

ETD Archive

---

2013

## A Multi-Taxonomic Approach to Assess the Impact of Overabundant White-Tailed Deer (*Odocoileus Virginianus*) in Forest Ecosystems Across Northeast Ohio

Sara A. Laux  
*Cleveland State University*

Follow this and additional works at: <https://engagedscholarship.csuohio.edu/etdarchive>



Part of the [Environmental Sciences Commons](#)

[How does access to this work benefit you? Let us know!](#)

---

### Recommended Citation

Laux, Sara A., "A Multi-Taxonomic Approach to Assess the Impact of Overabundant White-Tailed Deer (*Odocoileus Virginianus*) in Forest Ecosystems Across Northeast Ohio" (2013). *ETD Archive*. 174.  
<https://engagedscholarship.csuohio.edu/etdarchive/174>

This Dissertation is brought to you for free and open access by EngagedScholarship@CSU. It has been accepted for inclusion in ETD Archive by an authorized administrator of EngagedScholarship@CSU. For more information, please contact [library.es@csuohio.edu](mailto:library.es@csuohio.edu).

A MULTI-TAXONOMIC APPROACH TO ASSESS THE IMPACT OF  
OVERABUNDANT WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN  
FOREST ECOSYSTEMS ACROSS NORTHEAST OHIO

SARA A. LAUX

Bachelor of Science in Zoology  
Ohio State University  
June 2000

Master of Science in Wildlife Ecology  
University of North Dakota  
May 2004

Submitted in partial fulfillment of requirement of the degree  
DOCTOR OF PHILOSOPHY IN REGULATORY BIOLOGY  
at the  
CLEVELAND STATE UNIVERSITY  
MAY 2013

This dissertation has been approved for  
the Department of Biological, Geological,  
and Environmental Sciences and for the  
College of Graduate Studies of  
Cleveland State University

by

\_\_\_\_\_ Date: \_\_\_\_\_  
Dr. B. Michael Walton, BGES/CSU  
Major Advisor

\_\_\_\_\_ Date: \_\_\_\_\_  
Dr. Robert A. Krebs, BGES/CSU  
Advisory Committee Member

\_\_\_\_\_ Date: \_\_\_\_\_  
Dr. Terry L. Robison, Cleveland Metroparks  
Advisory Committee Member

\_\_\_\_\_ Date: \_\_\_\_\_  
Dr. Julie A. Wolin, BGES/CSU  
Advisory Committee Member

\_\_\_\_\_ Date: \_\_\_\_\_  
Dr. F. Paul Doerder, BGES/CSU  
Internal Examiner

\_\_\_\_\_ Date: \_\_\_\_\_  
Dr. Carl A. Anthony, JCU  
External Examiner

To Harlan and Harrison,  
you weren't born when I started this endeavor but you  
were my motivation to finish.

## ACKNOWLEDGMENTS

I would like to extend my gratitude to all those who have contributed to the success of this project. Without their support and contributions this project would not have been possible. I want to especially thank my advisor, Dr. Mike Walton, for taking me on as a student, for having the confidence in my abilities to successfully carry out this project, and for his patience and advice in writing this dissertation. I also wish to thank committee members Dr. Robert Krebs, Dr. Terry Robison, and Dr. Julie Wolin, who provided helpful advice, direction and encouragement throughout this study and to Dr. Paul Doerder and Dr. Carl Anthony for agreeing to read and comment on my dissertation.

A special thanks to Cleveland Metroparks and Cuyahoga Valley National Park for providing support and encouragement throughout the duration of the project. I would especially like to thank Dan Pettit for encouraging me to take on a Ph.D. and for his time and advice in the early stages of this project. I would also like to thank Lisa Petitt, Chuck Thomas, and Rick Tyler for sharing their time and knowledge when choosing field sites and getting to know the study area.

Last but not least, I would like to express my gratitude to all my field assistants; Emily Roach for her help and insight into project methods and for her sense of humor while checking traps at dawn each day and Anna Barry for her dedication, sticking with me for multiple field seasons. I would also like to thank my fellow students at CSU for their support and advice. Finally, a heart felt thanks to my family for their confidence and encouragement, and to Dan for his patience and understanding.

**A MULTI-TAXONOMIC APPROACH TO ASSESS THE IMPACT OF  
OVERABUNDANT WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN  
FOREST ECOSYSTEMS ACROSS NORTHEAST OHIO**

**SARA A. LAUX**

**ABSTRACT**

Browsing by white-tailed deer has altered plant species diversity of the forest understory across much of North America. A reduced understory may lead to the simplification of the forest-floor microhabitat, causing broad scale shifts in the community composition and abundance of litter-dwelling arthropods and small mammals. The objectives of this study were to 1) document changes in the forest-floor microhabitat as a result of over-browsing by deer and 2) determine if differential browsing pressures indirectly affect faunal biodiversity (litter-dwelling arthropods and small mammals) of forest ecosystems. I predicted that browsing within the understory will reduce structural complexity of the forest-floor microhabitat, and its dependent community. A combination of comparative (high vs. low deer impact) and exclosure studies were used to document the effects of herbivory on forest ecosystems. Fewer seedlings and less herbaceous and canopy cover occurred in areas outside exclosures and in areas heavily impacted by deer in contrast to those impacted less, and as percent herbaceous cover correlated strongly with leaf litter biomass and depth, browsing reduces structural complexity of the forest-floor microhabitat. More mesofauna, Coleoptera and Araneae, were present inside than outside deer exclosures. Non-native species (i.e., centipedes, gastropods, isopods and millipedes) were more abundant in areas of high deer impact compared to areas of lower impact. No differences in small mammal abundance were detected in response to the indirect effects of browsing; however, areas of low

impact were more speciose and supported significantly more insectivorous small mammals (Soricidae). Soricids require moist habitats with adequate cover and ample invertebrate prey. Capture rates of the Masked Shrew, *Sorex cinereus*, were positively correlated with litter depth and invertebrate abundance of the preceding year. These findings suggest that even where total soricid and arthropod abundance did not vary in response to differential levels of deer impacts, simplification of the forest-floor microhabitat can reduce diversity and species composition of litter-dwelling animals. Deer may also facilitate the invasion of non-native species and alter trophic cascades within the forest-floor ecosystem.

TABLE OF CONTENTS

LIST OF TABLES ..... x

LIST OF FIGURES ..... xi

CHAPTER

I. INTRODUCTION ..... 1

    Study Design ..... 10

        Comparative Study ..... 10

        Exclosure Study ..... 12

    Significance of Proposed Research & Objectives of Study ..... 14

II. DOCUMENTATION OF CHANGES TO THE FOREST FLOOR  
MICROHABITAT IN CLEVELAND METROPARKS AND CUYAHOGA  
VALLEY NATIONAL PARK ..... 19

    Abstract ..... 19

    Introduction ..... 20

    Methods ..... 22

        Study Area ..... 22

        Data Collection ..... 24

        Statistical Analysis ..... 25

    Results ..... 26

    Discussion ..... 28

    Literature Cited ..... 31

III. BROWSING EFFECTS ON LITTER-DWELLING ARTHROPOD  
COMMUNITIES IN NORTHEAST OHIO: AN EXCLOSURE STUDY ... 33

    Abstract ..... 33

    Introduction ..... 34



Methods .....	37
Study Area .....	37
Data Collection .....	37
Statistical Analysis .....	39
Results .....	40
Discussion .....	45
Management Implications .....	50
Literature Cited .....	51
IV. THE IMPACT OF BROWSING BY WHITE-TAILED DEER ON LITTER DWELLING ARTHROPOD POPULATIONS IN NORTHEAST OHIO: A COMPARATIVE STUDY .....	55
Abstract .....	55
Introduction .....	56
Methods .....	58
Study Area .....	58
Data Collection .....	59
Statistical Analysis .....	60
Results .....	61
Discussion .....	69
Management Implications .....	72
Literature Cited .....	75
V. THE EFFECT OF OVER-BROWSING BY WHITE-TAILED DEER ON SMALL MAMMAL POPULATIONS INHABITING THE FOREST FLOOR .....	79
Abstract .....	79

Introduction .....	80
Methods .....	82
Study Area .....	82
Data Collection .....	83
Statistical Analysis .....	85
Results .....	85
Discussion .....	91
Management Implications .....	95
Literature Cited .....	96
VI. HABITAT AND PREY ASSOCIATIONS FOR TWO SPECIES OF SHREW IN NORTHEAST OHIO .....	99
Abstract .....	99
Introduction .....	100
Methods .....	102
Statistical Analysis .....	106
Results .....	106
Discussion .....	110
Management Implications .....	111
Literature Cited .....	113
VII. CONCLUDING REMARKS AND MANAGEMENT RECOMMENDATIONS .....	116
Summary .....	116
Management Recommendations .....	121
VIII. LITERATURE CITED .....	125

## LIST OF TABLES

Table	Page
2.1 Estimates of deer density .....	23
2.2 Characterization of microhabitat by deer impact .....	28
3.1 Characterization of microhabitat at deer exclosures .....	42
4.1 Community level response by macrofauna to browsing .....	64
4.2 Community level response by mesofauna to browsing .....	67
4.3 Major hypotheses proposed to explain biological invasions .....	73
5.1 Total mammalian species captured .....	87
6.1 Microhabitat variables measured at successful and non-successful traps.....	108
7.1 Mean earthworm density .....	120

## LIST OF FIGURES

Figure	Page
1.1 Historical estimates of deer numbers .....	3
1.2 Perceived interactions between deer and their environment .....	7
1.3 Map of comparative study locations, Cleveland Metroparks & Cuyahoga Valley National Park, Ohio .....	11
1.4 Exclosure location map, Lake County Metroparks, Ohio .....	13
2.1 Mean canopy cover and seedling density by site .....	27
3.1 Percent cover inside and outside exclosures .....	41
3.2 Total invertebrate abundance .....	43
3.3 Mean invertebrates per gram leaf litter .....	44
4.1 Litter-dwelling arthropod response to browsing .....	63
4.2 Yearly taxonomic shifts in macrofauna .....	65
4.3 Proportion of native vs. non-native taxa .....	66
4.4 Yearly taxonomic shifts in mesofauna .....	68
4.5 The role of deer in facilitating biological invasions .....	74
5.1 Mean captures of insectivores and rodents .....	88
5.2 Mean rodent capture rate .....	89
5.3 Mean insectivore capture rate .....	90
6.1 Relationship between soricid captures and invertebrate biomass .....	109

## CHAPTER 1

### INTRODUCTION

“Just as a deer herd lives in mortal fear of its wolves, so does a mountain live in mortal fear of its deer. And perhaps with better cause, for while a buck pulled down by wolves can be replaced in two or three years, a range pulled down by too many deer may fail of replacement in as many decades.”

*Aldo Leopold, Sand County Almanac 1949*

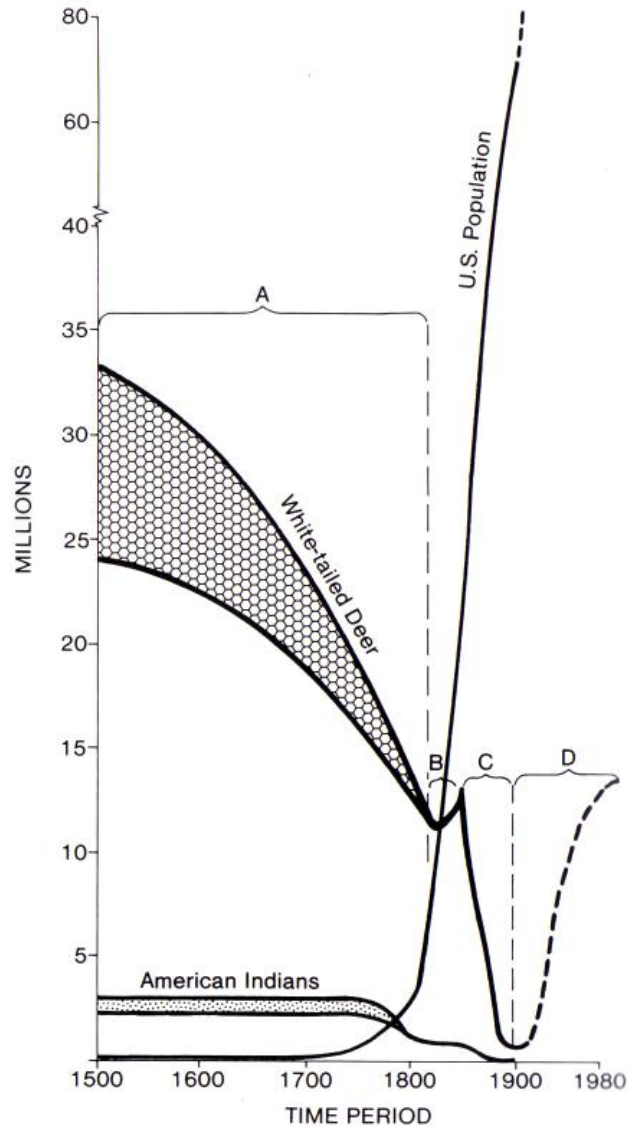
The overpopulation of deer herds in the United States is a common problem confronting conservation (Leopold 1949). Today, the issue of overabundance still commands considerable attention as the effects of urbanization, habitat fragmentation, extirpation of large predators, introduction of exotic species, and restrictions on hunting have exacerbated the problem (Hobbs 1996). White-tailed deer (*Odocoileus virginianus*) have expanded their geographic range and increased in abundance over the last several decades. Archaeological and anthropological data have estimated pre-European densities at 3 - 4 deer/ km<sup>2</sup> (McCabe and McCabe 1997; Figure 1.1). Today, however, it is common to see densities of over 30 deer/km<sup>2</sup> (R. Tyler, Cleveland Metroparks, unpublished data 2004; Alverson et al. 1988). This is problematic because deer degrade habitat and reduce biological diversity at densities less than 25% of carrying capacity (deCalesta and Stout 1997; McCabe and McCabe 1997). More specifically, deCalesta

(1997) and others have documented significant species loss, both plant and animal, at densities approaching 7 deer/km<sup>2</sup> in northern deciduous forests (Tilghman 1989; Augustine and Frelich 1998).

