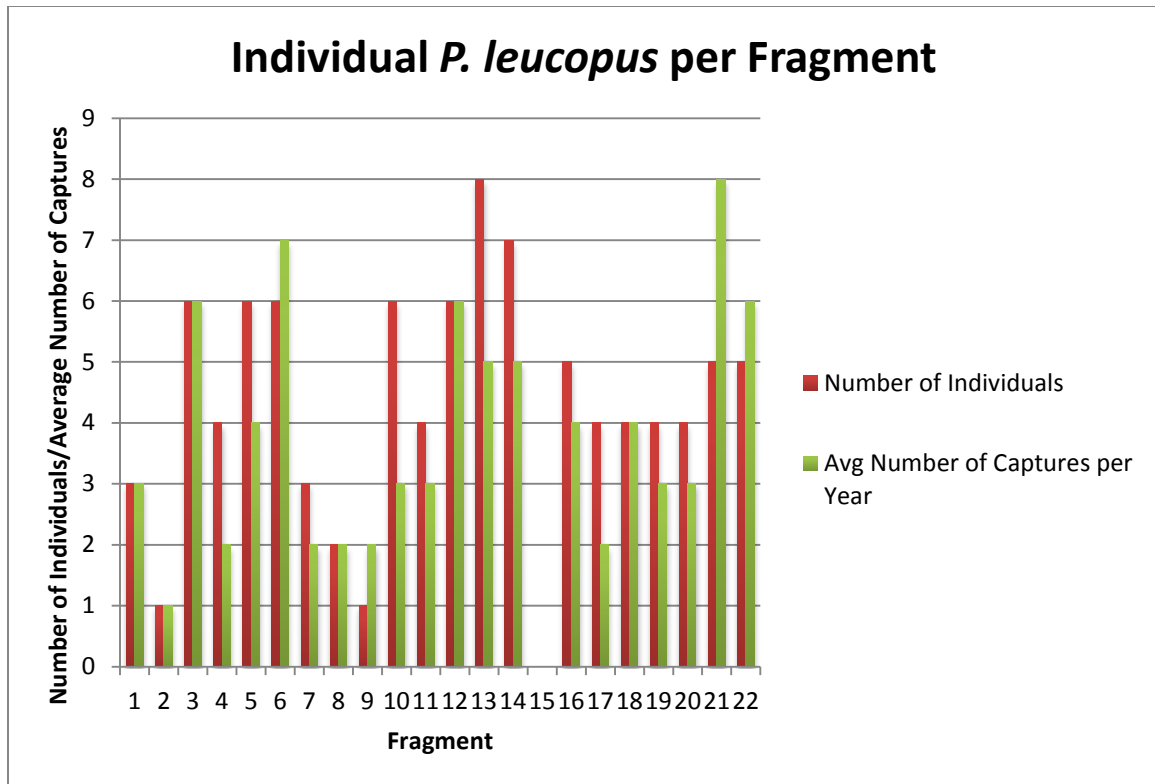
Figure 2: *Peromyscus leucopus* captured in fragments for the summers of 2012 and 2013. Fragments 2 and 15 were replaced with fragments 21 and 22 for 2013. No mice were captured in fragment 15.

Differences between Fragment, Forest, and Matrix

Vegetation provides cover and food to small mammals. Overall, 93 plant species, consisting of flowering plants and conifers, were identified across the three habitats. Comparison of plant diversity for both years combined demonstrated that the habitats were significantly different (ANOVA: $F_{(2,57)}=16.08$, $p<0.0001$) between the fragment and the matrix and the fragment and the forest, but no difference between forest and matrix (Tukey HSD: X=8.45, SD=2.17 for fragment, X=5.7, SD=1.74 for matrix, and X=5.6, SD=1.43 for forest). Fragments had the highest average number of plant species, while the matrix and forest habitats were roughly equivalent (See Table 3).

Table 3: Plant diversity parameters by habitat, where the minimum and maximum values refer to the number of species and average plant diversity (number of species) is followed by standard deviation (SD)

Habitat	Minimum	Maximum	Average Plant Diversity (Species)+ SD
Forest	3	8	5.6 + 1.43
Matrix	2	10	5.7 + 1.74
Fragment	6	15	8.45 + 2.17

Predation risk may be greater in the matrix if plant cover is reduced and predator abundance is high. Cameras placed on lines of GUD and control bait trays captured predators investigating the GUD and control trays, while photographic evidence of foraging mammals was limited to the baited trays. Predators were photographed in both day and evening. Main predators observed were raccoons (*Procyon lotor*) and black bears (*Ursus americanus*). Mammals foraged between 2200 and 0800, with a peak in activity between 0300 and 0600. The only small mammal photographed was *Peromyscus leucopus* (See Table 4).

Table 4: Camera detections by species in each habitat type. Bait=standard GUD setup with seeds, control=tray with wood chips only.

Species	Fragment		Matrix		Forest		Total Number of Detections
	Bait	Control	Bait	Control	Bait	Control	
Procyon lotor	4	6	3	2	1	5	21
Ursus americanus	0	0	1	1	0	0	2

| *Peromyscus leucopus* | 0 | 1 | 0 | 0 | 10 | 4 | 15 |

Mice (*Peromyscus* leucopus) and shrews (*Blarina* brevicauda) respond differently to fragmentation depending on the amount of cover and risk of predation. For *Peromyscus leucopus*, the differences between habitat types were significant (ANOVA: $F_{(2,117)}=10.24$, $p<0.0001$). *Post hoc* Tukey HSD testing indicated that mice were more prevalent in the fragment (X=4.65, SD=4.45) and forest (X=4.15, SD=3.85) than the matrix (X=1.33, SD=1.76), but there was no significant difference between the fragment and forest. Overall, shrews (*B. brevicauda*) did not forage significantly differently in any of the three habitat types (ANOVA: $F_{(2,117)}=0.763$, $p=0.468$), although they exhibited a slight preference for matrix habitat (X=0.5 captures per line, SD=1.24) over the fragment (X=0.8, SD=1.14) or forest (X=0.55, SD=1.38).

Giving-up densities (GUD's) indicate how much foraging occurred as a function of perceived predation risk. Average GUD's differed between year and habitat type (see Table 5); yearly differences were significant (ANOVA: $F_{(1,4)}=20.0$, $p=0.011$). Correcting for year as a covariate, animals foraged in each habitat differently during both years combined (ANCOVA: $F_{(2,116)}=10.72$, $p<0.0001$). The average weight of remaining bait was significantly lower in the fragment and forest than matrix habitat, but not significantly different in the fragment and forest habitats (Tukey HSD: X=2.00, SD=1.64 forest, X=2.08, SD=1.50 fragment, and X=2.94, SD=1.12 matrix)

Table 5: GUD results by year for fragment, forest, and matrix, out of an original 4.00 g seeds. Higher GUD's indicate that less food has been consumed.

		2012			2013	
Habitat	Sample size (n)	Avg Amount Remaining (GUD) (g)	% Consumed	Sample size (n) per matrix treatment	Avg Amount Remaining (GUD) (g)	% Consumed
Fragment	40	3.68	7.91	40	0.947	76.3
Matrix	40	3.83	4.29	40	2.25	43.7
Forest	40	3.24	19.0	40	0.713	82.2