The rise in deer numbers across North America is best described in four stages: 1) pre-settlement (pre-1700), 2) regrowth (1800s-1865), 3) exploitation (early 1900s) and 4) restoration (Late 1900s; Leopold 1943 and McShea et al.1997; Figure 1.1). The pre-settlement era can be defined by a period of massive harvest by Native Americans. During this time, hunting pressure in combination with periodic harsh winters and ample predator presence helped maintain low deer densities (Figure 1.1). During the 1800's, however, European settlement brought major changes to North America, including widespread habitat modification, predator elimination, and legislation to restrict Native Americans to small reservations, thus reducing their influence on deer populations. As a result, deer numbers experienced a period of re-growth (Figure 1.1). However, this period lasted only a few decades, followed by a period of market hunting and exploitation. During this time, deer were hunted to near extinction (Figure 1.1). In an attempt to restore deer numbers, wildlife managers restricted hunting, created preserves with ample food and started deer translocation programs across North America (Figure 1.1). Deer responded positively to these management efforts and began expanding their range, eventually achieving densities far surpassing historical numbers.

The effects of increasing deer populations on plant species richness and composition are well documented (McCabe and McCabe 1997). However, less is known of how these changes affect the species richness and composition of other taxa and how taxonomic shifts in dominance effect overall ecosystem functioning. Because of an increasing

emphasis on overall ecosystem function, resource managers are now faced with the challenge of



**Figure 1.1 Historical estimates of deer numbers.** Estimated white-tailed deer population numbers across North America, 1500-1980. Sections labeled a-d represent different eras in deer population status; a) pre-settlement, b) re-growth, c) exploitation, and d) restoration (Adapted from McCabe and McCabe 1997).

managing deer herds not only to maintain plant species biodiversity, but also to maintain overall taxonomic diversity and ecosystem function. The question is now, how do the browsing activities of deer impact overall taxonomic diversity and at what density should deer be managed to preserve ecological integrity? Or, should management toward a goal ‘threshold’ density, often based on broad scale vegetation data, be used at all?

In recent decades, an array of methodologies has been used to study the interaction between ungulates and forest ecosystems, each with their own caveats and limitations. The most commonly applied methodologies can be broadly grouped into two classes: 1) experimental, based on grazing simulations and use of exclosures and 2) non-experimental comparative studies. Grazing simulation techniques aim to mimic ungulate foraging behavior to evaluate individual plant responses to herbivory. Although useful for understanding species-specific responses to herbivory, scaling up these effects to understand community level responses across larger spatial scales can be difficult. Exclosure studies, based on pair-wise fenced and unfenced plots, prove useful for studying both individual and population level plant response to herbivory (Milchunas and Lauenroth 1993; Ammer 1996). However, an increasing number of studies now focus on broader taxonomic and community level responses to herbivory (e.g. Baines et al. 1994; Suominen 1999, ground-dwelling invertebrates and Hazebrock et al. 1995, small mammals) and ecosystem processes (McInnes et al. 1992; Pastor 1993). Exclosure data provide a method to experimentally assess the impact of ungulates on multiple taxonomic and ecosystem level processes; however, the general applicability of exclosure data is often low (Hester et al. 2000; Berstrom and Edenius 2003). Meta-analyses of exclosure studies indicate an over-representation of exclosures erected on poor to moderately



productive sites in areas already impacted by deer (Berstrom and Edenius 2003).

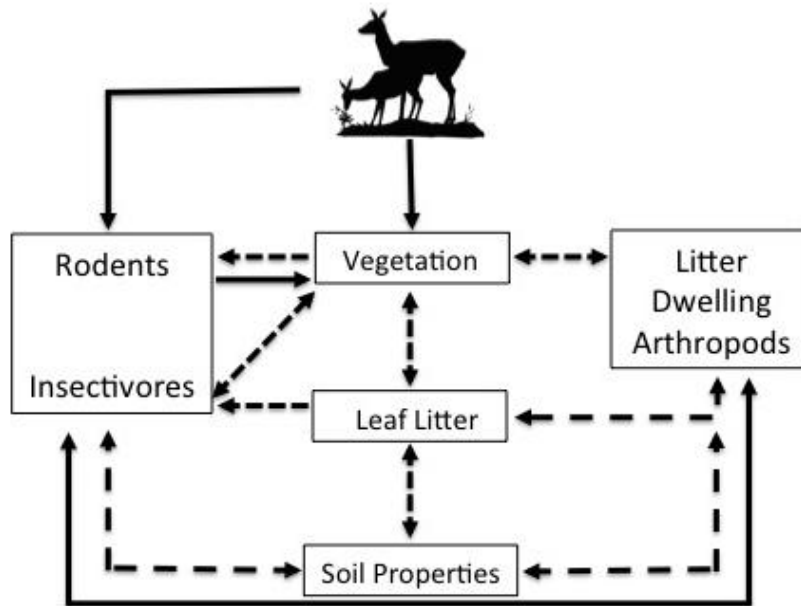
Additionally, ungulates are usually completely excluded from exclosures and control plots are usually small making it difficult to accurately assess browsing pressure outside exclosures (Hester et al. 2000). This means that what is actually being studied within exclosures is a recovery phase rather than a population or community level response to herbivory across a known density gradient. Finally, confounding factors associated with the exclosures often complicate interpretation of exclosure data. Exclosures themselves may create unnaturally small “islands”, supporting altered plant community dynamics and microhabitat features that in turn may attract or deter other species, such as litter-dwelling arthropods or small mammals (Bergstrom and Edenius 2003).

Non-experimental approaches make use of natural or uneven distributions of ungulates to evaluate both spatial and temporal patterns of ungulate behavior and their effects. These techniques are appropriate for gauging the impact of herbivory on plant interactions across broad landscapes and can also be used to investigate higher levels of ecological complexity. Non-experimental approaches are often logistically feasible, allowing large areas to be surveyed across a more natural biologically relevant setting and allowing a range of scales to be covered. Disadvantages of these techniques include lack of controls and difficulty in replicating sites. Additionally, confounding factors such as differences in land use history and site productivity can make clear interpretation of results difficult.

I characterize the impacts of overabundance on a suite of ecologically significant taxa present on the forest floor and important in driving ecological processes by using a combination of experimental and non-experimental methodologies. The following

research discussion focuses on the indirect effects of deer overabundance on local small mammal and invertebrate species composition. By introducing a new, more community based approach to investigating the issue of overabundance, I hope to provide supporting data to help managers develop a framework around which to evaluate the impacts of browsing within each park reservation. This shift in focus away from managing deer based on the ecological carrying capacity of the land, a measure difficult to quantify often based solely on plant responses to herbivory, to a more integrated approach evaluating how an ecosystem, in terms of taxonomic diversity, is responding to the local browsing pressure is critical if managers are to fully understand the impacts of browsing on forest ecosystems.

The rationale for this approach derives from recent findings that white-tailed deer are keystone herbivores within forest ecosystems (McShea and Rappole 1992; Waller and Alverson 1997; Rooney 2001) and therefore play an integral role in forest ecosystem dynamics. Deer are selective foragers, preferentially feeding on some plants while avoiding others; this increases the relative abundance of browse-tolerant species while browse-intolerant species decline (Augustine and McNaughton 1998). As a result, sustained over-browsing can have far reaching impacts on forest floor communities. These impacts occur through two pathways: 1) directly, through competition for and alteration of available resources (Gill 1992) and 2) indirectly, through the modification or removal of preferred habitat (Gill and Beardall 2001 and Rooney and Waller 2003; Figure 1.2). My focus will be on the indirect effects of deer on the taxonomic diversity of forest ecosystems.



**Figure 1.2 Perceived interactions between deer and their environment.** The above flow chart highlights perceived direct and indirect interactions between the browsing activities of deer and forest floor fauna—small mammals (insectivores and rodents) and litter-dwelling arthropods. Direct interactions are represented by a solid line, indirect interactions are represented by a dashed line.

Indirect effects arise in ecosystems when the influence of one species is transmitted through the habitat to a third ‘receiver species’ (Morin 1999). The indirect effects of chronic over-browsing cause shifts in overall plant species composition by altering competitive interactions among understory plant species and facilitating the invasion and establishment of unpalatable or non-native species (Augustine and McNaughton 1998; Gill and Beardall 2001; Lessard et al. 2012). Combined, these effects can negatively impact the forest floor microhabitat. Browsing induced changes to the functional composition of the plant community may alter the quantity of litter production and

quality of litter inputs on the forest floor thus altering habitat structure and resource availability for litter-dwelling taxa (Leboutan 2005). In addition, reduced plant and litter cover may increase light penetration to the forest floor causing a decline in soil moisture and humidity, which may alter soil pH. Collectively, these effects alter the forest floor microclimate and disrupt nutrient cycling regimes and decomposition rates (Rooney and Waller 2003; Figure 1.2). Leaf litter accumulation and biomass are important components of forest floor ecosystem dynamics, mediating a cascade of effects within forest communities (Hairston and Hairston 1993; Polis and Strong 1996; Bardgett and Wardle 2003; Lessard et al. 2012). An important, but poorly understood, deer-induced change to the forest floor microhabitat is the initiation of a cascade of effects on litter-dwelling arthropods and small mammals (Flowerdew and Ellwood 2001). Simplification of habitat structure brought on by shifts in species composition and reduced litter biomass are likely to result in a reduction of litter-dwelling arthropod diversity and abundance (Bultman and Uetz 1982; Rambo and Faeth 1999; Wagner et al. 2003; Langellotto and Denno 2004). For many litter-dwelling arthropods, the structural diversity of the forest floor microhabitat dictates habitat suitability by providing foraging sites, refugia from the elements and protection from predators (Langellotto and Denno 2004). The nature and strength of these effects will depend on the taxa in question; nonetheless, the potential for the interaction between the browsing activities of deer and arthropod abundance and diversity is great.

The impact of browsing on small mammals may not be quite as obvious. Browsing by deer can reduce the amount of forest floor vegetation cover, thereby making small mammals more visible and thus more susceptible to predation. On the other hand, the

creation of more open habitats may facilitate the colonization of species who prefer open forest habitats within the forest interior, such as the eastern chipmunk (*Tamias striatus*), or allow a competitive biological release for some species to increase in abundance because of a lack of competition with more habitat sensitive specialist species.

The impact of deer on forest microhabitat may be especially detrimental to shrews (*Blarina* and *Sorex*), which are a particular focus in this study. Shrews are semi-fossorial insectivores with a high metabolism; therefore, they require ample cover and invertebrate prey species to sustain daily activities. Additionally, and related to their high metabolism, shrews require moist habitats to offset high rates of evapotranspiration. A major component within the forest floor microhabitat determining invertebrate prey availability and regulating forest microclimate is the amount of litter accumulation on the forest floor; therefore, the indirect removal of the litter layer through browsing may negatively impact shrew populations.

Although few empirical studies have specifically addressed the effects of overabundant deer populations on the forest floor dynamics of small mammals and invertebrate populations, the above evidence suggests that interactions exist between deer and forest floor communities. Based on this evidence, I hypothesize that:

***H<sub>1</sub>***: Habitat modifications caused by deer over-browsing reduce structural complexity and habitat quality of the forest floor microhabitat;

***H<sub>2</sub>***: The loss of forest understory and resulting changes to forest floor microhabitat result in a decline in invertebrate diversity and abundance;

**H<sub>3</sub>:** Habitat modifications reduce invertebrate abundance and the subsequent reduction in food availability will result in lower small mammal diversity and abundance in areas of high deer density.

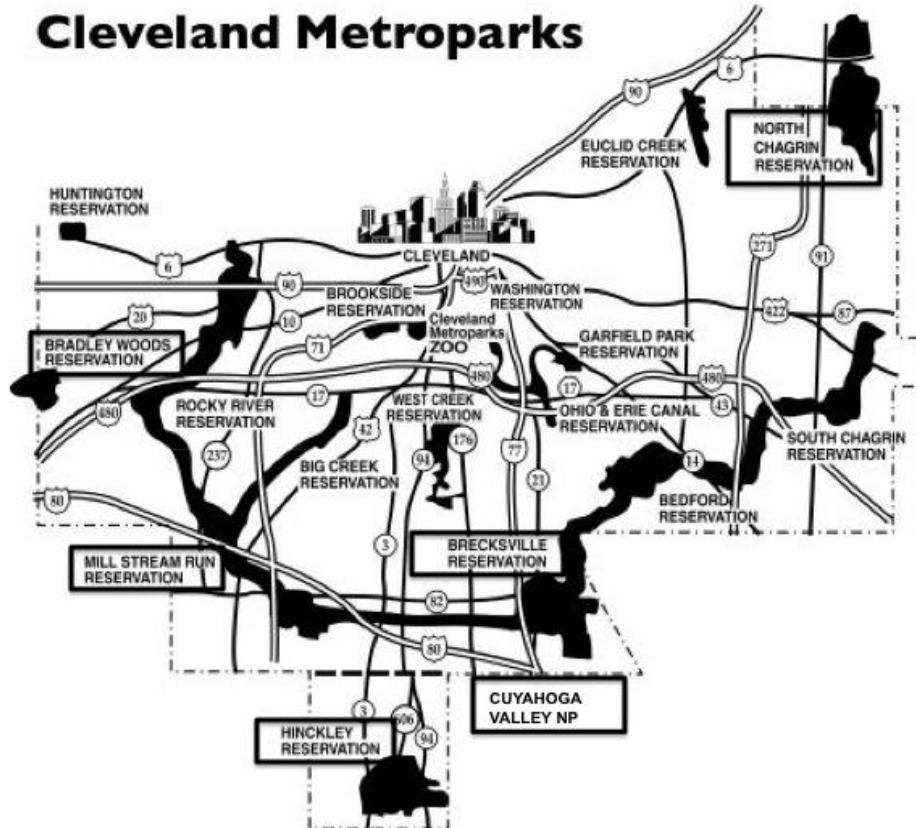
## **Study Design**

A combination of comparative and enclosure methodologies will be used to assess the impact of deer on the taxonomic diversity of the forest floor microhabitat. This approach will provide a framework around which the impact of browsing by deer can be assessed across multiple spatial scales. The park systems of Northeast Ohio provide an excellent opportunity to conduct such experiments and thus serve as study sites for my research.