Comparison of habitat types under the tall and short matrix treatments yielded different results for each species (See Figure 3). During the two treatments, only the height of the matrix vegetation was changed through mowing. *P. leucopus* used the tall matrix habitats to a greater extent than those of the short matrix. The forest and matrix habitats were used similarly, while the fragment habitat was used significantly more than the matrix (ANOVA: $F_{(2,45)}=7.13$, p=0.002; Tukey HSD: X=2.44, SD=1.49 for forest, X=1.56, SD=1.86 for matrix, and X=3.88, SD=1.78 for fragment). On the other hand, the short matrix habitats were used less frequently and habitats were more clearly distinguished (ANOVA: $F_{(2,45)}=5.31$, p=0.009). The fragment and forest habitats were clearly delineated from the matrix, with (Tukey HSD: X=3.13, SD=2.36 for fragment, X=3.00, SD=2.45 for forest, and X=0.94, SD=1.44 for matrix). In contrast with *P. leucopus*, shrews (*Blarina brevicauda*) exhibited no difference in occupancy of the habitats between matrix treatments (ANOVA: $F_{(2,45)}=3.70$, p=0.375 for tall and $F_{(2,45)}=2.80$, p=0.071 for short).
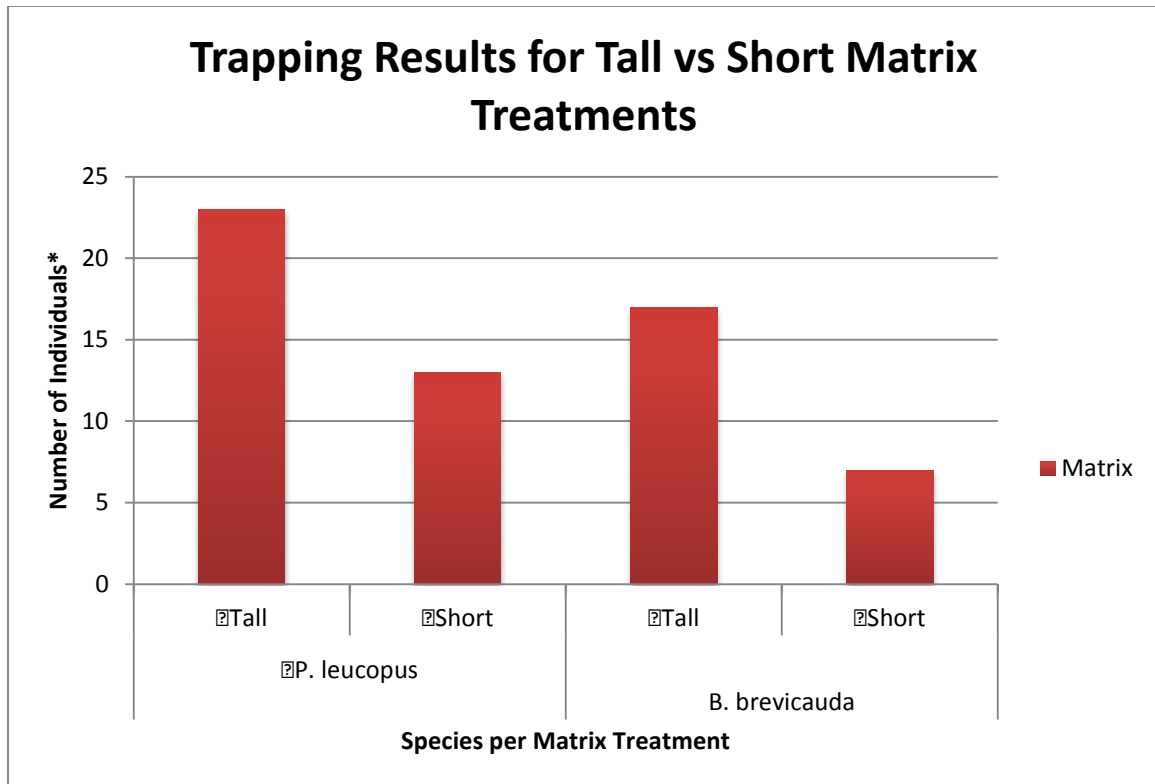
Figure 3: Number of individual *Peromyscus leucopus* and *Blarina brevicauda* captured in the matrix during each matrix treatment. *B. brevicauda* were not marked, so all captures were counted as individuals.

Similarly, foraging patterns reflected the impact of matrix height. For the GUD trials, the taller matrix increased connectivity between habitats and encouraged more foraging than with the short matrix (ANOVA: $F_{(2,42)}=4.17$, $p=0.02$). While the fragment and matrix were similar in amount of foraging, the forest was distinguished from matrix habitat (Tukey HSD: X=1.26, SD=0.97 for fragment, X=2.00, SD=1.26 for matrix, and X=0.88, SD=0.92 for forest). Under influence of the short matrix with less cover and elevated perceived predation risk, the habitats were distinct and less foraging occurred (ANOVA: $F_{(2,45)}=26.3$, $p<0.0001$). Fragment and forest habitats were each significantly different from the matrix, but similar to each other in terms of foraging activity (Tukey

HSD: X=0.24, SD=0.34 for forest, X=0.57, SD=0.65 for fragment X=2.88, SD=1.80 for

matrix).

Four of the lines were not mown and the matrix vegetation remained tall

throughout the summer; these were treated as controls to determine whether any

differences between the tall and short matrices were due to seasonal animal movements.

Most captures occurred in the forest, followed by the fragments, followed by the matrix

for earlier and later sampling efforts respectively (X=4.5, SD=2.65 and X=5, SD=1.71 for

forest, X=3, SD=1.83 and X=2.75, SD=1.71 for fragment, and X=1.75, SD=1.71 and

X=2.25, SD=0.5 for matrix). Habitat usage was not significantly different between forest,

fragment, and matrix for either sampling period (ANOVA: $F_{(2,9)}=1.717$, p=0.234 for

early-season sampling and $F_{(2,9)}=3.96$, p=0.058 for late-season sampling). Similarly,

amount of foraging at GUD trays did not differ significantly between the habitat types for

either round of sampling (ANOVA: $F_{(2,6)}=5.09$, p=0.051 for early-season sampling and

$F_{(2,6)}=0.77$, p=0.50 for late-season sampling).

Effects of Fragmentation on Small Mammal Species

Though age, sex, and reproductive ratios varied across the small mammal

community, generally more adults, males, and non-reproductive animals were captured

(See Table 6). *Peromyscus leucopus* and *Blarina brevicauda* were captured most often;

however, *B. brevicauda* captures were indistinguishable as individuals, so *P. leucopus*

data were used to elucidate the effects of fragmentation on population demographics.

Table 6: Species trapped during both seasons and demographic information, where n=number of individuals, male:female=ratio of males to females, juvenile:adult=ratio of juveniles to adults, Avg Weight=average weight of individuals, Lac=number of lactating females, Scrotal=number of scrotal males, and Non-Repro=individuals not in reproductive condition.

Species	n	male:female	juvenile:adult	Avg Weight (g)	Lac	Scrotal	Non-Repro
Peromyscus leucopus	254	156:98	77:177	21.7	29	68	157
Blarina brevicauda	74	N/A	3:71	16.15	N/A	N/A	74
Microtus pennsylvanicus	3	2:1	1:2	32.67	0	2	1
Zapus hudsonius	2	1:1	0:2	15.5	0	1	1
Tamias striatus	2	0:2	0:2	58	0	0	2

Individuals in the forest and fragments were significantly different in terms of sex, weight, and reproductive status. Males (ANOVA: $F_{(2,63)}=17.1$, $p<0.0001$), individuals of intermediate weight (20 – 25 g) ($F_{(2,63)}=14.1$, $p<0.0001$), and non-reproductive males ($F_{(2,63)}=10.6$, $p=0.0001$) differed significantly between these two habitats and matrix habitat. The fragments were further distinguished from the matrix (but not the forest) in terms of age (adult: $F_{(2,63)}=16.6$, $p<0.0001$) sex (female: $F_{(2,63)}=7.94$, $p=0.0008$), weight (26 – 30 g: $F_{(2,63)}=3.72$, $p=0.03$) and reproductive status (lactating: $F_{(2,63)}=5.90$, $p=0.004$). The number of scrotal males was not significantly higher in the forest than the fragment ($F_{(2,63)}=4.25$, $p=0.02$), though the forest did differ significantly from the matrix. The number of juveniles (ANOVA: $F_{(2,63)}=1.16$, $p=0.32$), low weight individuals (<20 g) ($F_{(2,63)}=0.90$, $p=0.41$), high weight individuals (>30 g) ($F_{(2,63)}=0.15$, $p=0.86$), and non-reproductive females

(F(2,63)=2.52, p=0.09) was not significantly different among the three habitats (See

Table 7).

Table 7: Demographic attributes of *Peromyscus leucopus* individuals for each habitat type, where X=average number of individuals per line and SD=standard deviation of each sample category

Demographic Profile of *P. leucopus*: Age and Sex

Habitat	Adult	Juvenile	Male	Female
Fragment	2.91+1.69	1.14+1.39	2.09+1.15	0.86+1.13
Matrix	1.0+0.82	0.64+0.85	0.95+1.0	0.68+0.84
Forest	3.27+1.55	1.05+1.17	2.95+1.25	1.36+1.09

Demographic Profile of *P. leucopus*: Weight

Habitat	<20 g	20 - 25 g	26 - 30 g	>30 g
Fragment	1.23+1.57	1.73+1.32	0.86+1.13	0.09+0.29
Matrix	0.73+0.88	0.64+0.66	0.18+0.50	0.09+0.29
Forest	1.05+1.21	2.64+1.59	0.5+0.74	0.14+0.35

Demographic Profile of *P. leucopus*: Reproductive Status

Habitat	Male		Female	
	Non-Repro	Scrotal	Non-Repro	Lactating
Fragment	1.09+0.81	1.0+0.82	1.18+1.10	0.77+0.87
Matrix	0.50+0.60	0.45+0.67	0.55+0.80	0.14+0.35
Forest	1.77+1.23	1.18+1.05	1.05+1.05	0.32+0.57