### ***Comparative Study***

Cuyahoga Valley National Park (CVNP) and the Cleveland Metroparks (CMP) consist of multiple reserves encompassing approximately 21,500 ha surrounded by the Greater Cleveland-Akron metropolitan area of Northeast Ohio (Figure 1.3). Hunting is prohibited in both park systems; however, CMP has been culling deer herds since 1998. CVNP on the other hand, does not allow any form of deer management. Such management regimes have resulted in densities ranging between 8 and 30 deer/ km<sup>2</sup> in CMP to densities > 52 deer/km<sup>2</sup> at CVNP (Underwood and Coffey 1999; R. Tyler, Cleveland Metroparks, unpublished data 2004). This continuum of deer densities within and among park reservations provided an opportunity for a comparative assessment of the ecological impacts of deer in a natural, biologically relevant setting without the use of enclosures. Within these park systems, seven field sites were chosen based on over ten years of data concerning the impact and density of deer population on forest vegetation.

## Cleveland Metroparks



**Figure 1.3 Map of comparative study locations, Cleveland Metroparks & Cuyahoga Valley National Park, Ohio.** Field sites (highlighted by boxes) used for the comparative study investigating the impact of deer on the taxonomic diversity of the forest floor. Sites were defined by overall deer impact and grouped into high or low impact categories based on a combination of indices including vegetation data (C. Thomas, Cleveland Metropark, unpublished data 2000), culling records, aerial and spotlight surveys and pellet counts between the years of 1998 and 2004. Sites characterized as low impact include, two sites at Hinkley Reservation and one site at Bradley Woods Reservation. Sites characterized as high impact include sites at Cuyahoga Valley National Park, Brecksville, Mill Stream Run, and North Chagrin Reservations.

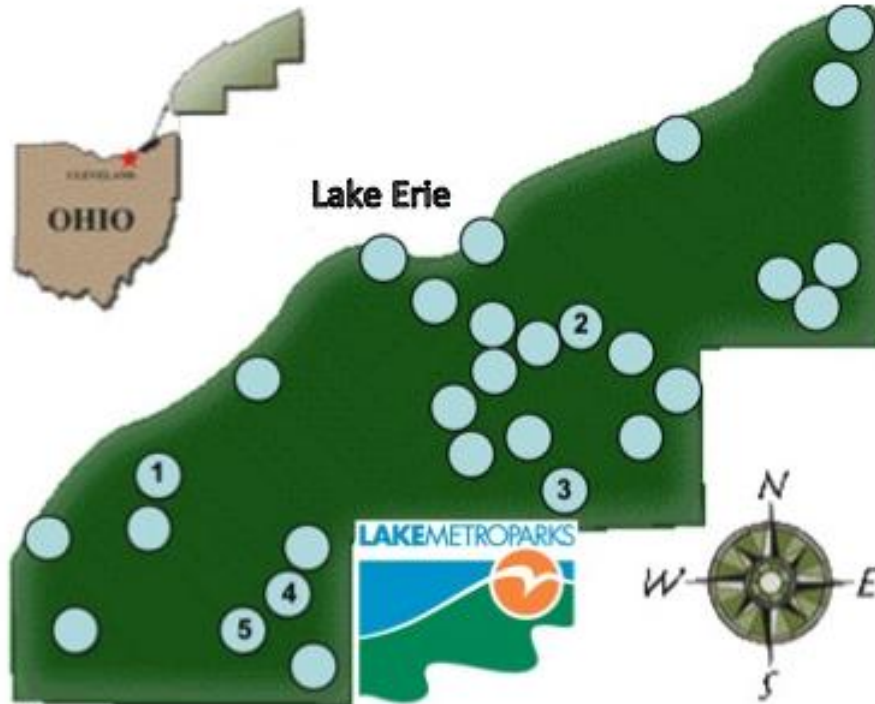
These sites varied in overall deer impact from low to moderately low to high or very high (Figure 1.3). Data on small mammal and invertebrate abundance, as well as a suite of microhabitat variables were collected seasonally between the years of 2005 - 2007 at each site to document the impact of browsing on forest floor communities. I used a series

of trapping grids using Sherman live traps ([www.shermantraps.com](http://www.shermantraps.com)) and pitfall traps (6.4 liter tin cans) to estimate population size and small mammal diversity at each field site. Data on the diversity and abundance of litter-dwelling arthropods were collected using both pitfall traps and Berlese extraction of leaf litter samples. Habitat quality was accessed around a subset of small mammal trapping stations to estimate: % ground cover, leaf litter depth, % herbaceous cover, and % canopy cover. In addition, % cover and decay state for all downed woody debris larger than 10-cm in diameter was estimated at each site. Data on soil condition, moisture and pH were collected at monthly intervals across each field site.

### *Exclosure Study*

Lake Metroparks manages 42 rural and suburban park reservations encompassing over 7,600 ha of mixed deciduous forest and riparian habitat along the Lake Erie watershed (Figure 1.4). Hunting and any other form of deer management are prohibited within park boundaries. As a result, deer densities average between 18 and 48 deer/km<sup>2</sup> (T. Adair, Lake Metroparks, unpublished data). In 1993, park managers installed four 30 X 60 m (0.18-ha) deer exclosures within three park reservations to study the effect of browsing on forest regeneration and plant species diversity. Park managers established three additional exclosures in 2000. Research at Lake County Metroparks then, provided an ideal framework to study the impacts of deer using exclosures.





**Figure 1.4 Exclosure location map, Lake County Metroparks, Ohio.** Exclosure site locations with the 7,600 ha Lake County Metropark System. Each circle represents a different park reservation. Each of the five labeled reservations represents a different exclosure site: 1) Chagrin River Park (2 exclosures), 2) Indian Point, 3) Girdle Road, 4) Penitentiary Glen, and 5) Chapin Forest.

In 2008, a study was initiated to compare the abundance and taxonomic diversity of invertebrates inside and outside of the five previously established exclosure sites (Figure 1.4). Similar methods were used to collect data on the taxonomic diversity and abundance of litter-dwelling invertebrates inside vs. outside deer exclosures as described above. Data were also collected on a suite of microhabitat variables inside the enclosed treatment area and in unfenced control plots adjacent to the exclosures. Because of the relatively small area covered by the exclosure and paired control sites, data on small mammal population indices were not collected as part of this study.

## **Significance of Proposed Research & Objectives of Study**

Data provided by this study will give managers another set of tools to help make decisions regarding the population management of deer. By understanding the potential impact of deer on litter-dwelling arthropods and small mammals, and knowing how to recognize these interactions in the field; managers will be able to assess the impact of deer on overall ecosystem dynamics using a suite of ecologically important taxa, instead of focusing solely on plant species responses. These data will also help managers design a framework around which success of management practices can be monitored. Rather than determining success solely on maintaining a predetermined ‘threshold’ density or looking at plant species recovery, information on how other ecologically important taxa—litter-dwelling arthropods and small mammals—respond to herbivory will allow managers to incorporate guidelines and expected norms for indirect impacts of deer into management practices. Success would then be determined by the response of select indicator species to deer manipulations rather than maintaining ‘threshold’ densities alone. In other words, if a ‘threshold’ density of 6 deer/km<sup>2</sup> is reached but the expected taxonomic diversity is absent, then management objectives were not reached and further research or management efforts are needed to restore taxonomic diversity.

Below is a brief synopsis of my research organized into five subsequent data chapters followed by a final chapter of concluding remarks.

**Chapter 2:** *Documentation of changes to the forest floor microhabitat as a result of deer browsing in Cleveland Metroparks and Cuyahoga Valley National Park*

Sustained over-browsing by white-tailed deer have caused extensive damage to the forest ecosystems across much of North America. Many management regimes rely on

broad scale shifts in plant species diversity and crude estimates of deer abundance to dictate management efforts and gauge success of management goals. However, these efforts, useful in broad ecosystem assessments, may be missing changes happening at a more localized scale. Much of the biodiversity present in forest ecosystems, litter-dwelling arthropods and small mammals, occupy niches within the forest floor microhabitat at scales much smaller than those used to currently assess the impact of deer. The objectives of this study are to 1) employ a more localized approach to document changes in the forest understory and compare these estimates to previously documented estimates of deer numbers across a broader landscape and 2) show how different browsing pressures indirectly affect the forest floor microhabitat, a niche important in supporting much of the faunal biodiversity in forest ecosystems. Results indicate that changes in the forest understory correspond to changes in the structural complexity of the forest floor microhabitat.

**Chapter 3:** *Browsing effects on litter-dwelling arthropod communities in Northeast Ohio: An exclosure study*

This study aims to document the response of litter-dwelling arthropods to deer-induced changes in the structural complexity of the forest floor microhabitat. I used a combination of pitfall traps and Berlese litter extractions to document differences in litter-dwelling arthropod abundance and community composition inside versus outside of deer exclosures. I hypothesized that 1) browsing by deer results in a decline in habitat structural complexity on the forest-floor, and that 2) changes in habitat quality will correspond to a decrease in abundance of litter-dwelling arthropods. I found the structural complexity of the forest floor microhabitat was greater inside exclosures

compared to unfenced control plots. The simplification of the forest microhabitat negatively impacted the species composition of litter-dwelling arthropods, especially small litter dependent mesofauna.

**Chapter 4:** *The impact of browsing by white-tailed deer on litter-dwelling arthropod populations in Northeast Ohio: A comparative study*

Here I use a comparative study to document the impact of deer on the abundance and taxonomic composition of litter-dwelling arthropods in Northeast Ohio. I hypothesized lower overall abundance of litter-dwelling arthropods in areas of high relative to low browsing impact. I also expected an overall shift in species composition between areas of high and low impact. Specifically, I expected areas heavily impacted by deer to support a disproportionate assemblage of non-native species. A series of pitfall and Berlese extractions were used to document arthropod abundance and taxonomic diversity in areas of high and low deer impact within Cleveland Metroparks and Cuyahoga Valley National Park. Results suggest that the disturbances caused by the browsing activities of deer may facilitate and support the invasion of non-native species further escalating the threats of overabundant deer to local species diversity.

**Chapter 5:** *The impact of over-browsing by white-tailed deer on small mammal populations inhabiting the forest floor*

A comparative study was designed to assess the indirect effects of deer on small mammal population dynamics in Northeast Ohio. I used a combination of Sherman live traps and pitfall arrays to assess differences in small mammal abundance and diversity between areas of low and high deer impact. I expected areas of low impact to support increased small mammal abundance and species diversity, especially insectivorous

species such as shrews. Results suggest higher abundance and species diversity in areas of low impact relative to sites more heavily impacted by deer. This study suggests an indirect interaction between deer and small mammals. I found an increase in abundance and species diversity, especially insectivorous shrews, in areas of low impact relative to high impact sites.

**Chapter 6:** *Habitat and prey associations for two species of shrew in Northeast Ohio*

This study is designed to define associations between habitat quality and the abundance of shrews. I approached this aim from two different scales: 1) microhabitat, defined as the habitat immediately surrounding a trap site and 2) macro-habitat, defined as the collective quality of habitat, including food availability, across the broader study site over several years (2005-2007). This study suggests that the structural composition of the forest microhabitat is more important in determining soricid presence than the overall characterization of the macro-habitat and abundance of invertebrate prey.

**Chapter 7:** *Concluding remarks and management recommendations*

Managing deer with the goal of maintaining deer at a “threshold” density based on carry capacity or broad scale plant responses to browsing may not be the most effective way to manage deer for increased biodiversity within forest ecosystems. Deer are highly mobile and behaviorally flexible, capable of modifying their behavior depending on both the biotic and abiotic surroundings of their habitat. It has been suggested that deer will preferentially browse on different plant species, even those thought to be browse tolerant, in different areas based on availability and competition (C. Thomas, personal communication 2004). This makes it difficult to apply universal conditions or assumptions about deer browsing activities and their impact across a landscape.

Therefore, density estimates alone are unlikely to be good predictors of the impact of deer on their environment. Instead, management decisions should be made on the basis of known interactions between deer browsing and the abundances and species composition of other ecologically important taxa. The indirect effects of deer on the forest microhabitat have the potential to alter the abundance and species composition of both litter-dwelling invertebrates and small mammals. Therefore, I suggest managers incorporate data on the diversity of forest floor taxa, both at the local and landscape level, into their management plans. Accounting for how local and broad scale changes in vegetation, from browsing activities of deer affect taxonomic diversity will allow managers to gain better insight into the impacts of deer on forest ecosystems and provide a more relevant means to gage the success of deer management and ecosystem restoration efforts.

## CHAPTER II

### DOCUMENTATION OF CHANGES TO THE FOREST FLOOR MICROHABITAT IN CLEVELAND METROPARKS AND CUYAHOGA VALLEY NATIONAL PARK

#### ABSTRACT

Sustained over-browsing by white-tailed deer has caused extensive damage to the forest ecosystems across much of North America. Many management regimes rely on broad scale shifts in plant species diversity and crude estimates of deer abundance to dictate management efforts and gauge success of management goals. However, this approach, useful in broad ecosystem assessments, may be missing changes happening at a more localized scale. The objectives of this study are to 1) employ a more localized approach to document changes in the forest understory and compare these estimates to previously documented estimates of deer numbers across a broader landscape and 2) show how different browsing pressures indirectly affect the forest floor microhabitat, a niche important in supporting much of the faunal biodiversity in forest ecosystems. Seven field sites were chosen and grouped as high or low impact based on previous estimates of deer density. Data on canopy cover and seedling density ( $\#/m^2$ ) were collected at each site to verify browsing pressure and impact. Results indicate that changes in the forest understory correspond to changes in the structural complexity of the

forest floor microhabitat. On average, areas chosen *a priori* as low impact had 5% more canopy coverage and more than four-fold increase in the number of seedlings present per unit area than areas of high impact. This suggests that sites were correctly classified as either experiencing low or high deer impact. Leaf litter was 0.56 cm deeper at low impact sites with an average of 60 g more leaf litter biomass/m<sup>2</sup> compared to areas of high deer impact. Additionally, overall herbaceous cover was 6% higher in areas lower deer impact and soils were on average 14% drier in high impact areas and

## INTRODUCTION

Over-browsing by white-tailed deer (*Odocoileus virginianus*) has caused extensive changes in understory plant communities throughout much of North America (Fuller and Gill 2001; Vázquez 2003; Côte et al. 2004). Several experimental and comparative studies have indicated that long-term over-browsing decreases plant size, growth & survival, reduces plant fecundity and alters plant species dominance and overall species diversity (Augustine and Frelich 1998; Russell et al. 2001; Rooney and Waller 2003; Côte et al. 2004; Eschtruth and Battles. 2009; Gill and Morgan 2010). These shifts in understory plant demography have the potential to alter the quality and quantity of the forest floor microhabitat, i.e., leaf litter accumulation, ground cover, and consequently reduce availability of habitat for forest floor communities (Souminen et al. 1999; McShea and Rappole 2000). Reduction in the overall herbaceous layer result in less leaf litter accumulation; this, in combination with increased light penetration to the forest floor, can result in warmer, more xeric soils (Fuller 2001). These changes have been documented to affect seedling growth rates and prevent canopy tree recruitment (Tilghman 1989; Inouye et al. 1994; Alverson and Waller 1997; Strange and Shea 1998; Liang and Seagle



2002). Decreases in seedling densities (Putman et al. 1989; Healy 1997; Liang and Seagle 2002; but see Tilghman 1989) and the underrepresentation of browse sensitive species in favor of browse tolerate species (Rooney et al. 2000) have lead to decreased species richness (Tilghman 1989; Rooney and Dress 1997; Augustine et al. 1998) and a shift in species dominance to less palatable species (VanDeelen et al. 1996). The presence of less favorable plant species in the leaf litter layer may slow decomposition rates, altering nutrient cycling regimes and the ability of native species to maintain their presence in heavily impacted areas. Additionally, those animal species reliant on the forest floor for food, shelter, and temperature regulation represent the majority of species diversity in forest ecosystems. Therefore, understanding how deer influence resource availability for species living within the forest understory and on the forest floor is important for preserving the integrity of ecosystems where deer are overabundant.

To understand the impact of deer on the flora and fauna living within the forest floor microhabitat, it is important to understand the scale at which these processes occur. Because I am interested in how deer affect habitat quality as it relates to small mammals and litter-dwelling arthropods, species that live within much smaller home ranges than deer, I wanted to document the level of browsing intensity within smaller, more local habitats, rather than rely on landscape level estimates of browsing pressure. I chose two easily measured variables influenced by the browsing activities of deer to estimate local browsing impact: seedling density and percent understory canopy cover (Carter and Fredericksen 2007 and Putman et al. 1989). I also wanted to document how changes in the forest understory affect the quality of habitat on the forest floor. Again, I employed relatively simple, but meaningful, methods to document changes to the forest floor rather

than detailed species-specific changes. For much of the fauna of the forest floor, the amount of shade, shelter and vertical structure are more important for organismal functions, e.g., web building, egg laying and prey capture, than are the specific plant species providing those functions.

One objective of this study was to verify the classifications of sites designated previously as high or low deer impact sites. I used two criteria: seedling density and percent canopy cover (Carter and Fredericksen 2007). Sites most heavily impacted by deer should have fewer seedlings/m<sup>2</sup> and less canopy cover than sites with less severe deer browse. The second objective was to determine if differential browsing pressure affects features of the forest floor microhabitat, including leaf litter biomass and depth, percent ground cover, and soil moisture. I expect areas of high deer impact to have reduced seedling density and reduced herbaceous and understory canopy cover relative to low impact sites. I also expect less leaf litter accumulation on the forest floor leading to drier soils in areas with increased deer activity.

## METHODS

### **Study Area**

A continuum of deer densities can be found within and among park districts and reservations in Northeast Ohio, presumably caused, at least in part, by variation among management regimes employed by Cleveland Metroparks (CMP) and Cuyahoga Valley National Park (CVNP). As a result, I designed a comparative assessment of the ecological impacts of deer browsing activities within a natural, biologically relevant

**Table 2.1 Estimates of deer density.** Mean estimates of deer impact based on several measures of deer impact (pellet counts, aerial infrared, spotlight and browse index surveys) between 1997-2003 and within Cleveland Metroparks (CMP) and Cuyahoga Valley National Park (CVNP). Combined methods focused on management sites within the CMP. Data on browse index surveys were taken within 400 m of selected study sites for this study. These data were used to make *a priori* classification of sites based on deer impact.

Site	Park District	Combined Methods Estimate		Browse Index Survey	Overall Impact
		Mean (#/km <sup>2</sup> )	Range (#/km <sup>2</sup> )		
Riding Run (RR)	CVNP	31	N/A	Very High Browse	High Impact
Ottawa Point (OP)	Brecksville Reservation, CMP	17	8-27	High Browse	High Impact
Royal View (RV)	Mill Steam Run Reservation, CMP	16	11-23	High Browse	High Impact
North Chagrin (NC)	North Chagrin Reservation, CMP	12	10-16	High to Medium High Browse	High Impact
Bradley Woods (BW)	Bradley Woods Reservation, CMP	21	16-27	Low to Medium Browse	Low Impact
Hinckley 1 (H1)	Hinckley Reservation, CMP	17	8-23	Low Browse	Low Impact
Hinckley 2 (H2)	Hinckley Reservation, CMP	17	8-23	Low to Medium Browse	Low Impact

setting without the use of deer exclosures. Seven field sites were chosen based on several measures of deer impact (Table 2.1). Because the current structure and species diversity within the forest understory likely to reflect the influence of past browsing events, browse estimates from the years leading up to the study were weighted more heavily than current estimates. Pellet count data, aerial infrared and spotlight surveys, and population estimates based upon culling efforts conducted between 1997 and 2003 were used to obtain estimates of park-wide deer density. Using these data, average density estimates

ranged from 8- 27 deer/km<sup>2</sup> (Table 2.1). However, because deer are known to browse preferentially in certain habitats relative to others and have been documented by park personnel to prefer certain areas within the parks (C. Thomas, personal communication 2004), localized estimates of deer impact were also used to document browse severity near each potential field site. Since 1998, CMP has been conducting detailed multi-point vegetation surveys to assign a browse severity index, ranging from low to very high within several of its park reservations. With these data and visual assessments of each potential field site by qualified park personnel, seven field sites were chosen: three low and four high impact sites (Table 2.1).

### **Data Collection**

Data on a suite of forest floor microhabitat variables were collected once each year during the 2005-2007 field seasons. A 1-m radius circular sampling frame was used to estimate ground cover and estimate numbers of seedlings and mature trees. At each site, I placed the frame at 69 points within a previously established sampling grid (see Chapter 5; total area 0.92 ha). Within the sampling frame, I estimated measures of ground cover visually, including % herbaceous cover, % leaf litter cover, and % cover of downed woody debris (DWD). I also counted the number of seedlings (height < 15 cm) and saplings (trunk DBH < 10 cm) and mature trees (trunk DBH ≥ 10 cm) within each sampling frame. Percent canopy cover was estimated using a spherical crown densiometer at the center of each circular plot. Estimates of canopy cover were taken in each of the four cardinal directions at the center of each sampling grid and averaged to obtain an overall estimate. Measurements on leaf litter depth to the nearest 0.5 cm were collected at 4 points along the perimeter of each sampling grid (totaling 275

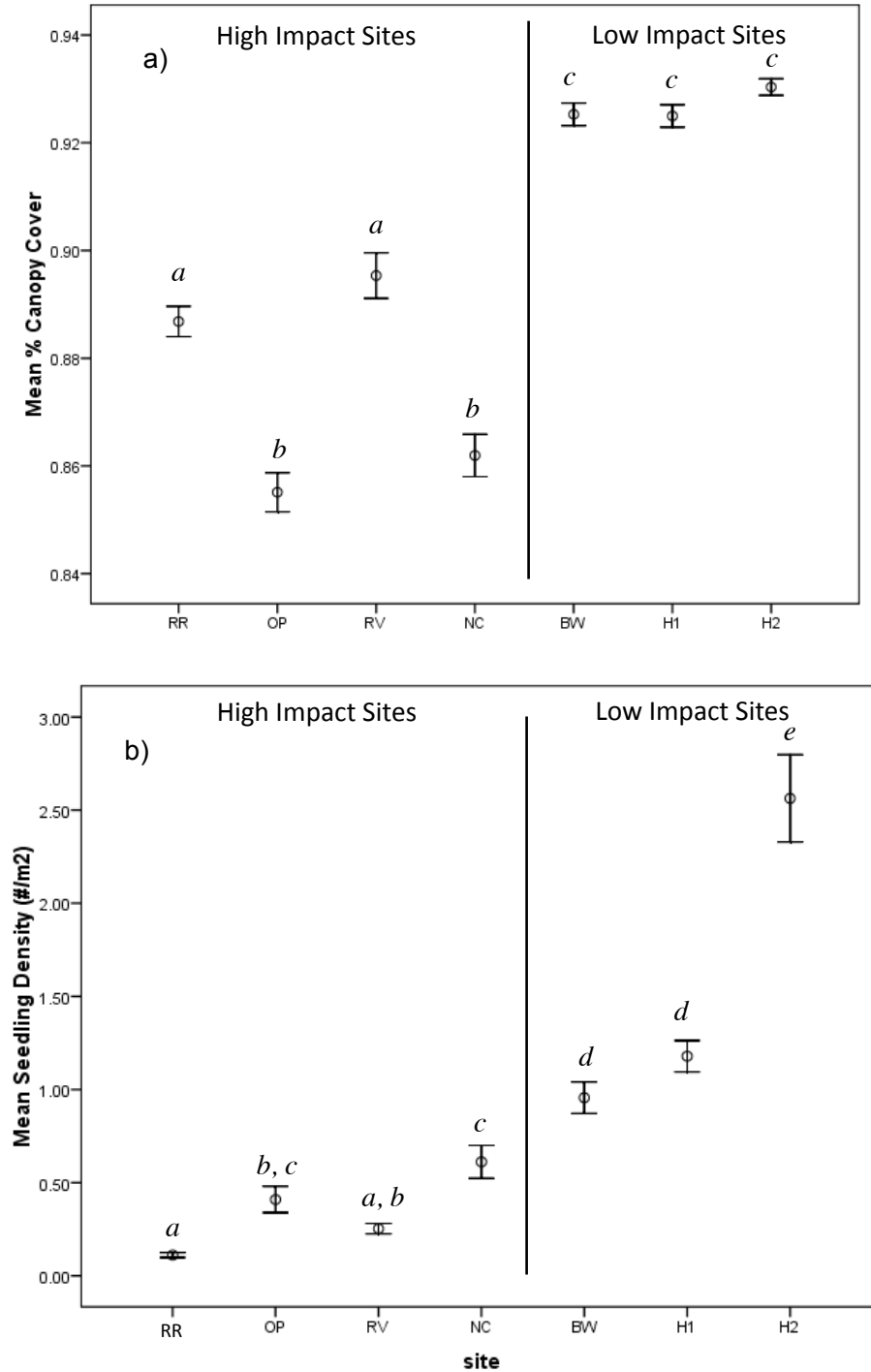
measurements/site). Soil moisture was measured with a Kelway® soil pH and moisture meter at 15 cm depth at 109 locations spaced at each trap station along the previously established small mammal trapping grid. Dry weight of leaf litter were established using litter samples collected for invertebrate extraction as part of a related study on the impacts of deer on forest floor invertebrates. Leaf litter samples were collected three times each field season during the months of June, August and October. Twenty-eight random locations were identified each month at each site for litter collection. A 189 cm<sup>2</sup> circular frame was placed at 28 random locations within the previously established trapping grid. All litter within the frame was removed by hand and placed in a 1 gal plastic bag. Leaf litter samples were transported to a laboratory, weighed to the nearest 0.001g on an electronic balance and distributed randomly among 30 Berlese funnel extractors. Extractions were run for 48 hrs; dried leaf litter samples were reweighed to the nearest 0.001g to determine total dry litter biomass.

### **Statistical Analysis**

Analysis of variance (ANOVA) was used to test for differences in seedling density and canopy cover among field sites. Post hoc comparisons using Tukey HSD were used to characterize differences among sites. These data were used to verify previous groupings of sites into two categories, i.e. high or low impact. Pearson's correlations were used to explore relationships among microhabitat variables, canopy cover, and seedling density/m<sup>2</sup>. I then used multivariate analysis of variance (MANOVA) to test for differences in forest microhabitat variables between areas of high and low deer impact.

## RESULTS

An overall significant difference in seedling density ( $\#/m^2$ ) and percent canopy cover was found among field sites (Pillai's Trace = 0.662,  $F_{(12, 1752)} = 72.311$ ,  $p \leq 0.001$ ). Canopy cover differed strongly between sites characterized *a priori* by park personnel as low-impact sites and those characterized as high impact sites ( $F_{(6, 885)} = 101.95$ ,  $p \leq 0.001$ ; Fig. 2.1a). Similarly, seedling density was significantly greater at sites characterized *a priori* as low-impact than those deemed high-impact sites ( $F_{(6, 885)} = 87.94$ ,  $p \leq 0.001$ ; Fig 2.1b.). Post hoc comparisons using Tukey HSD tests support these site groups (Figures 2.1a & b). On average, areas of low impact had 5% more canopy coverage and more than two fold increase in the number of seedlings present per unit area than areas of high impact (Table 2.2). The structure and complexity of the forest floor microhabitat also differed between areas of high and low impact. Of the variables measured, all but percent leaf litter cover was found to vary significantly between areas of high and low impact (Table 2.2). On average, leaf litter was 0.56 cm deeper at low impact sites with an average of 60 g more dry litter biomass/ $m^2$  compared to areas of high deer impact (Table 2.2). Additionally, soils were on average 14% drier in high impact areas and overall herbaceous cover was 6% higher in areas of lower deer impact (Table 2.2).



**Figure 2.1 Mean canopy cover and seedling density by site.** Estimates of (a) % canopy cover and (b) seedling density used to classify field sites as high or low impact. High impact sites averaged 88% ( $\pm 0.3$  SE) canopy cover and 0.41 ( $\pm 0.057$  SE) seedling density. Low impact sites averaged 93% ( $\pm 0.2$  SE) canopy cover and 1.60 ( $\pm 0.139$ ) seedling density. Similar italicized letters represent site groupings indicated by post hoc Tukey HSD tests of homogeneity.