Multivariate analysis of demographic data organized by habitat reflected the patterns of habitat usage in the ANOVA tests. Non-metric multidimensional scaling depicted most of the fragment and forest points associated with high values on Axis 2, while most of the matrix points were associated with low values on Axis 2 (see Figure 4). However, the NMS graph did not display any obvious clusters of points based on habitat.
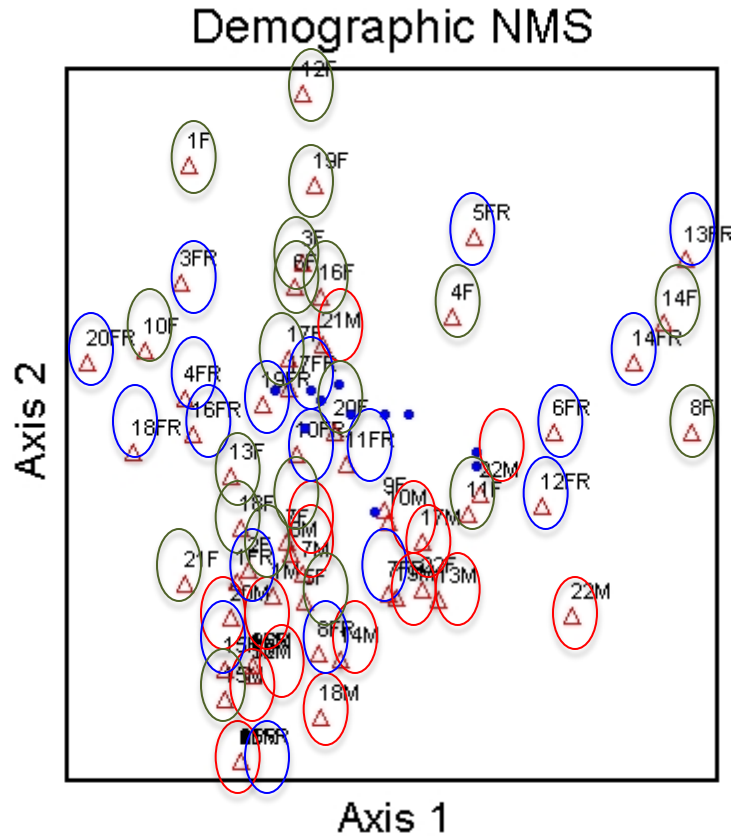
Figure 4: NMS ordination of transects based on demographics of *P. leucopus* individuals, in which fragment (blue), matrix (red), and forest (green) trapping stations were grouped based on habitat type (i.e., forest stations A and B combined for line 1). Lines (Δ) are labeled according to habitat type (FR=fragment, M=matrix, F=forest). Demographic attributes are clustered near the center (•).

Manipulating the height of the matrix resulted in varied demographic composition of the mouse population. As with the habitat type analyses, the matrix habitat generally hosted the fewest individuals in each demographic category (See Figure 5). In addition, the number of adults, juveniles, males, females, non-reproductive animals, lactating animals and scrotal individuals was higher under the tall matrix treatment. However, the differences between the tall and short matrix demographic distributions were non-

significant when tested with ANOVA (See Table 8). In these tests, the data was divided

by matrix treatment and then by habitat type, and results reflect the comparison between

the number of individuals in each habitat for the tall matrix and the number of individuals

per habitat for the short matrix.
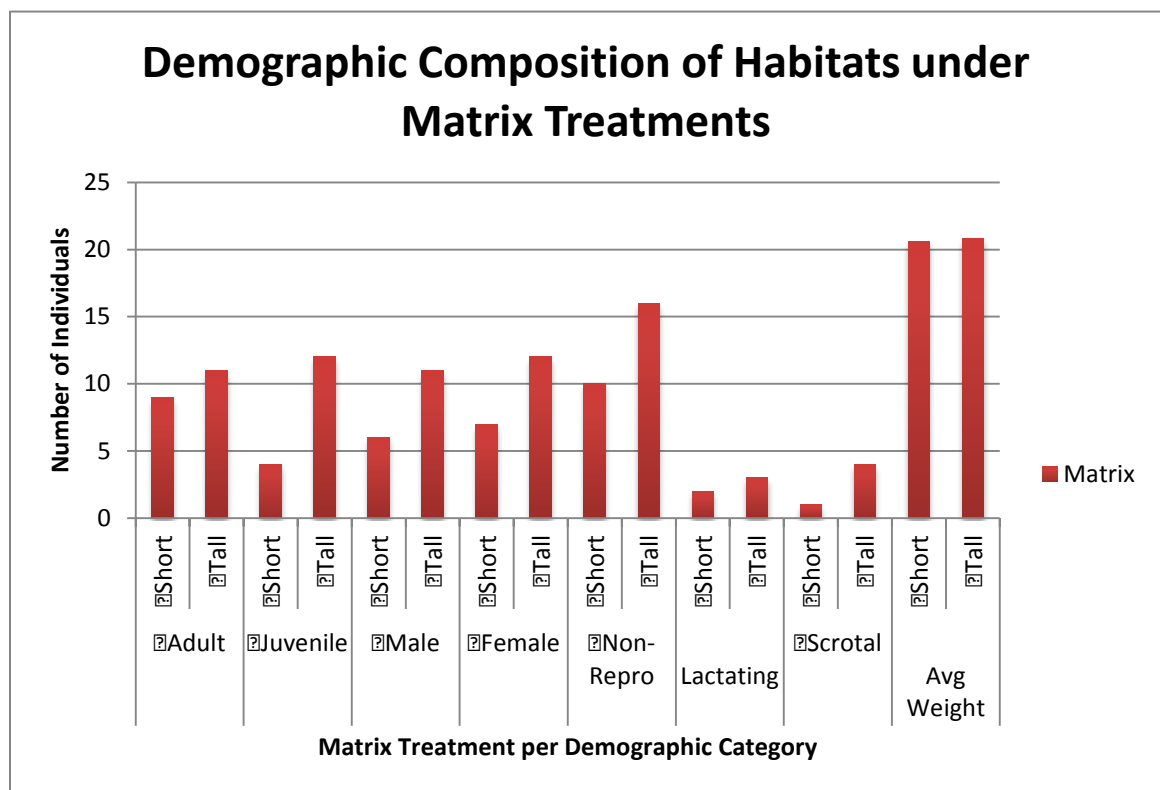
Figure 5: Demographic characteristics (adult, juvenile, male, female, non-reproductive, lactating, scrotal, and average weight) for *P. leucopus* individuals in matrix habitat for the tall and short matrix trials

Table 8: ANOVA results for comparisons between short and tall matrix treatments within demographic categories. For example, the adult category compares the number of individuals in each habitat type between tall and short matrix treatments

ANOVA Results by Demographic Category			
Demographic	df (between, within)	F	p-value
Adult	1,4	0.23	0.66
Juvenile	1,4	7.23	0.055
Male	1,4	0.34	0.59
Female	1,4	1.90	0.24
Non-reproductive	1,4	1.70	0.26
Lactating	1,4	4.23	0.11
Scrotal	1,4	0.01	0.92
Weight (g)	1,4	5.89	0.07