**Table 2.2 Characterization of microhabitat by deer impact.** Mean values for several microhabitat variables influenced by the activities of deer in areas of high and low deer impact during the 2005-2007 field seasons. High impact sites include those at Riding Run (CVNP) and Ottawa Point, North Chagrin and Royal View Reservations (CMP). Low impact sites include those at Bradley Woods and Hinckley Reservations (CMP).

Microhabitat Variable	High Impact		Low Impact		<i>p</i>
	Mean	SE	Mean	SE	
Leaf Litter Biomass (g/m <sup>2</sup> )	950.98	17.41	1010.95	17.34	≤ 0.001
Leaf Litter Depth (cm)	0.97	.014	1.59	0.028	≤ 0.001
Seedling Density (#/m <sup>2</sup> )	0.41	.06	1.60	0.14	≤ 0.001
Mature Tree Density (#/m <sup>2</sup> )	0.081	0.009	0.055	0.008	0.06
% Herbaceous Cover	20%	4.5	78%	0.9	≤ 0.001
% Canopy Cover	88%	0.3	93%	2.0	≤ 0.001
% Downed Woody Debris	9%	4.6	12%	0.8	0.001
% Leaf Litter Cover	84%	1.1	85%	1.0	0.701
% Soil Moisture	47%	0.40	61%	0.50	≤ 0.001

Statistical significance was calculated using MANOVA. *p* values ≤ 0.05 were considered significant.

## DISCUSSION

Reliable assessments of the impact of deer on forest ecosystems require accurate indices of deer abundance and density of deer. Several methods have been employed to determine relative abundance and other indices of deer density each with their own limitations and caveats. Two issues of concern that arise when relying on estimates of relative abundance or density to describe a specific local site are 1) the scale at which the numbers were estimated and applied and 2) differential use of habitats within the area studied.



The first area of concern, the scale at which the data are collected, is important because park wide estimates of abundance are often made using a sampling of density within a relatively small area that is then extrapolated to larger areas within the park district. Depending on the intended use of this information, large-scale estimates may be useful, i.e. to follow trends or changes over time within a larger population. However, because deer are highly mobile and are known to preferentially browse in small patches within a larger more heterogeneous landscape, large-scale density estimates may not accurately reflect deer activity within these smaller habitat patches. This is important to consider when interested in finer scale questions such as how browsing activities by deer affect forest floor habitat quality and how these changes correlate to changes in community composition and abundance of those species whose home range activities occur at much smaller scales, such as small mammals and forest floor invertebrates. Therefore, in addition to overall estimates of density at the larger scale, it is important to gather information on the browsing activities of deer within a smaller more localized region.

Here I applied two relatively simple measures of deer impact, canopy cover and seedling density, to gain a more localized assessment of the deer activity at each of seven field sites within six larger park districts or reservations. With these data and data collected over the past 10 years (R. Tyler, Cleveland Metroparks, unpublished data) I was able to verify and group these sites into areas of either high or low deer impact. I expected low impact sites to have increased seedling density and percent canopy cover compared with sites classified as high impact. Figure 2.1 helps illustrate a natural break in the data indicating that canopy structure is relatively similar between sites previously

determined to experience high or low deer impact. This break in data, although more prominent for low impact sites, helps support the decision to lump field sites into two broad categories of high and low impact. Using these measures I was able to relate differential browsing pressure across field sites to differences in the quantity and quality of the forest floor microhabitat (Carter and Fredericksen 2007). In support of my original hypotheses, areas of high deer impact had less understory herbaceous cover and leaf litter biomass and depth, and had drier soils compared to areas of lower impact. Characterizing the impact of deer on the forest floor microhabitat is important first step in understanding how deer may indirectly affect taxonomic diversity within the forest floor microhabitat.

## LITERATURE CITED

- Alverson, W. S. and Waller, D. M. (1997) Deer populations and the widespread failure of hemlock regeneration in northern forests. p. 280-297. In: W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.). *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C.
- Augustine, D. J., and Frelich, L. E. (1998) Effects of white-tailed deer on populations of an understory forb in fragmented forests. *Conservation Biology* 12, 995-1004.
- Augustine, D. J. and McNaughton, S. J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62, 1165-1183.
- Carter, W.K. and Fredericksen, T.S. (2007) Tree seedling and sapling density and deer browsing incidence on recently logged and mature non-industrial private forestlands in Virginia, USA. *Forest Ecology and Management* 242, 671-677.
- Côté, S. D., Rooney, T. P., Tremblay, J., Dussault, C., and Waller, D. M. (2004) Ecological impact of deer overabundance. *Annual Review of Ecology and Systematics* 35, 113-147.
- Eschtruth, A. K. and Battles, J. J. (2009) A generalist herbivore accelerates exotic plant invasion in a forested ecosystem. *Conservation Biology* 23(2), 388-399.
- Fuller, R. J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanism. *Forestry* 74, 289-298.
- Fuller, R. J. and Gill, R. M. A. (2001) Ecological impacts of increasing numbers of deer in British woodlands. *Forestry* 74, 193-199.
- Gill, R. M. A. and Morgan, G. (2010) The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry* 83, 53-63.
- Liang, S. Y. and Seagle, S. W. (2002) Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83(1), 212-227.
- McShea, W. J. and Rappole, J. H. (1992) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology* 14 (4), 1161-1170.
- McShea, W. J. and Rappole, J. H. (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology* 14,1161-1170.
- Rooney, T. P. and Dress, W. J. (1997) Species loss over sixty-six years in the ground layer vegetation of Heart's Content, an old growth forest in Pennsylvania, USA. *Natural Areas Journal* 17, 297-305.

- Rooney, T. P. and Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181, 165-176.
- Russell, F. L., Zippin, D. B., and Fowler, N. L. (2001) Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations, and communities: A review. *American Midland Naturalist* 146, 1-26.
- Strange, E. E. and McShea, K. L. (1998) Effects of deer browsing, fabric mats and tree shelters on *Quercus rubra* seedlings. *Restoration Ecology* 6, 29-34.
- Suominen, O., Danell, K., and Bryant, J. P. (1999) Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. *Ecoscience* 6, 505-510.
- Tilghman, N. G. (1989) Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53, 524-532.
- VanDeelan, T. R., Pregitzer, K. S., and Haufler, J. B. (1996) A comparison of pre-settlement and present-day forests in two northern Michigan deer yards. *American Midland Naturalist* 135, 181-195.
- Vázquez, D. P. and Simberloff, D. (2003) Changes in interaction biodiversity induced by an introduced ungulate. *Ecological Letter* 6, 1077-83.

## CHAPTER III

### BROWSING EFFECTS ON LITTER-DWELLING ARTHROPOD COMMUNITIES IN NORTHEAST OHIO: AN EXCLOSURE STUDY

#### ABSTRACT

The litter-dwelling arthropod community composition and abundance on the forest floor is predicted to change in response to the browsing activities of deer. Habitat heterogeneity and structural complexity are important determinates of litter-dwelling arthropod species abundance and diversity and thus important in defining community composition and trophic level organization. A combination of pitfall traps and Berlese litter extractions were used to extract litter-dwelling arthropods inside versus outside of deer exclosures. The structural complexity of the forest floor microhabitat was greater inside exclosures compared to unfenced control plots, but no overall effect of treatment on species density (ANOVA,  $F_{1,58} = 1.404$ ,  $P = 0.241$ ) or the number of native (ANOVA,  $F_{1,58} = 2.257$ ,  $P = 0.138$ ) and nonnative (ANOVA,  $F_{1,58} = 1.059$ ,  $P = 0.308$ ) taxa. However, during the month of August when differences in leaf litter differences were greatest between control and treatment plots, there was an observable treatment effect for arthropods samples via Berlese extraction. This effect was driven largely by the presence of more Coleoptera and Araneae inside vs. outside exclosures (Coleoptera: ANOVA,  $F_{1,$

$t_{28} = 7.626, P = 0.010$ ; Araneae: ANOVA,  $F_{1, 28} = 2.640, P = 0.090$ ). The simplification of the forest microhabitat negatively impacted the species composition of litter-dwelling arthropods, especially small litter depend mesofauna. A strong correlation between % herbaceous cover and leaf litter biomass ( $r = 0.915, p = 0.029$ ) and thickness ( $r = 0.925, p = 0.025$ ) suggests browsing of the shrub zone likely reduces the structural complexity of the forest floor habitat and indirectly arthropod species composition.

## INTRODUCTION

The loss of species biodiversity in recent decades and the subsequent loss of ecosystem function has led to an increased awareness of the importance of maintaining biological diversity as a goal of ecosystem management. In light of this increased awareness, natural resource managers have adopted a more ecosystem-level approach to management emphasizing the need to conserve biological diversity and ecological integrity (Thomas 1994; Bergstrom and Edenius 2003). Related to this shift in management objectives is the awareness of the role of ungulates in structuring forest community composition and structure (McShea et al. 1997; Côté et al. 2004).

White-tailed deer (*Odocoileus virginianus*) have long been recognized as keystone herbivores in forest ecosystems (McShea and Rappole 1992; Waller and Alverson 1997; Rooney and Waller 2003). However, when overabundant, these keystone herbivores can threaten local and regional biodiversity by altering plant-animal interactions and, ultimately, changing the path of forest succession (Waller and Alverson 1997). While the effects of sustained over-browsing on plant species diversity and understory structural diversity have been well documented (Alverson and Waller 1997; Rooney and Dress

1997; Augustine and Frelich 1998; Gill and Beardall 2001), less is known of how these changes affect the population dynamics and interactions of terrestrial arthropods.

Although, the importance of habitat structural complexity as a major driver of terrestrial arthropod population dynamics has long been recognized (Wagner et al. 2003; Miyashita et al. 2004), the magnitude of these effects depends on the taxon in question, browsing intensity, scale and overall site productivity (Facelli 1994; Pastor et al. 1993; Suominen et al. 1999 a & b; Wardle et al. 2001; Suominen et al. 2003; Allombert et al. 2005). In general, arthropods inhabiting the forest understory or shrub zone respond negatively to increased browse pressure (Baines et al. 1994; Hartley et al. 2003; Miyashita et al. 2004; but see Suominen et al. 1999b, Lessard et al. 2012) but contrasting results have been documented for ground dwelling invertebrates (Rambo and Faeth 1999; Suominen et al. 1999b; McShea and Rappole 2000; Allombert et al. 2005). In areas heavily impacted by browsing, litter-dwelling arthropods respond negatively to the effects of habitat loss; resulting in an overall decline in abundance and diversity (Suominen et al. 2008). In contrast, in areas of light to moderate browsing, litter-dwelling arthropods may respond positively to increased spatial heterogeneity (Suominen et al. 2003; Melis et al. 2007). Yet other studies have found no clear effect of browsing by deer on litter-dwelling arthropods (Dennis et al. 1998; Allombert et al. 2005). Although the specific effects of browsing by deer on terrestrial arthropod population dynamics are unclear, the potential exists for trophic level interactions to induce a cascade of effects on abundance, composition, and distribution of terrestrial arthropods (de Calesta 1994; McShea and Rappole 2000; Flowerdew and Ellwood 2001; Fuller 2001; Smit et al. 2001).

In Northeast Ohio, urbanization, reduced hunting pressure, extirpation of predators, and habitat fragmentation has caused white-tailed deer populations to increase in local parks and reserves to historically high densities (McCabe and McCabe 1984). Recent surveys across the region estimate deer densities between 1-48 deer/km<sup>2</sup> (Underwood and Coffey 1999; Fulton et al. 2004; R. Tyler, Cleveland Metroparks, unpublished data 2004). As a result, area biologists have identified deer to be the principal threat to biodiversity in area parks and reserves (Dengg 2002; J. Bissell, Cleveland Museum of Natural History, personal communication 2006). However, a recent study investigating the effects of deer exclosures on ground-dwelling herpetofauna and invertebrates at Cuyahoga Valley National Park, Summit County, Ohio suggested that browsing by deer can have a positive indirect effect on components of faunal diversity (Greenwald et al. 2008). Species diversity increases noted in this particular study, seem largely associated with opportunistic, non-native species (i.e. gastropods) and species that prefer more open habitats; conditions favored by browsing. Clearly, more research is needed to understand the complex interactions between deer, their habitat and ultimately overall species diversity in forest ecosystems.

The objectives of the present study were to assess litter-dwelling arthropods inside and outside of deer exclosures and to relate any observed differences to deer-induced changes to the structural complexity of the forest floor. I hypothesized that 1) browsing by deer results in a decline in habitat structural complexity on the forest-floor, and that 2) changes in habitat quality will correspond to shifts in overall species composition and decreased abundance of litter-dwelling arthropods. Knowledge of how deer may indirectly affect the diversity and abundance of litter-dwelling arthropods is important for



the future management of parks and reserves where overabundant deer threaten biological diversity and overall ecosystem functioning.

## METHODS

### **Study Area**

This study took place in Lake Metroparks, Lake County, Ohio, USA, (41° 35' 44"N, 81° 19' 91"W). Lake Metroparks was established in 1958 and currently includes 42 rural and suburban park reservations encompassing over 7,600 ha of mixed deciduous forests and riparian habitat within the Lake Erie watershed. Hunting and other forms of deer management are prohibited within park boundaries. As a result, deer densities average between 18 and 48 deer/km<sup>2</sup> (T. Adair, Lake Metroparks, unpublished data 2008).

### **Data Collection**

In 1993, four 30 m x 60 m (0.18-ha) deer exclosures were established in 3 park reservations to study the effects of browsing on forest regeneration and plant species diversity. An additional 3 exclosures were established in 2000. In 2008, 5 of these exclosures were chosen to compare the abundance and taxonomic diversity of litter-dwelling arthropods inside vs. outside exclosed areas. Adjacent to each fenced exclosure, a 30 m x 60 m (0.18ha) unfenced control plot was established, 15 m from the exclosure edge. Data were collected on a suite of microhabitat variables within the enclosed treatment area and unfenced control plots. I used 1 m radius circular plots placed at random at three locations inside and outside of exclosures to estimate vegetation characteristics and ground cover. Within each plot I measured: % leaf litter cover, % bare ground, % downed woody debris, % herbaceous cover and number of

seedling and saplings/m<sup>2</sup>. Percent canopy cover was estimated using a spherical densiometer at the center of each circular plot. Soil moisture and pH were measured using a Kelway<sup>®</sup> soil pH and moisture probe, and leaf litter depth was estimated to the nearest 0.5 cm at 10 random points both inside and outside each exclosure.

Arthropod abundance was estimated, once each, in early June and mid-August 2008. Invertebrates were sampled using a combination of pitfall traps and Berlese extraction of leaf litter. Three pitfall traps (16 oz double stacked plastic cups) were placed at 20 m intervals within each exclosure 15 m from the fence edge. An additional three pitfall traps were similarly placed within the unfenced control plot. Each pitfall was dug flush to ground and filled with an aqueous soap-salt solution to trap litter-dwelling arthropods. After a 36 hr sampling period all invertebrates were transferred to vials containing 70% ethanol. Invertebrates were separated from ethanol by filtration and analyzed under a dissecting scope to determine taxonomic diversity at the family level, total abundance and species density (# species/ sampling unit). Invertebrates were also grouped based on whether they were generally considered native or nonnative to the region. Non-native taxa included those arthropods classified as Isopoda, Diplopoda (Julidae), Chilopoda (Lithobidae) and Gastropoda.

Small litter-dwelling arthropods, i.e. mesofauna, were extracted from leaf litter samples collected during each sampling period. First, a circular sampling frame (189 cm<sup>2</sup>) was placed at random in three locations inside and outside of deer exclosures. All litter within the frame, as well as any invertebrates observed on the litter or soil surface, were removed by hand and placed in 1gal plastic bags. Leaf litter samples were transported to the laboratory within 3 hrs of collection, weighed to the nearest 0.001g on

an electronic balance and distributed randomly among 30 Berlese funnel extractors. Extractions were run for 48 hrs into 70% ethanol. Once extractions were complete, all invertebrates were separated by filtration and analyzed under a dissecting scope to determine total abundance, taxonomic diversity, species and invertebrate density (individuals/ g dry leaf mass) and total number of native and nonnative taxa present. Dry leaf litter samples were then reweighed to the nearest 0.001g to determine total dry litter biomass.

### **Statistical Analyses**

A total of 4,226 (June, N = 2191; August, N = 2035) invertebrates were collected representing 63 families and 21 orders during 2008. Because of the paucity of data at the family level all data were grouped to order. Analyses of individual taxa were then confined to those taxa accounting for  $\geq 1$  % of total number of invertebrates collected. This resulted in a total of 14 orders and one morphogroup (larvae) for analysis including: Acari, Araneae, Chilopoda, Collembola, Coleoptera, Diplopoda, Diptera, Hymenoptera, Isopoda, Oligocheata, Opiliones, Orthoptera, Pseudoscorpiones and Thysanoptera. Further analysis at the family level was conducted for the most abundant taxa. Sample size restrictions and a lack of replication resulted in pooling all data across sites to test for treatment and seasonal effects.

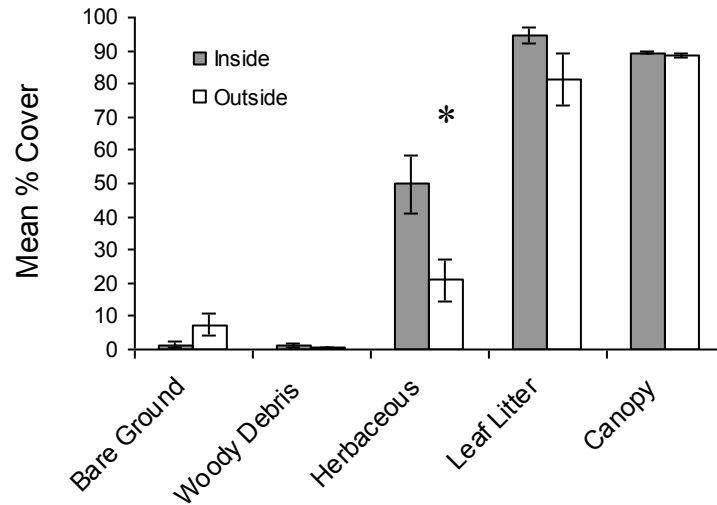
Simple pairwise comparisons of microhabitat variables inside vs. outside deer exclosures were made using Mann-Whitney *U*-tests. Differences in total leaf litter biomass inside vs. outside exclosures were examined using one-way analysis of variance (ANOVA). For all analyses, dry litter mass was log-transformed ( $\log_{10}(x+1)$ ) and % soil

moisture, ground and canopy cover were arcsine-square-root transformed to improve conformance to normality.

The effect of treatment on species density and number of native vs. non-native taxa was assessed using one-way ANOVA where data were pooled across site and sampling method. Multivariate analysis of variance (MANOVA) was used to test for any differences in total invertebrate abundance of the most numerous taxa (those accounting for  $\geq 1\%$  of individuals) among treatment and sampling period. Multivariate analysis of covariance (MANCOVA) was used to test for the effect of treatment on invertebrate abundance and available leaf litter biomass. For these analyses data were split by season (month); exclosure treatment was used as the fixed effect and leaf litter biomass was treated as a covariate.

## RESULTS

The number of seedlings and saplings/m<sup>2</sup> served as a proxy for estimating browse pressure and thus the impact of deer inside and outside of exclosures (Rooney and Waller 2003; see Chapter 2). Pairwise comparisons revealed browse pressure was higher outside compared to inside exclosures (Mann-Whitney *U*-test,  $p = 0.006$  seedling/m<sup>2</sup> and  $p < 0.001$ , sapling/m<sup>2</sup>). Percent herbaceous cover was significantly higher inside exclosures (Mann-Whitney *U*-test,  $p = 0.009$ ) compared to areas outside exclosures (Figure 3.1) suggesting that more habitat structure was available to invertebrates in the shrub zone inside compared to outside exclosures. Percent canopy cover (Mann-Whitney *U*-test,  $p = 0.398$ ) and number of mature trees/m<sup>2</sup> (Mann-Whitney *U*-test,  $p = 0.947$ ) did not differ between treatments implying that upper canopy layer was similar between treatments and



**Figure 3.1 Percent cover inside and outside exclosures.** Percent ground cover within 1 m circular plots inside and outside of deer exclosures in Lake Metroparks, Ohio 2008. Error bars represent  $\pm 1$  SE.

unaffected by browse pressure in this study. Although no treatment effect was detected for percent leaf litter cover (Mann-Whitney  $U$ -test,  $p = 0.383$ ), a significant treatment effect was observed for leaf litter depth (Mann-Whitney  $U$ -test,  $p < 0.001$ ). On average, leaf litter was 1.0 cm deeper inside vs. outside exclosures during both sampling periods (Table 3.1). In addition, significant treatment (ANOVA,  $F_{1,56} = 9.678$ ,  $p = 0.003$ ) and seasonal effects (ANOVA,  $F_{1,56} = 9.479$ ,  $p = 0.003$ ) were observed for dry leaf litter biomass (Table 3.1). When months were analyzed separately, no treatment effect was observed in June (ANOVA,  $F_{1,28} = 1.208$ ,  $p = 0.281$ ); however, a highly significant effect was observed in August (ANOVA,  $F_{1,28} = 11.157$ ,  $p = 0.002$ ). In August, leaf litter biomass was nearly 2-fold greater inside vs. outside deer exclosures (Table 3.1).

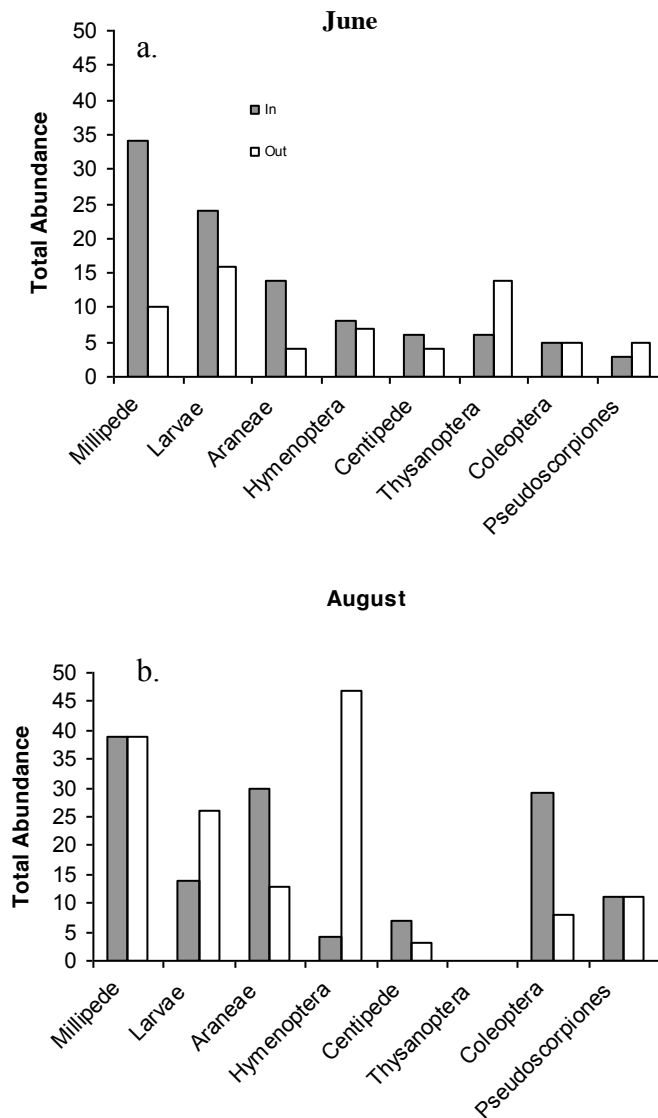
**Table 3.1 Characterization of microhabitat at deer exclosures.** Mean values for % soil moisture, leaf-litter depth, and leaf litter biomass inside and outside deer exclosures in Lake County, Ohio during the months of June and August 2008

	June				August			
	Inside Exclosure		Outside Exclosure		Inside Exclosure		Outside Exclosure	
	x	SE	x	SE	x	SE	x	SE
% Soil Moisture	19.07	0.933	18.53	0.92	7.4	0.438	6.89	0.488
Leaf Litter Depth (cm)	1.93*	0.083	0.887*	0.069	1.75*	0.095	0.827*	0.071
Leaf Litter Biomass (g)	39.69	5.16	32.27	3.56	32.69*	4.38	16.67*	2.1

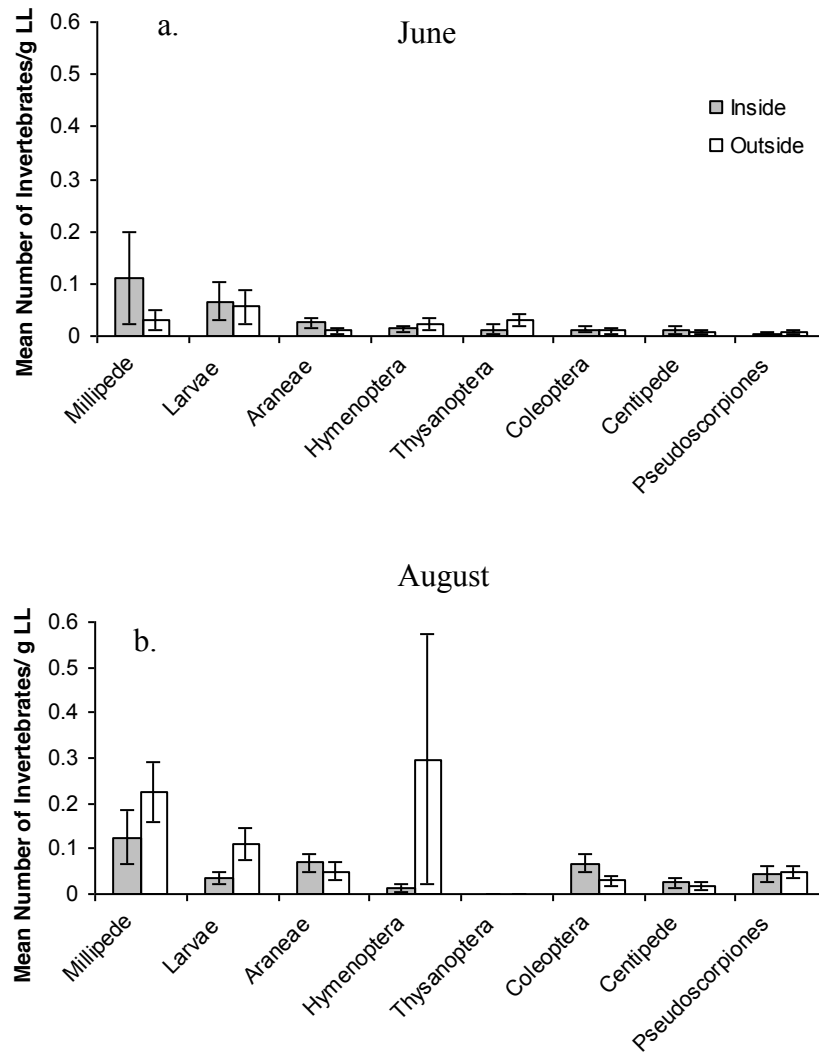
\* Indicates significant differences between treatments ( $p < 0.01$ )

Analysis of percent soil moisture revealed no treatment effect (ANOVA,  $F_{1,295} = 0.383$ ,  $p = 0.537$ ), but a significant seasonal effect (ANOVA,  $F_{1,295} = 265.697$ ,  $p < 0.001$ ) was observed. Soil moisture was nearly 3-fold higher in June compared to August (Table 3.1).

No overall effect of treatment on species density (ANOVA,  $F_{1,58} = 1.404$ ,  $p = 0.241$ ) or the number of native (ANOVA,  $F_{1,58} = 2.257$ ,  $p = 0.138$ ) and nonnative (ANOVA,  $F_{1,58} = 1.059$ ,  $p = 0.308$ ) taxa was observed. However, an overall effect of treatment on litter-dwelling arthropod abundance was observed during the month of August for invertebrates sampled via Berlese extraction. This effect was driven largely by the presence of more Coleoptera and Araneae inside vs. outside exclosures (Coleoptera: ANOVA,  $F_{1,28} = 7.626$ ,  $p = 0.010$ ; Araneae: ANOVA,  $F_{1,28} = 2.640$ ,  $p = 0.090$ ; Figure 3.2). Once the effect of differences in leaf litter biomass between treatment and controls were accounted for, any significant treatment effect during the month of August was lost (MANCOVA,  $\lambda = .538$ ,  $F_{9,19} = 1.810$ ,  $P = 0.132$ ; Figure 3.3). This result implies the strong role of leaf litter biomass as a driver of litter-dwelling arthropod abundance on the forest floor.