The Impacts of Size and Isolation

The size and isolation of a fragment can influence how many animals can occupy that fragment. The number of animals captured in small and large fragments did not differ significantly (ANOVA: $F_{(1,36)}=0.23$, $p=0.63$) nor did the number of captures in near and far fragments ($F_{(1,36)}=0.06$, $p=0.81$). Transects did not group by either size or location in the NMS ordination (See Figures 6 and 7). Since the demographic attributes were most closely associated with Axis 3 (final stress for real data=2.62, stress for randomized data=8.4, $p=0.004$), those driving the variance in the data best fit Axis 2. Adult (r=0.766), male (r=0.368), intermediate weight (20 – 25 g)(r=0.682), and lactating status (r=0.525) drove the variance; these were similar to the habitat type analyses. The large and small fragments were not significantly different (MRPP: A=-0.01, p=0.68), nor were the more and less isolated fragments (A=-0.02, p=0.83).
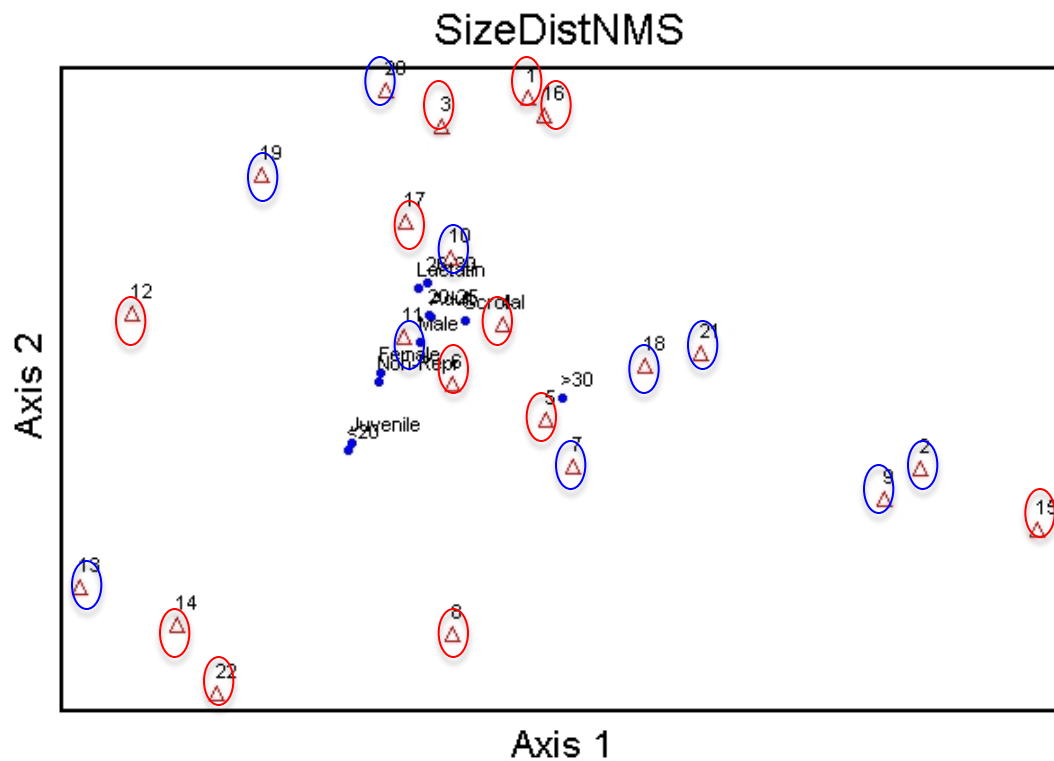
Figure 6: NMS ordination of transects (Δ) utilizing demographic attributes (•). Transects circled in blue contain small fragments, while those circled in red contain large fragments. Axis 1 accounts for the greatest percentage of the variance, followed by Axis 2, Axis 3 and any subsequent axes. High values on Axis 1 indicate that the transects or attributes are more closely associated with Axis 1, while high values on Axis 2 indicate that transects or attributes are more closely associated with Axis 2.
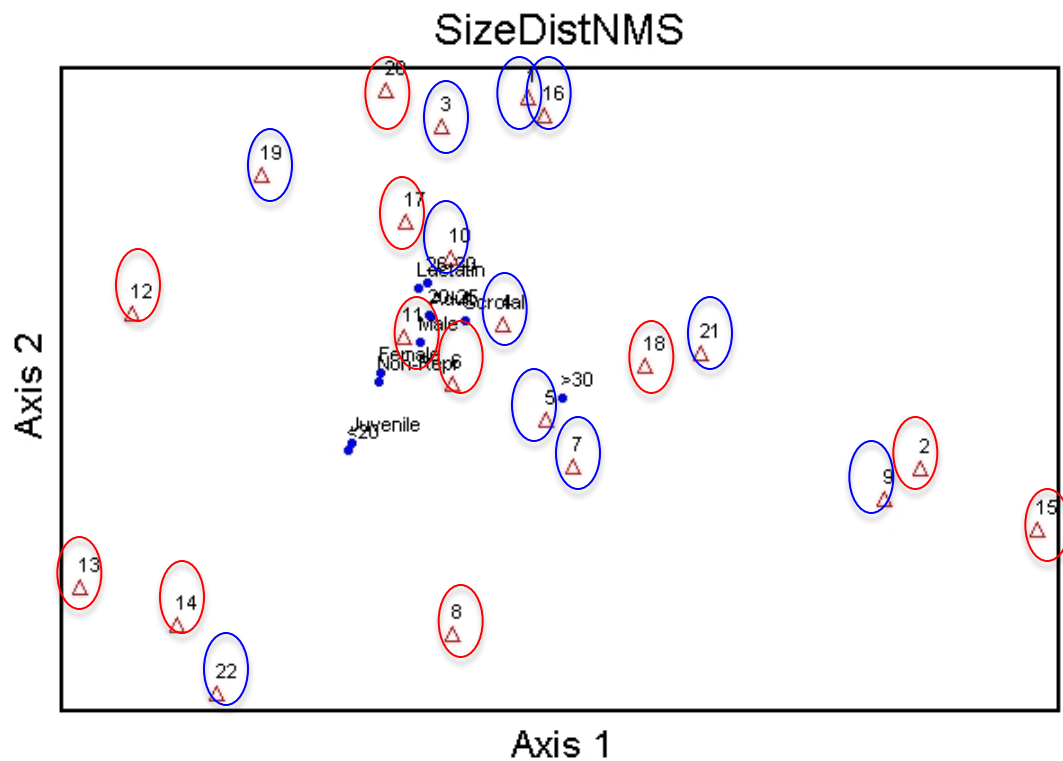
Figure 7: NMS ordination of transects (Δ) utilizing demographic attributes (•). Transects circled in blue contain less isolated fragments, while those circled in red contain more isolated fragments. Axis 1 accounts for the greatest percentage of the variance, followed by Axis 2, Axis 3 and any subsequent axes. High values on Axis 1 indicate that the transects or attributes are more closely associated with Axis 1, while high values on Axis 2 indicate that transects or attributes are more closely associated with Axis 2.

5. DISCUSSION

White-footed mice dominated both years, with shrews making up a larger proportion of the captures during the second summer. Jumping mice (*Zapus hudsonius*), voles (*Microtus pennsylvanicus*), and chipmunks (*Tamias striatus*) comprised only a small number of captures, and these species were not trapped during both summers.

As expected, foraging and habitat usage were lower in the matrix than in the fragment or forest habitats overall; analysis also generated lower capture probabilities for *P. leucopus* individuals in the matrix. Foraging in the fragments also often exceeded foraging in the forest for *Peromyscus*. These patterns were reflected in both the trapping efforts and the GUD trials. The matrix was significantly different from the fragment and forest, while the fragment and forest themselves were not significantly different in terms of habitat usage. Conversely, shrews foraged slightly more in the matrix than either of the other habitats, though this pattern was not significant. Shrews are fossorial, venomous mammals (Lomolino 1984, Rappole 2007), and therefore may present less of a target to predators in the matrix than the rodent species. Shrews may also have greater success capturing insect prey in the matrix habitat, as opposed to the more herbivorous rodent species.

For the GUD tests, the same pattern held, with a higher percentage of seeds eaten in the forest, a lower percentage in the fragment, and the lowest in the matrix. These

groups were significantly different between matrix and fragment and matrix and forest, but not fragment and forest. The results of the GUD trials are logical, because giving-up density reflects the benefits (food) and costs (predation) of foraging in a certain location. Since animals must spend time sorting through the wood chips in each tray to access the seed, they are variably exposed to predation (see Hughes et al. 1994). Thus, areas with the least amount of cover and the greatest predation risk should not be visited as often nor as long as areas with more cover (see Jacob and Brown 2000).

Although the initial prediction was that foraging would occur most often in continuous forest, followed by fragments, followed by the matrix, the trapping and GUD measures of foraging behavior in the fragments over the forest are not entirely surprising. According to Allan et al. (2003), *P. leucopus* can reach high population densities in fragments, so these results may simply represent the outcome of the increased number of mouse encounters within a small area. In fact, in support of this concept, the number of recaptures was slightly higher in fragments than the forest for both summers. Conversely, the results could indicate that the animals are more likely to supplement their food resources with bait in fragments, since fragments contain fewer large trees and other seed-producing plants.

Several overall trends emerged over the course of the two field seasons pertaining to small mammal demographics. Animals foraging in the fragmented landscapes were more likely to be adult, male, and non-reproductive, similar to the findings of Cummings and Vessey (1994). Fragment occupants were equally likely to be male or female, while forest occupants were more likely to be male. Animals moving greater than 10 m were

almost always scrotal males. This observation is in contrast with Krohne et al. (1984), who suggested that scrotal males are more likely to remain in one territory. The 2012 and 2013 data suggest that not all scrotal males disperse such distances, so those that do may have recently attained scrotal status and are attempting to establish new territories with enhanced access to females. Maximizing reproductive potential for smaller scrotal males may outweigh the risk of moving long distances in the matrix to access new territories. Established males in habitats with more food and cover are more likely to win in intraspecific competitions for food and mates (Fuxjager et al. 2010). The mice captured in fragment and matrix habitats were more likely adult, of intermediate weight (20 – 25 g), and non-reproductive Indeed, adult mice of this size may not be large enough to occupy a territory in the highest quality mouse habitat (assumed to be continuous forest), so consequentially choose to forage in lower quality habitats. Taken together, the long-distance dispersers and demographic patterns in the fragmented habitats could indicate that fragments are more likely to be colonized by young male animals that are more willing to cross the matrix to obtain a territory.

Central to the responses of small mammals to fragmentation is movement. This transcends an individual's foraging behavior, in that dispersal ability dictates fragment occupancy and persistence of a metapopulation (Ewers and Didham 2006, Fahrig and Merriam 1994). The population within a fragment is supplemented with births and immigration, and depleted with deaths and emigration. If the death and emigration rate exceeds the birth and colonization rate, the population will go locally extinct (Fahrig and Merriam 1994). Fahrig and Merriam (1994) write that immigration has the largest impact

on population persistence; however, immigration is impeded in fragmented landscapes for small mammals because they have to cross a matrix with (usually) a higher risk of predation. Thus, the predator avoidance behavior of the animal determines whether and how far it will disperse. Scrotal males may accept the predation risk and move longer distances, serving as a possible source of immigration to fragments. Synchronous juvenile dispersal to flood predators with prey may also serve as another source of immigration to more isolated patches, though this effect was not specifically explored.

Small mammals choose foraging habitats with a sufficient quantity and quality of food and cover (Barnum et al. 1992, Getz and McGuire 2008). Multiple authors cite matrix structure and complexity in determining where an animal will forage (Barnum et al. 1992, Cummings and Vessey 1994, Yahner 1983). A tall matrix provides more cover from predation than a short matrix, so more activity should occur in tall matrices than short matrices. For *P. leucopus*, habitat usage with the tall matrix treatment was statistically similar for the fragment and matrix habitats, indicating similar usage patterns though the fragment and matrix habitats were inherently different. For the short matrix treatment, the fragment and forest habitat types were the only ones that were not significantly different. These patterns were similar for the GUD trials in the tall and short matrices. The forest and matrix were significantly different for the tall matrix, the matrix differed from both fragment and forest for the short matrix, and the fragment and forest did not significantly differ in either matrix treatment. Thus, increasing the structural complexity of the matrix does seem to provide adequate cover for foraging. However, matrix structure does not entirely dictate habitat usage, as exemplified by the significant

difference between fragment and matrix for the tall matrix trials. Comparison of the tall matrices in the control lines yielded no significant difference between the earlier season captures and the later season captures; thus, seasonal migrations did not affect the number of captures in the lines between the tall and short treatment phases. However, seasonal foraging patterns may have exerted an impact on GUD results between the early and later sampling efforts, as more seeds were removed from the later GUD trays. In addition, most of the *Peromyscus* demographic categories exhibited increased numbers of individuals during the tall matrix phase for the fragment and matrix habitats. Notably, access to fragments was enhanced for multiple demographic groups, including reproductive males and females. A tall matrix may therefore improve immigration rates to fragments, and allow colonization of low density and empty fragments. This also imparts genetic benefits to a *Peromyscus* population, as genetic material from the forest and other fragments is more likely to reach other fragments and persist over a larger area. Unlike *Peromyscus*, shrews are tolerant of the matrix, and therefore can range more easily between forest and fragment habitats. However, shrews still respond to predation risk in the matrix; under the short matrix treatment, fewer shrews were captured in all of the three habitat types.

Floristic composition of the matrix and fragments may also affect small mammal usage. Quadrat plant surveys in the three habitat types showed higher average plant diversity in the fragments than either of the other habitats, and about the same average plant diversity in the forest and matrix habitats. Since the fragments under observation were so small, they had higher degree of edge effects stemming from the increased

penetration of sunlight further into the interior of each fragment. According to Yahner (1988), edge effects can result in greater vegetative complexity, since edge-loving plants and original fragment plants contribute to the overall plant diversity. Many of the fragments under observation contained at least one mature tree, as well as a host of shrubs and herbaceous plants, whereas the matrix was limited to herbs and some seedling shrubs (specifically Coralberry, *Symphoricarpos orbiculatus*). Plant diversity was lower in the forest than the fragments, and was about the same as the matrix plant diversity. This was somewhat unexpected because white-footed mice, which comprised the majority of the captures for both summers, favor wooded habitats. However, the forest had more tall trees, which provide food and woody debris for small mammals. The forest also likely had more trees per unit area than either of the other habitat types, though this was not quantified. The interplay of vegetative structure and plant quality, rather than the strong effects of one factor or the other, likely influences where an animal forages.

As previously stated, cover protects small mammals from predation. The animals under observation are prey items for a plethora of terrestrial and aerial fauna, including black bears (*Ursus americanus*), red-tailed hawks (*Buteo jamaicensis*), raccoons, (*Procyon lotor*), black ratsnakes (*Pantherophis allegheniensis*), and others. Even other small mammals, mainly *Blarina brevicauda*, have been observed preying upon juvenile and adult cricetids (Burt and Grossenheider 1976, Lomolino 1984). Camera traps recorded *U. americanus* and *P. lotor* in the matrix (bears and raccoons), fragments (raccoons), and forests (raccoons). *Blarina brevicauda* tolerates matrix habitat according to the results of this study, and therefore constitute another possible source of juvenile

mammal mortality. Direct sightings of these animals and others tended to occur most often in the matrix habitat as well, lending credence to the risk it poses to small mammals relative to the other habitat types with more cover. Additionally, direct observations have an advantage over camera trapping in that they allow detection of aerial predators that the cameras may fail to capture. However, more extensive use of camera traps would allow the exact terrestrial predator foraging areas to be more precisely defined.

Modified island biogeography theory postulates that larger fragments and those closer to continuous habitat or other fragments will harbor more biodiversity (Bierregaard et al. 2001, Laurance 2008). Although more animals were captured on average in large than in small fragments, this difference was not statistically significant. Small and large fragments and those closer to and farther away from the matrix did not order by size or isolation in the ordination, nor were they significantly different. The similarity between small and large fragments may stem from the increased number of trap encounters in small fragments, which could liken a small fragment with fewer animals to a larger fragment with many animals. The small range of fragment sizes may also have affected the size comparisons, since population density might not differ depending on small increments in fragment area. Finally, connectivity between fragments and forest may have been established as a function of matrix height, promoting movement into the matrix during the tall phase.

Future studies within similarly fragmented habitats could be modified to include a larger range of patches and encompass the population cycles of the native mammal species. This particular investigation details the small mammal community's response to

a pre-existing fragmented landscape, in which the initial fragmentation event took place decades prior to commencement of the project. As a result, the small mammal community has had more time to adapt to the fragmented conditions than in the case of an experimentally fragmented landscape. The fields are maintained through mowing; however, fragments have the potential to expand when woody vegetation sprouts on the edge. In addition, certain fields had small patches (<100 m), sometimes consisting only of shrubs, which the animals nevertheless may have used to "island-hop" further into the matrix or to other fragments. Certain fragments that met or exceeded the size requirements were too close to the forest to allow proper placement of the traps, and conversely certain patches that were very isolated in the matrix were too small to include in the study. Future studies in the same general area could include some of these additional patches by examining the differences between very isolated patches and groups of several small patches. Larger patches near the forest could also be vegetatively contrasted with the forest itself, especially in terms of plant density and diversity. The effects of fragment shape were not explored, since most fragments were elliptical and presented roughly the same proportion of edge. However, elongated fragments and those with amorphous shapes present more edge, and may harbor different ratios of small mammals than fragments with more regular shapes. Increasing the frequency of matrix mowing could facilitate multiple rounds of sampling over the course of the season, rather than restricting sampling to two main phases.

In terms of trapping, this study was conducted over a short period of time (two field seasons). Extending the timeline for future studies would provide larger datasets,

more strongly support the differences between habitats and fragment sizes, and minimize the impact of temporal population fluctuations. Both the trapping and GUD results portrayed the dramatic difference in mammal activity between 2012 and 2013, with significantly more captures and lower GUD's in 2013. The 2012 season was roughly 8 weeks shorter than the 2013 season (since matrix treatments were not performed), but even correcting for time the number of captures did not approach the 2013 data. Other trapping studies in Virginia during the summer of 2012 resulted in similarly low capture rates (personal communication), so a population crash could explain the marked difference between capture rates during both field seasons. As Elias et al. (2004) observed, *P. leucopus* populations undergo population peaks and crashes on a four-year cycle. Temperature may have also impacted small mammal populations; temperatures were higher in 2012 than 2013, and fewer animals were captured on very hot nights. However, seasonal movements of animals may also contribute to the variations in capture rate.