**Figure 3.2 Total invertebrate abundance.** Total abundance of invertebrates representing >1% of total captures excluding Collembola and Acari collected using Berlese extraction in Lake County, Ohio during the months of June (a) and August (b) 2008.



**Figure 3.3 Mean invertebrates per gram leaf litter.** Mean number of invertebrates excluding Collembola and Acari per gram leaf litter sampled using Berlese extraction inside and outside of deer enclosures in Lake County, Ohio during the months of June (a) and August (b) 2008. Error bars represent  $\pm 1$  SE.



I analyzed abundance at the family level for the two orders responding most notably to treatment effects, Coleoptera and Araneae. Four families of beetles and six families of spiders (including a group of unidentified juvenile spiders) representing  $\geq 1\%$  of specimens collected were analyzed separately. Significantly more carabid beetles were found inside compared to outside exclosures ( $F_{1,56} = 4.539, p = 0.042$ ). More staphylinid beetles ( $F_{1,56} = 3.500, p = 0.072$ ), juvenile spiders ( $F_{1,28} = 3.376, p = 0.077$ ) and amaurobiid spiders ( $F_{1,28} = 3.088, p = 0.090$ ) were found inside the exclosure as well, although differences were only marginally significant.

## DISCUSSION

Litter-dwelling arthropod community composition and abundance on the forest floor varies in response to the browsing activities of deer. Habitat heterogeneity and structural complexity of the forest floor are important determinates of arthropod species abundance and diversity and thus important in defining community composition and trophic level organization (Bultman and Utez 1982; Langellotto and Denno 2004, Wardle and Bardgett 2004, Lessard et al. 2012). Key factors determining overall habitat heterogeneity include percent herbaceous cover, soil moisture, leaf litter depth and biomass (Facelli 1994; Wise and Chen 1999). Variation in litter depth may influence several variables such as litter complexity, prey abundance, temperature and humidity. Therefore, I can assume that the deeper litter and increased biomass present inside deer exclosures, where deer browsing was eliminated, provided a more structurally complex and heterogeneous habitat favored by litter-dwelling arthropods than areas outside the exclosures browsed by deer. Because I found a positive correlation between % herbaceous cover and leaf litter biomass ( $r =$

0.915,  $p = 0.029$ ) and thickness ( $r = 0.925$ ,  $p = 0.025$ ) we can infer that browsing of the shrub zone indirectly affects the structural complexity of the forest floor habitat.

Although I found no overall treatment effect on arthropod abundance on a broad scale, we did find a significant treatment effect for smaller litter-dwelling beetles and to some extent spiders (Coleoptera and Araneae). This effect was most obvious during the month of August. This is biologically significant because in August differences in forest-floor habitat between exclosures and controls were greatest (Table 3.1). Of the beetles, the carabids responded most to differences in habitat between controls and exclosed areas. In general, carabid beetles are relatively abundant and fill many ecological roles and trophic levels in forest ecosystems ranging from predators to prey, herbivores and scavengers, and as such have been considered by some as ecological indicators of overall ecosystem health and functioning (Niemela 2001; Rainio and Niemela 2003; see also Work et al. 2008). Factors important to carabid abundance include percent ground cover, soil moisture, and overall habitat heterogeneity, and some have suggested that carabid abundance and diversity are often highest at intermediate levels of disturbance (Souminen et al. 2003; Melis et al. 2007). The finding of more carabid beetles inside exclosures where more habitat was available is consistent with the intermediate disturbance hypothesis, especially because the area within the exclosures may be more representative of intermediate disturbance than complete relief from browsing pressure (see below). However, without species data I can only infer that changes in carabid abundance are indicative to changes in habitat quality as a result of browsing by deer.

The finding of more juvenile and amaurobid spiders, although not statistically significant, is still biologically relevant. Spiders are important members of the detrital

food web, because these predators can shape ecosystem dynamics through top-down forces that initiate cascade effects influencing plant community composition, nutrient cycling and other trophic level interactions (Wise 2001; Sanders et al. 2008). Differences in spider abundance were most obvious during the month of August. Again, this is noteworthy because during the month of August differences in the structural complexity of the forest floor between exclosures and controls were greatest (Table 3.1). Structurally complex habitats facilitate spider abundance and diversity by increasing prey abundance and providing unique foraging sites for a diversity of spiders (i.e. web-building or active hunting cursorial species; Uetz 1992; Miyashita et al. 2004; Souminen et al. 2008). One possible explanation for an increase in abundance of Amaurobids, a web-building spider, may have been that more structure was available for web building sites inside compared to outside deer exclosures. Because generalist predators are known to be positively correlated with litter structural complexity (Bultman and Uetz 1982; Langellotto and Denno 2004), these observed differences in the structural make-up of the forest floor between exclosures and control plots may explain the finding of more spiders in exclosed areas, especially the web building spiders, who may be more strongly affected by the indirect effects of browsing by deer than active hunting cursorial spiders.

The expected negative response by litter-dwelling arthropods to reduced habitat complexity was only observed for the smaller litter-dwelling mesofauna sampled via Berlese extraction. This may be because the larger more mobile macrofauna, typically sampled by pitfall trapping, may have the ability to move between fenced and unfenced areas based on prey availability or cover. Additionally, capture rate is often dependent on invertebrate activity level and habitat, not necessarily on invertebrate abundance (Uetz et

al. 1976). As a result, invertebrates may more often be captured in open habitats thus leading to an increased probability of capture in reduced cover. For this reason, pitfall trapping may have been insensitive to the detection of changes in abundance and diversity in this study. Additionally, a lack of replication over multiple years and within each park forced us to combine data across all study sites. Combining site data may have limited our ability to detect any local differences in arthropod response to browsing and thus may have hindered our ability to discover changes in invertebrate abundance. More specific information on arthropod populations over a longer time scale may be necessary to accurately quantify the effect of browsing on arthropod populations.

Interpreting exclosure data is difficult because exclosures eliminate all browsing pressure creating an unnatural condition, not representative of the natural pressures of browsing across a density gradient. Instead, they illustrate recovery from browsing influenced more by past browsing events than current management practices and may actually represent conditions representative or similar to those under intermediate or even high deer densities. The potential that areas within exclosures are representative of habitats under intermediate disturbance regimes complicates interpretation of exclosure data. The intermediate disturbance hypothesis refers to a complex set of mechanisms, which promote the coexistence of species through temporal and spatially patchy disturbance dynamics; local species diversity is maximized when ecological disturbance is neither too rare nor too frequent (Grime 1973; Connell 1978). Under this hypothesis the coexistence of species within ecological communities is determined by the availability of multiple ecological niches within a patchwork of varying habitats maintained in space and time by intermediate disturbances to the system. This is

problematic because the underlying mechanism driving differences in community interactions within exclosures may not be truly caused by deer but instead by mechanisms outlined under the intermediate disturbance hypothesis. This may have been evident in this study. The finding of more carabid beetles within exclosures may not have been caused by a relief in browsing pressure, but instead different carabid species may have coexisted in exclosed areas because at intermediate disturbance levels more habitat and thus ecological niches are available for more species to exploit in a given area. As a result, caution should be made when making broad statements about the complex interactions between ungulates and their environment using exclosure data.

An additional mechanism may be acting on this system between exclosed and unexclosed areas (Milchunas 1998). The exclosures themselves may have trapped litter within their confines that would have otherwise blown or been washed away from the site if not enclosed by fencing. As a result, litter accumulation and biomass inside the exclosures may have been a side effect of the exclosures rather than a causal effect of reduced deer browsing. Regardless of the cause however, this study has shown the importance of increased litter accumulation and biomass on the structural complexity of the forest floor habitat and species abundance. Studies across a natural gradient of deer density will help narrow down the cause and effect relationship between the impact of browsing and the structural complexity of the forest floor. Data from these studies in combination with exclosure studies are necessary to fully understand the complex interactions between deer and their environment.

## **Management Implications**

The successful management of overabundant ungulate populations under the larger goal of maintaining biological diversity and ecological functioning of ecosystems depends on the understanding of how browsing affects ecological communities. This study suggests that deer may negatively impact large functional groups of litter-dwelling arthropods, which have the potential to drive ecological processes in forest ecosystems. However, these interactions are complex and depend on several factors. Therefore, broad statements about how change to litter-dwelling arthropod community composition, as a result of deer herbivory, affects ecosystem functioning are beyond the scope of this paper. However, it is important to acknowledge the potential for increasing densities of deer to indirectly affect forest floor food webs and recognize that more emphasis needs to be placed on community interactions within forest ecosystems when developing management protocols concerning overabundant deer.

This study reiterates the importance of being objective in interpreting enclosure data, and although popular in the past, more needs to be done to fully understand the impact of ungulates on their environment. In the future we suggest abandoning the use of enclosures to study any cause and effect relationship among browsers and their environment. Instead I suggest testing theories developed from previous enclosure studies to design comparative experiments along gradients of deer density, as well as manipulative experimental studies, e.g., deer removal or grazing simulation experiments, to further our understanding of the effects of browsing on forest-floor communities.

## LITERATURE CITED

- Allombert, S., Stockton, S., and Martin, J. L. (2005) A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology* 19(6), 1917-1929.
- Augustine, D. J. and Frelich, L. E. (1998) Effects of white-tailed deer populations of an understory forb in fragmented deciduous forests. *Conservation Biology* 12, 995-1004.
- Baines, D., Sage, R. B., and Baines, M. M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology* 31, 776-783.
- Bergstrom, R. and Edenuis, L. (2003) From twigs to landscapes—methods for studying the ecological effects of forest ungulates. *Journal for Nature Conservation* 10, 203-211.
- Bultman, T. L. and Uetz, G. W. (1982) Abundance and community structure of forest floor spider communities following litter manipulation. *Oecologia* 55, 34-41.
- Connell, J. H. (1978) Diversity in tropical rainforests and coral reefs. *Science* 199, 1302-1310.
- Côté, S. D., Rooney, T. P., Tremblay, J., Dussault, C., and Waller, D. M. (2004) Ecological impact of deer overabundance. *Annual Review of Ecology and Systematics* 35, 113-147.
- deCalesta, D. S. (1994) Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58, 711-718.
- Dengg, E. L. (2002) Cuyahoga Valley National Park 2001 deer exclosure report. National Park Service, Brecksville, Ohio, USA.
- Dennis, P., Young, M. R., and Gordon, I. J. (1997) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 23, 253-264.
- Facelli, J. M. (1994) Multiple indirect effects on plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75, 1727-1735.
- Flowerdew, J. R. and Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry* 74, 277-287.
- Fuller, R. J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanism. *Forestry* 74, 289-298.

- Fulton, D. C., Skerl, K., Shank, E. M., and Line, D. W. (2004) Beliefs and attitudes toward lethal management of deer in Cuyahoga Valley National Park. *Wildlife Society Bulletin* 32, 1166-1176.
- Gill, R. M. A. and Beardall, V. (2001) The impact of deer woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74(3), 209-218.
- Greenwald, K. R., Petit, L. J., and Waite, T. A. (2008) Indirect effects of a keystone herbivore elevate local animal diversity. *The Journal of Wildlife Management* 72(6), 1318-1321.
- Grime, J. P. (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242, 344-247
- Hartley, S. E., Gardner, S. M., and Mitchell, R. J. (2003) Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. *Journal of Applied Ecology* 40, 793-803.
- Langellotto, G. A., and Denno, R. E. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139, 1-10.
- Lessard, J. P., Reynolds, W. N., Bunn, W. A., Genung, M. A., Gregger, M. A., Felker-Quinn, E., Barrios-Garcia, M.N., Stevenson, M. L., Brown, C. B., Patrick, M., Rock, J.H., Jenkins, M. A., Bailey, J. K., and Schweitzer, J. A. (2012) Equivalence in the strength of deer herbivory on and above and below ground communities. *Basic and Applied Ecology* 13, 59-66.
- McCabe, T. R. and McCabe, R. E. (1997) *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C.
- McShea, W. J. and Rappole, J. H. (1992) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology* 14 (4), 1161-1170.
- McShea, W. J., Underwood, H. B., and Rappole, J. H. (1997) *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- Miyashita, T., Takada, M., and Shimazaki, A. (2004) Indirect effects of herbivory by deer reduce abundance and species richness of web-building spiders. *Ecoscience* 11:74-79.
- Milchunas, D. G., Sala O. E., Lauenroth, W. K. (1988) A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. *American Naturalist* 132, 87-106.



- Melis, C. (2007) The role of moose *Alces alces* L. in boreal forests—the effect on ground beetles (Coleoptera, Carabidae) abundance and diversity. *Biodiversity Conservation* 16, 1321-1335.
- Niemelä, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *European Journal of Entomology* 98(2), 127-132.
- Pastor, J., Dewey, B., Naiman, R. J., McInnes, P., and Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74, 467-480.
- Rainio, J. and Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity Conservation* 12, 487–506.
- Rambo, J. L. and Faeth, S. H. (1999) Effects of vertebrate grazing on plant and insect community structure. *Conservation Biology* 13, 1047-1054.
- Rooney, T. P. (2001) Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74, 201–8.
- Rooney, T. P. and Dress, W.J. (1997) Species loss over sixty-six years in the ground layer vegetation of Heart's Content, an old growth forest in Pennsylvania, USA. *Natural Areas Journal* 17, 297-305.
- Rooney, T. P. and Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181, 165-176.
- Sanders, D., Nickel, H., Grützner, T., and Planter, C. (2008) Habitat structure mediates top-down effects of spiders and ants on herbivores. *Basic and Applied Ecology* 9, 152-160.
- Smit, R., Bokdam, J., den Ouden, J., Olf, H., Schot-Opschoor, H., and Schrijver, M. (2001) Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology* 155, 119-127.
- Suominen, O., Danell, K., and Bergstrom, R. (1999a) Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests *Oikos* 84, 215-226.
- Suominen, O., Danell, K., and Bryant, J. P. (1999b) Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. *Ecoscience* 6, 505-510.
- Suominen, O., Niemelä, J., Martikainen, P., Niemelä, P., and Kojola, I. (2003) Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography* 26, 503-513.