To summarize with regard to the original hypotheses, small mammals choose areas of more cover and greater structural complexity (fragment and forest habitat) over areas with less cover and complexity (matrix habitat). Small mammals face a greater risk of predation in habitats with less cover; as a result, they spend less time foraging in GUD trays and use matrix habitats less frequently. Habitat type, along with year, has the strongest influence on small mammal distribution. Taller matrices help increase connectivity between fragments, and consequentially more animals move within tall matrices and more time is spent foraging at GUD trays. Although size and isolation are

expected to influence the number of animals occupying fragments, these parameters were not as important in this study. High population densities and the small range of fragment sizes resulted in the smaller fragments approximating the larger fragments in terms of the number of individuals captured. Fragments differ from forest demographically for *Peromyscus leucopus*. While forest individuals were more likely to be adult males, fragment individuals were more likely to be adults of either sex. Captures in the tall and short matrices resulted in higher numbers of individuals in fragment and matrix habitats for most demographic categories.

Implications for Species Interactions

Habitat fragmentation is not as detrimental to small mammals as other species, such as interior forest birds, that cannot thrive outside original habitat. However, because fragmentation affects where animals forage, it also limits their movements compared to continuous habitat, and shifts patterns of occupancy. Altered interactions with plants and other animals further modify where, when, and how small mammals use fragment and matrix habitats, and in turn affect other species that rely on small mammals as a food source or seed dispersal agent. For example, the initial fragmentation process creates a matrix that changes over time (Jules and Shahani 2003). Successful matrix plants must be tolerant of the initial matrix conditions and future conditions that arise as plant communities in the matrix develop. Thus, future disturbances affect the availability of cover and forage plants for herbivores (Jules and Shahani 2003). Climate change may also instigate food source changes among small mammals. Northward flora and fauna migrations are expected to occur with rising temperatures, but differing rates of migration

could cause mismatches between herbivores and plant species. This may necessitate mammals to rely on plant species that are tolerant of both fragmentation and a larger range of climactic conditions. These factors combined can limit a species' range (Ewers and Didham 2006).

Interspecific interactions can also affect small mammal populations. Predator release in very small fragments can increase *P. leucopus* density, but interspecific competition with other small mammals for food resources can limit population growth when mammals are restricted to the area of the fragment. Resource quality in the fragment plays a role in enhancing survivorship and the chance of reproductive success of individual animals as well (Johnson 2007), so if certain species or individuals dominate the highest quality resources, the other species will exhibit lower reproductive rates at the very least. Hughes et al. (1994) explain that when the population density of one competitor increases, other competitors must either spend more time foraging to fulfill their energetic requirements, or reduce the amount of energy spent foraging. This decreases the amount of energy left for reproduction. Lower fecundity among small mammals equates to a greater chance of the patch population going extinct, and therefore a diminished food source for predators that may enter the fragment.

Fragmentation also enhances disease transmission, because small mammals and disease vectors are found at higher densities in fragments (Allan et al. 2003). Lyme disease and other tick-borne diseases exhibit higher transmission rates in fragmented landscapes, and *P. leucopus* often transmit this disease (Ewers and Didham 2006, Allan et al. 2003). In smaller fragments, Allan et al. (2003) reported that nymphal tick density

was significantly higher than in larger fragments. Fragmentation also occurs alongside human development (Bierregaard et al. 2001), thereby exposing more people to higher tick densities. Thus, fragmented landscapes pose more of a tick-borne disease risk to humans. On the other hand, isolation within a fragmented habitat may remove animals from some endemic disease areas. Small mammals may in this case evolve lower resistance to diseases more often encountered in continuous habitat, weakening the population's ability to recover if an epidemic should occur (Hoffmeister et al. 2005).

Conservation and Management

Habitat fragmentation is detrimental to species, populations, and individuals. In terms of species diversity, fragmented habitats are often more prone to negative effects from other anthropogenic activities such as hunting, wildfires, and species introductions in addition to the direct fragmentation effects (Laurance 2008). Preventing further fragmentation is the best strategy for maintaining small mammal populations and preventing the spread of Lyme disease (Allan et al. 2003). Small mammals are less able to move in fragmented landscapes, and with the northward range expansion of ticks in response to climate change, fragmentation is more likely to result in higher mouse and tick densities over a larger area. This can translate to higher frequencies of tick-borne disease outbreaks in humans and animals (Allan et al. 2003, Ewers and Didham 2006). Restoring vertical structure and vegetative complexity minimizes the impact of predators that hunt preferentially along the edge, by providing more cover (Yahner 1988). In agricultural regions where cover is limited, tall crops provide adequate shelter for foraging mice (Cummings and Vessey 1994). However, in extremely fragmented, disease

68

endemic areas, minimizing matrix height may be advised to discourage ticks and their mammalian hosts from occupying areas in close contact with humans and pets.

Corridors promote connectivity between habitat patches for sensitive species, and can connect communities across landscapes (Beier and Noss 1998, Ewers and Didham 2006). Landscape connectivity can increase a pathogen's spread to other patches, but generally the benefits of connectivity outweigh the costs (McCallum and Dobson 2002). The potential for species to move away from areas of infection or recolonize extinct patches compensates for the disease risk. Furthermore, populations unaffected by the disease can colonize patches once disease has eliminated competing populations or species (McCallum and Dobson 2002). The data for matrix height in 2013 indicate that maintaining a taller matrix generally benefits small mammals, whereas if the management goal is deterring small mammals, matrix habitat should be kept short to prevent dispersal. However, corridor lengths and the prevalence of small mammals elsewhere in the landscape indicate that corridor construction to suit small mammal species alone is likely to be too costly to justify the benefits (see Beier and Noss 1998). Preserving remaining fragments of a certain quality can be invaluable for providing source and sink populations to maintain demographic and genetic diversity among local populations. They can also serve as refugia for dispersing animals, and aid mammals in shifting their ranges as the climate changes.

Although small mammal populations appear to be stable and somewhat tolerant of fragmentation, these species' importance as prey and seed dispersers merit attention in a wider scheme of ecological conservation.

6. CONCLUSION

Human-induced habitat fragmentation creates a mosaic of fragment, matrix, and original habitats. Apart from the loss of habitat alone, altered species composition, population density and distribution, and ecological interactions can arise as a consequence of the novel habitat configurations and environmental conditions manifesting in fragmented habitats (Bierregaard et al. 2001, Fahrig 2003). Previous studies of small mammals in fragmented habitats have demonstrated the complexity of the interactions between fragment and matrix habitats, as well as quantity and quality of habitat. For example, animals may favor the benefits of food availability in the matrix over the higher predation risk associated with less cover, and forage in the matrix when food resources are abundant (Diffendorfer et al. 1995). However, this behavior is maximized when the matrix is more structurally and vegetatively complex (Cummings and Vessey 1994, Merriam and Lanoue 1990, Yahner 1983).

Habitat fragmentation strongly influences where and how small mammals forage. Habitat type, fragment size, matrix height, plant composition, and predator distribution determine how and for how long mammals will use different habitats. Conversion of one habitat type to another may exclude some species while favoring others. Larger fragments host more species, but are also more likely to contain more predators. Some predators may vanish from certain landscapes, allowing small mammal populations to

flourish in their absence, while others may alter their search patterns, increasing predation pressure on the edge. Plant species composition and matrix height can contribute to fragment and matrix quality, either serving as alternate foraging sites or precluding foraging altogether. Fragmentation also affects dispersal ability, and can dictate which demographic characteristics will be favored for dispersing individuals. Other factors, including intra- and interspecific competition, can modify these effects and restructure the interactions between small mammals and other organisms in the ecosystem. Even though small mammals are fairly abundant, conserving them also protects their role in the ecosystem, and may allow certain fragmented ecosystems to persist even as they continue to evolve.

7. APPENDIX
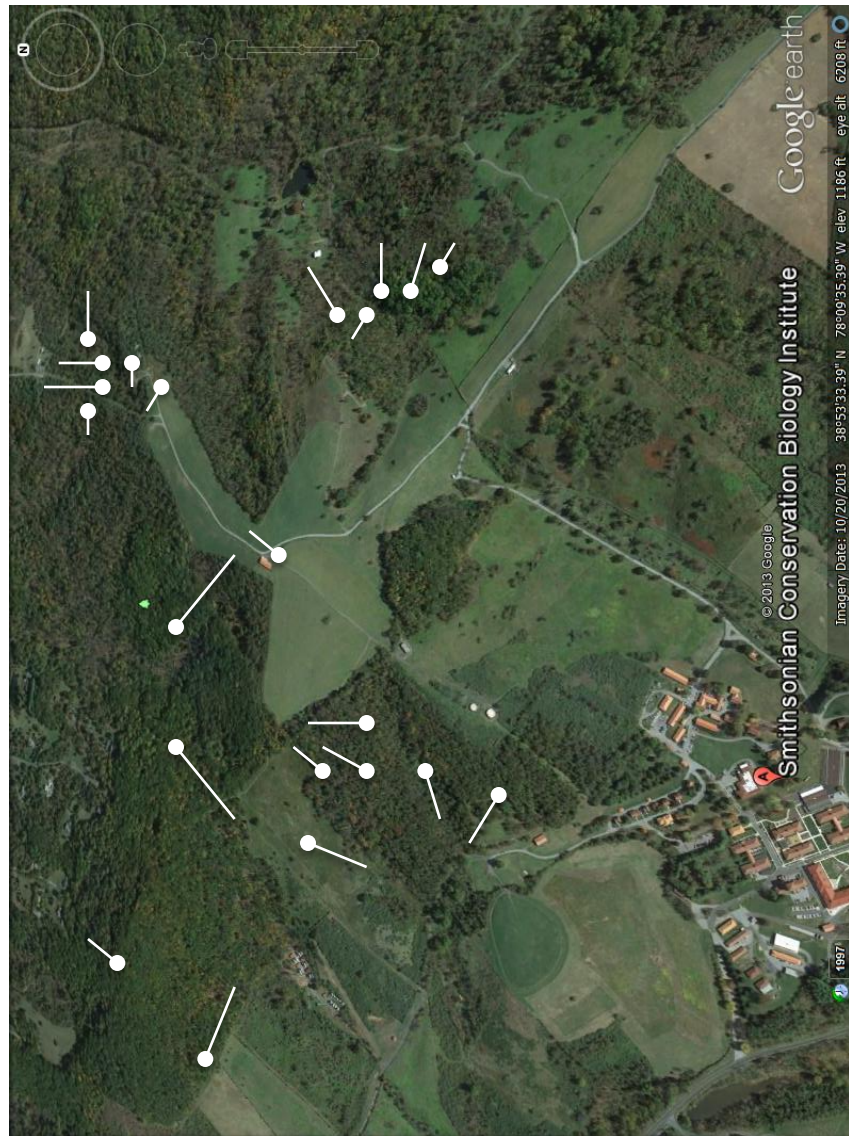
Figure 8: Satellite image of the study site, with fragments as dots and transects as lines. 20 fragments were sampled each field season.

REFERENCES

Allan, Brian F., Felicia Keesing, and Richard S. Ostfeld. "Effect of Forest Fragmentation on Lyme Disease Risk." *Conservation Biology* 17, no. 1 (2003): 267–272. <http://onlinelibrary.wiley.com>.

Anderson, Christine S., and Douglas B. Meikle. "Genetic Estimates of Immigration and Emigration Rates in Relation to Population Density and Forest Patch Area in Peromyscus Leucopus." *Conservation Genetics* 11.5 (2010): 1593–1605. <http://link.springer.com>.

Barnum, Sarah A., Christiana J. Manville, John R. Tester, and William J. Carmen. "Path Selection by Peromyscus Leucopus in the Presence and Absence of Vegetative Cover." *Journal of Mammalogy* 73, no. 4 (November 1, 1992): 797–801. <http://www.jstor.org>.

Beier, Paul, and Reed F. Noss. "Do Habitat Corridors Provide Connectivity?" *Conservation Biology* 12, no. 6 (1998): 1241–1252. <http://onlinelibrary.wiley.com>.

Bierregaard Jr., R. O., Claude Gascon, Thomas E. Lovejoy, and Rita Mesquita. *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, 2001.

Bowers, Michael A., Kristina Gregario, Courtney J. Brame, Stephen F. Matter, and James L. Dooley Jr. "Use of Space and Habitats by Meadow Voles at the Home Range, Patch and Landscape Scales." *Oecologia* 105, no. 1 (January 1, 1996): 107–115. <http://jstor.org>.

Brady, Megan J. et al. "Matrix Is Important for Mammals in Landscapes with Small Amounts of Native Forest Habitat." *Landscape Ecology* 26.5 (2011): 617–628. <http://link.springer.com>.

Burt, William Henry and Richard Philip Grossenheider. *A Field Guide to the Mammals: North America North of Mexico*. Houghton Mifflin Harcourt, 1976.

Cummings, John R., and Stephen H. Vessey. "Agricultural Influences on Movement Patterns of White-Footed Mice (Peromyscus Leucopus)." *American Midland Naturalist* 132, no. 2 (October 1, 1994): 209–218. <http://www.jstor.org>.

Debinski, Diane M., and Robert D. Holt. "A Survey and Overview of Habitat Fragmentation Experiments." *Conservation Biology* 14, no. 2 (2000): 342–355. <http://www.onlinelibrary.wiley.com>.

Diffendorfer, James E., Michael S. Gaines, and Robert D. Holt. "Habitat Fragmentation and Movements of Three Small Mammals (Sigmodon, Microtus, and Peromyscus)." *Ecology* 76, no. 3 (April 1, 1995): 827–839. <http://www.esajournals.org>.

Do, Randy, Julia Shonfield, and Andrew G. McAdam. "Reducing Accidental Shrew Mortality Associated with Small-mammal Livetrapping II: a Field Experiment with Bait Supplementation." *Journal of Mammalogy* 94, no. 4 (August 2013): 754–760. <http://www.bioone.org>.

Elias, Susan P., Jack W. Witham, and Malcolm L. Hunter. "PEROMYSCUS LEUCOPUS ABUNDANCE AND ACORN MAST: POPULATION FLUCTUATION PATTERNS OVER 20 YEARS." *Journal of Mammalogy* 85, no. 4 (August 2004): 743–747. <http://www.jstor.org>.

Ewers, Robert M., and Raphael K. Didham. "Confounding Factors in the Detection of Species Responses to Habitat Fragmentation." *Biological Reviews* 81, no. 1 (2006): 117–142. <http://onlinelibrary.wiley.com>.

Ewers, Robert M., Raphael K. Didham, William D. Pearse, Véronique Lefebvre, Isabel M. D. Rosa, João M. B. Carreiras, Richard M. Lucas, and Daniel C. Reuman. "Using Landscape History to Predict Biodiversity Patterns in Fragmented Landscapes." *Ecology Letters* 16, no. 10 (2013): 1221–1233. <http://onlinelibrary.wiley.com>.

Fahrig, Lenore. "Effects of Habitat Fragmentation on Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 34 (January 1, 2003): 487–515. <http://www.jstor.org>.

Fahrig, Lenore, and Gray Merriam. "Conservation of Fragmented Populations." *Conservation Biology* 8, no. 1 (1994): 50–59. <http://onlinelibrary.wiley.com>.

Fuxjager, Matthew J. et al. "Deciding to Win: Interactive Effects of Residency, Resources and 'boldness' on Contest Outcome in White-footed Mice." *Animal Behaviour* 80.5 (2010): 921–927. *ScienceDirect*. <http://www.sciencedirect.com>.

Getz, Lowell L., and Betty McGuire. "Factors Influencing Movement Distances and Home Ranges of the Short-tailed Shrew (Blarina Brevicauda)." *Northeastern Naturalist* 15, no. 2 (June 1, 2008): 293–302. <http://www.bioone.org>.

Hanski, Ilkka. "The Theories of Island Biogeography and Metapopulation Dynamics: Science Marches Forward, but the Legacy of Good Ideas Lasts a Long Time." In Losos, Jonathan B., Robert E. Ricklefs and Robert H. MacArthur *The Theory of Island Biogeography Revisited*, 186 – 213. Princeton, NJ: Princeton University Press, 2010.

Hanski, Ilkka, Gustavo A. Zurita, M. Isabel Bellocq, and Joel Rybicki. "Species–fragmented Area Relationship." *Proceedings of the National Academy of Sciences* (July 15, 2013): 201311491. <http://pnas.org>.

Hindle, Allyson G., John M. Lawler, Kevin L. Campbell, and Markus Horning. "Muscle Senescence in Short-lived Wild Mammals, the Soricine Shrews Blarina Brevicauda and Sorex Palustris." *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 311A, no. 5 (2009): 358–367. <http://onlinelibrary.wiley.com>.

Hoffmeister, Thomas S., Louise EM Vet, Arjen Biere, Kent Holsinger, and Juliane Filser. "Ecological and Evolutionary Consequences of Biological Invasion and Habitat Fragmentation." *Ecosystems* 8, no. 6 (September 1, 2005): 657–667. <http://link.springer.com>.

Hughes, Jessica J., David Ward, and Michael R. Perrin. "Predation Risk and Competition Affect Habitat Selection and Activity of Namib Desert Gerbils." *Ecology* 75, no. 5 (July 1, 1994): 1397–1405. <http://jstor.org>.

Jacob, Jens, and Joel S. Brown. "Microhabitat Use, Giving-up Densities and Temporal Activity as Short- and Long-term Anti-predator Behaviors in Common Voles." *Oikos* 91, no. 1 (2000): 131–138. <http://onlinelibrary.wiley.com>.

Johnson, Matthew D. "Measuring Habitat Quality: A Review." *The Condor* 109, No. 3 (August 1, 2007): 489–504. <Http://Www.Bioone.Org>.

Jones, Calley G., and Erin S. Lindquist. "Utilization of Woody Debris by Peromyscus Leucopus in a Fragmented Urban Forest." *Southeastern Naturalist* 11, no. 4 (December 1, 2012): 689–698. <http://www.bioone.org>.

Jules, Erik S., and Priya Shahani. "A Broader Ecological Context to Habitat Fragmentation: Why Matrix Habitat Is More Important Than We Thought." *Journal of Vegetation Science* 14, no. 3 (2003): 459–464. <http://onlinelibrary.wiley.com>.

Kays, Roland W., and Don E. Wilson. *Mammals of North America: (Second Edition)*. Princeton University Press, 2009.

Kelly, Marcella J., and Erika L. Holub. "Camera Trapping of Carnivores: Trap Success Among Camera Types and Across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles County, Virginia." *Northeastern Naturalist* 15, no. 2 (June 1, 2008): 249–262. <http://www.bioone.org>.

Klein, Gregory P., and Guy N. Cameron. "Effect of Habitat Gradients on Space Use by White-footed Mice (Peromyscus Leucopus)." *Journal of Mammalogy* 93, no. 3 (June 28, 2012): 706–715. <http://www.bioone.org>.

Krohne, David T., Bradley A. Dubbs, and Ramone Baccus. "An Analysis of Dispersal in an Unmanipulated Population of Peromyscus Leucopus." *American Midland Naturalist* 112, no. 1 (July 1, 1984): 146–156. <http://www.jstor.org>.

Laurance, William F. "Fragmentation and Plant Communities: Synthesis and Implications for Landscape Management." *In* Bierregaard Jr., R.O., Claude Gascon, Thomas E. Lovejoy, and Rita Mesquita, Editors *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, 2001.

Laurance, William F. "Theory Meets Reality: How Habitat Fragmentation Research Has Transcended Island Biogeographic Theory." *Biological Conservation* 141, no. 7 (July 2008): 1731–1744. <http://www.sciencedirect.com>.

Levey, Douglas J., Benjamin M. Bolker, Joshua J. Tewksbury, Sarah Sargent, and Nick M. Haddad. "Effects of Landscape Corridors on Seed Dispersal by Birds." *Science* 309, no. 5731 (July 1, 2005): 146–148. <http://www.sciencemag.org>.

Linzey, Alicia V. et al.
"Effects of Habitat Disturbance on a Peromyscus Leucopus (Rodentia: Cricetidae) Population in Western Pennsylvania." *Journal of Mammalogy* 93.1 (2012): 211–219. *CrossRef*. < http://asmjournals.org/>.

Lomolino, Mark V. "Immigrant Selection, Predation, and the Distributions of Microtus Pennsylvanicus and Blarina Brevicauda on Islands." *The American Naturalist* 123, no. 4 (April 1, 1984): 468–483. <http://www.jstor.org>.

Marcello, Gregg J., Shawn M. Wilder, and Douglas B. Meikle. "Population Dynamics of a Generalist Rodent in Relation to Variability in Pulsed Food Resources in a Fragmented Landscape." *Journal of Animal Ecology* 77, no. 1 (2008): 41–46. <http://onlinelibrary.wiley.com>.

MacArthur, Robert H. *The Theory of Island Biogeography*. Princeton University Press, 1967.

McCallum, Hamish, and Andy Dobson.
    "Disease, Habitat Fragmentation and Conservation." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269, no. 1504 (October 7, 2002): 2041–2049. <http://rspb.royalsocietypublishing.org>.

McCune, Bruce, and James B. Grace. *Analysis of Ecological Communities*. M G M Software Design®, 2002.

McShea, William J. "The Influence of Acorn Crops on Annual Variation in Rodent and Bird Populations." *Ecology* 81, no. 1 (January 2000): 228. <http://www.jstor.org>.

McShea, William J., Christen Wemmer, and Michael Stüwe. "In My Experience: Conflict of Interests: A Public Hunt at The National Zoo's Conservation and Research Center." *Wildlife Society Bulletin* 21, no. 4 (December 1, 1993): 492–497. <http://www.jstor.org>.

Merriam, Gray, and Alain Lanoue. "Corridor Use by Small Mammals: Field Measurement for Three Experimental Types of Peromyscus Leucopus." *Landscape Ecology* 4, no. 2–3 (July 1, 1990): 123–131. <http://link.springer.com>.

Mortelliti, Alessio, Giovanni Amori, and Luigi Boitani. "The Role of Habitat Quality in Fragmented Landscapes: a Conceptual Overview and Prospectus for Future Research." *Oecologia* 163, no. 2 (June 1, 2010): 535–547. <http://link.springer.com>.

Munshi-South, Jason. "Urban Landscape Genetics: Canopy Cover Predicts Gene Flow Between White-footed Mouse (Peromyscus Leucopus) Populations in New York City." *Molecular Ecology* 21.6 (2012): 1360–1378. <http://www.onlinelibrary.wiley.com>.

Opdam, Paul, and Dirk Wascher. "Climate Change Meets Habitat Fragmentation: Linking Landscape and Biogeographical Scale Levels in Research and Conservation." *Biological Conservation* 117, no. 3 (May 2004): 285–297. <http://sciencedirect.com>.

Ostfeld, Richard S., and Felicia Keesing. "Biodiversity and Disease Risk: The Case of Lyme Disease." *Conservation Biology* 14, no. 3 (2000): 722–728. <http://onlinelibrary.wiley.com>.

Rankin-De Merona, Judy M., and Roger W. Hutchings H. "Deforestation Effects at the Edge of an Amazonian Forest Fragment." In Bierregaard Jr., R.O., Claude Gascon, Thomas E. Lovejoy, and Rita Mesquita, Editors *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*, 136–145. Yale University Press, 2001.

Rappole, John. *Wildlife of the Mid-Atlantic: A Complete Reference Manual*. University of Pennsylvania Press, 2007.

Rockwood, Larry L. *Introduction to Population Ecology*. John Wiley & Sons, 2009.

Sikes, Robert S., and William L. Gannon. "Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research." *Journal of Mammalogy* 92, no. 1 (February 16, 2011): 235–253. <http://www.mammalsociety.org/articles/guidelines-american-society-mammalogists-use-wild-mammals-research-0>.

Tewksbury, Joshua J., Douglas J. Levey, Nick M. Haddad, Sarah Sargent, John L. Orrock, Aimee Weldon, Brent J. Danielson, Jory Brinkerhoff, Ellen I. Damschen, and Patricia Townsend. "Corridors Affect Plants, Animals, and Their Interactions in Fragmented Landscapes." *Proceedings of the National Academy of Sciences* 99, no. 20 (October 1, 2002): 12923–12926. <http://www.jstor.org>.

Vlautin, Christian T., and Michael H. Ferkin. "The Outcome of a Previous Social Interaction with a Same-sex Conspecific Affects the Behavior of Meadow Voles, Microtus Pennsylvanicus." *Ethology* 119, no. 3 (2013): 212–220. <http://onlinelibrary.wiley.com>.

Verdolin, Jennifer L. "Meta-analysis of Foraging and Predation Risk Trade-offs in Terrestrial Systems." *Behavioral Ecology and Sociobiology* 60.4 (2006): 457–464. <http://link.springer.com>.

Wolff, Jerry O., and Bethia Hurlbutt. "Day Refuges of Peromyscus Leucopus and Peromyscus Maniculatus." *Journal of Mammalogy* 63, no. 4 (November 1, 1982): 666–668. <http://www.jstor.org>.

Yahner, Richard H. "Small Mammals in Farmstead Shelterbelts: Habitat Correlates of Seasonal Abundance and Community Structure." *The Journal of Wildlife Management* 47, no. 1 (January 1983): 74. <http://www.jstor.org>.

Yahner, Richard H. "Changes in Wildlife Communities Near Edges." *Conservation Biology* 2, no. 4 (1988): 333–339. <http://onlinelibrary.wiley.com>.

BIOGRAPHY

Meredith Penthorn graduated from University of Wisconsin-Madison in 2010, where she received a Bachelor of Science in Biological Aspects of Conservation. She obtained her Master of Science degree in Environmental Science and Policy from George Mason University in 2014.