- Suominen, O., Persson, I., Danell, K., Bergström, R. and Pastor, J. (2008) Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. *Ecography* 31, 636-645.
- Thomas, J. W. (1994) Trends in forest management in the United States. *The Forestry Chronicle* 70(5), 546-548.
- Uetz, G.W. (1992) Foraging strategies of spiders. *Trends in Ecology and Evolution* 7, 155-159.
- Uetz, G. W. and Unzicker, J. D. (1976) Pitfall trapping in ecological studies of wandering spiders. *Journal of Arachnology* 3, 101-113.
- Underwood, H. B and Coffey, M. A. (1999) Evaluation of distance sampling for deer density estimation at Cuyahoga Valley National Recreation Area (CUVA): part II. National Park Service, Brecksville, Ohio, USA.
- Wagner, J. D., Toft, S. and Wise, D. H. (2003) Spatial stratification in litter depth by forest-floor spiders. *The Journal of Arachnology* 31, 28-39.
- Waller, D. M., and Alverson, W. S. (1997) The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25, 217-226.
- Wardle, D. A. and Bardgett, R. D. (2004) Human-induced changes in large herbivorous mammal density: The consequences for decomposers. *Frontiers in Ecology and the Environment*. 2, 145-153.
- Wardle, D. A., Barker, G. M., Yeates, G. W., Bonner, K. I., and Ghani, A. (2001) Introduced browsing mammals in New Zealand natural forest: aboveground and belowground consequences. *Ecological Monographs* 71(4), 587-614.
- Wise, D. H. (2001) Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annual Review of Entomology* 51, 441-465.
- Wise, D. H. and Chen, B. (1999) Impact of intraguild predators on survival of a forest-floor wolf spider. *Oecologia* 121, 129-137.
- Work, T. T., Koivula, M., Klimaszewski, J., Langor, D., Spence, J., Sweeney, J., and Hébert, C. (2008) Evaluation of carabid beetles as indicators of forest change in Canada. *Canadian Journal of Entomology* 140, 393-414.

## CHAPTER IV

### THE IMPACT OF BROWSING BY WHITE-TAILED DEER ON LITTER-DWELLING ARTHROPOD POPULATIONS IN NORTHEAST OHIO: A COMPARATIVE STUDY

#### ABSTRACT

The browsing activities of deer indirectly affect forest ecosystems. Reduced understory and simplification of the forest floor microhabitat, as a result of over-browsing by deer, could lead to broad scale shifts in the community composition and abundance of litter-dwelling arthropods present on the forest floor. A series of pitfall and Berlese extractions were used to assess arthropod response to browsing in areas of high and low deer impact within Cleveland Metroparks and Cuyahoga Valley National Park (N=7). Total macro- or mesofauna abundance did not differ between areas of high and low deer impact (macrofauna, ANOVA,  $F_{(1, 1125)} = 0.318, p = 0.57$ ; mesofauna, ANOVA,  $F_{(1, 282)} = 0.027, p = 0.869$ ); however, a significant shift in overall community composition between areas of high and low impact was evident. This shift was largely driven by a disproportionately high assemblage of non-native species (i.e. gastropods and millipedes) in areas of high impact relative to low impact sites (macrofauna, ANOVA,  $F_{(1, 835)} = 22.614, p \leq 0.001$ ; mesofauna, ANOVA,  $F_{(1, 904)} = 9.727, p = 0.002$ ). These results suggest that the disturbances caused by the browsing activities of deer may

facilitate and support the invasion of non-native species further complicating the threats of overabundant deer to local species diversity.

## INTRODUCTION

Browsing activities of white-tailed deer (*Odocoileus virginianus*) can have significant impact on forest ecosystems (McShea et al. 1997; Russell et al. 2001; Côté et al. 2004). Deer browsing alters not only plant and animal species composition and diversity, but also the structural diversity of the forest understory and forest floor microhabitat (Rooney and Waller 2003). Combined, these effects may also facilitate invasion by non-native species (Bartuszevige and Endress 2008; Eschtruth and Battles 2009) further impacting forest ecosystems. Susceptible to these changes in forest ecosystem dynamics are the litter-dwelling arthropods. How these species respond to browsing is poorly understood and the magnitude of impact depends on the arthropod taxon in question, browsing intensity, scale and overall site productivity (Pastor et al. 1993; Facelli 1994; Suominen et al. 1999a & b; Wardle et al. 2001; Suominen et al. 2003; Allombert et al. 2005).

The species diversity and abundance of litter-dwelling arthropods often depends on local plant species diversity and the structural heterogeneity of available habitat (Wardle 2000, Wagner et al. 2003; Miyashita et al. 2004). Herbivory by deer alters plant species composition and removes understory vegetation, which decreases litter production and accumulation and as such directly impacts litter-dwelling arthropods by removing foliage and habitat important for food, shelter and egg deposition (Flowerdew & Ellwood 2001). Studies have documented a general negative response by understory invertebrate fauna to browsing of the forest understory (Baines et al. 1994; Hartley et al. 2003; Miyashita et al. 2004; but see Suominen et al. 1999b, Lessard et al. 2012). However, contrasting results

have been documented for litter-dwelling arthropods (Bromham et al. 1999; Rambo and Feath 1999; Suominen et al. 1999b; McShea and Rappole 2000; Allombert et al. 2005). In areas heavily impacted by browsing, litter-dwelling arthropods respond negatively to the effects of habitat loss; resulting in an overall decline in abundance and diversity (Suominen et al. 2008, but see Greenwald et al. 2008). In contrast, litter-dwelling arthropods may respond positively to the increased in spatial heterogeneity associated with areas experiencing light to moderate browsing (Suominen et al. 2003; Melis et al. 2007). Yet, other studies have found no clear effect of browsing on the abundance or species diversity of litter-dwelling arthropods (Dennis et al. 1997; Allombert et al. 2005). Although the specific effects of browsing on arthropod population dynamics is unclear, the potential to initiate a cascade of effects on the abundance, composition, and distribution of arthropods living within the forest floor microhabitat exists, especially in areas of deer overabundance (de Calesta 1994; McShea and Rappole 2000; Flowerdew and Ellwood 2001, Fuller 2001; Smit et al. 2001).

This study compares the impact of differential browsing by deer on the species composition and abundance of litter-dwelling arthropods in areas of high and low impact maintained through natural barriers without the use of exclosures. I hypothesize lower overall abundance of litter-dwelling arthropods in areas of high browse impact relative to low impact. I also expect an overall shift in species composition between areas of high and low impact; specifically, I expect areas of high impact to support a disproportionate assemblage of non-native species.

## METHODS

### **Study Site**

Research was conducted within Cleveland Metroparks (CMP) and Cuyahoga Valley National Park (CVNP) located Northeast Ohio. Cleveland Metroparks was founded in 1917 and currently manages 18 reservations encompassing 8,498 ha of interconnected parks and reserves located primarily along riparian corridors known as the Emerald Necklace of Greater Cleveland. Cuyahoga Valley National park consists of 8,230 ha of intermingled federal, state and private land surrounded by the suburbs of Akron, Ohio. Hunting is prohibited in both park systems; however, CMP has been culling deer herds annually since 1998. CVNP on the other hand, does not allow any form of deer management. Such management regimes have resulted in densities ranging between 8 and 30 deer/ km<sup>2</sup> in CMP to densities > 52 deer/km<sup>2</sup> at CVNP (Underwood and Coffey 1999). As a result I was able to design a comparative assessment of the ecological impacts of deer browsing activities in a natural, biologically relevant setting without the use of exclosures. Within these park systems, seven field sites were chosen based on several measures of deer impact. These include density estimates from pellet count, aerial infrared and spotlight surveys and data collected from culling efforts conducted between 1997 and 2003 (see Chapter 2, Table 2.1). Because the current structure and species diversity within the forest understory is most likely influenced from past browsing events, browse estimates from the years leading up to the study were more heavily weighted than current estimates of browse intensity that may have fluctuated as a result of current management efforts.

## Data Collection

Arthropod abundance was estimated three times each year, early June, August and October, during the 2006 and 2007 field seasons using a combination of pitfall traps and Berlese extraction of leaf litter. Twenty-nine pitfall traps (16 oz. double stacked plastic cups) were systematically placed within previously established sampling grids at each field site (see Chapter 1). Each pitfall was dug flush to ground and filled with an aqueous soap-salt solution to trap large active litter-dwelling arthropods (i.e., macrofauna). After a 36 hr. sampling period all invertebrates were transferred to a vial containing 70% ethanol. Invertebrates were separated from ethanol by filtration and analyzed under a dissecting scope to determine taxonomic diversity and total abundance. Invertebrates were also grouped based on whether they were generally considered native or nonnative to the region. Non-native taxa included those arthropods classified as Isopoda, Diplopoda (Julidae), Chilopoda (Lithobidae) and Gastropoda.

Small litter-dwelling arthropods were extracted from leaf litter samples collected during each sampling period. First, a circular sampling frame (189 cm<sup>2</sup>) was placed at random in 28 systematically identified sampling locations within the previously established sampling grid at each study site (see Chapter 1). All litter within the frame, as well as any invertebrates observed on the litter or soil surface, were removed by hand and placed in a 1 gal plastic bag. Each litter sample were transported to the laboratory within 3 hrs of collection, weighed to the nearest 0.001g on an electronic balance and distributed randomly among 30 Berlese funnel extractors. Extractions were run for 48 hrs. into 70% ethanol. Once extractions were complete, all invertebrates were separated by filtration and analyzed under a dissecting scope to determine total abundance and

overall taxonomic diversity. Organisms were then grouped by native and non-native taxa. Non-native taxa included those arthropods classified as Isopoda, Diplopoda (Julidae), Chilopoda (Lithobidae) and Gastropoda.

### **Statistical Analysis**

Studies at the community-level run the risk of Type I error because of multiple statistical tests on the several taxa within the community. However, typical methods for protecting against Type I error, e.g., sequential Bonferroni corrections, can be overly conservative and lead to dismissal of biologically-relevant results (Moran 2003; Garcia 2004; Nakagawa 2004). Therefore, the analyses employed here used strategies that have been recommended as measures to protect against Type I error while preserving the ability to examine multiple taxa simultaneously. First, univariate analyses of individual taxa were preceded by a multivariate test of the omnibus community response (Garcia 2004). Second, in addition to traditional significance values, e.g.,  $p < 0.05$ , I provide a probability value, referred to as Moran's  $p$ , which gives the probability of finding  $k$  significant results at  $\alpha < 0.05$  within a set of  $N$  multiple tests, calculated according to the Bernoulli process equation developed by Moran (2003):

$$p = [N! / (N - K)! K!] \times \alpha^K (1 - \alpha)^{N - K}$$

Hence, the omnibus, community level response by invertebrates to browsing impact was analyzed using multivariate analysis of variance (MANOVA). Analyses at the community level were confined to those taxa accounting for  $\geq 1$  % of the total invertebrates collected. This resulted in a total of 14 orders being analyzed including: Acari, Araneae, Chilopoda, Coleoptera, Collembola, Diplopoda, Hemiptera,



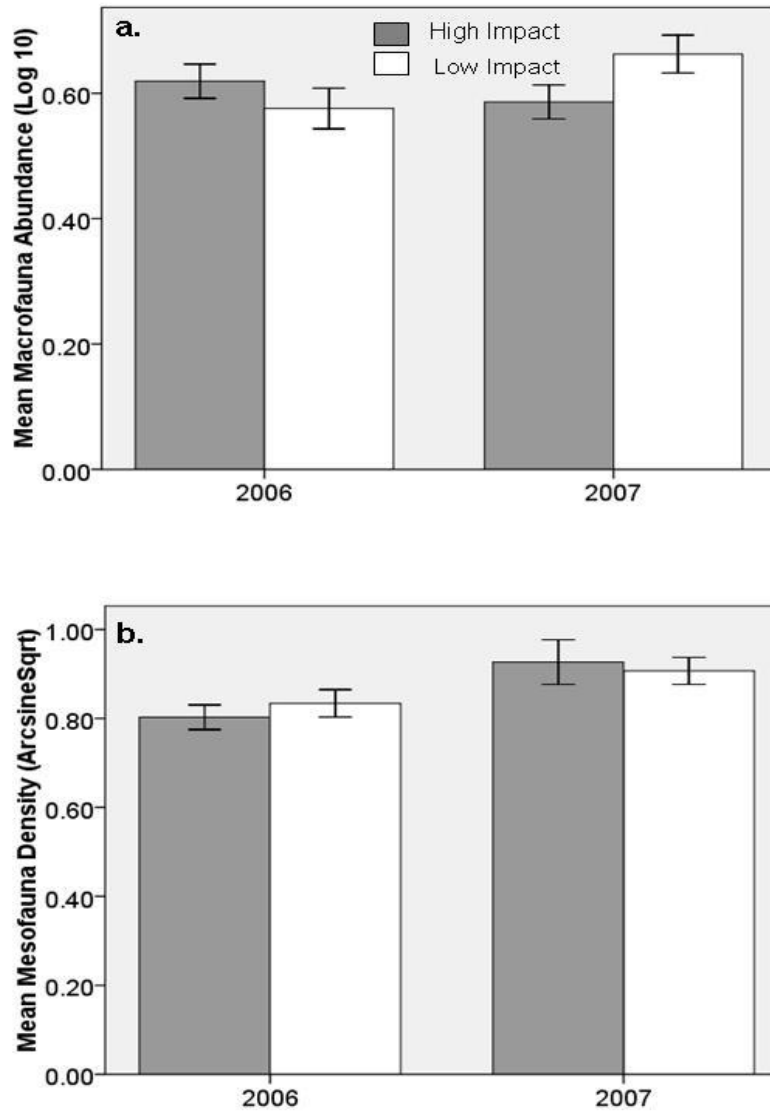
Hymenoptera (Formicidae), Isopoda, Oligocheata, Opiliones, Orthoptera, Pseudoscorpiones, and Thysanoptera. Univariate analysis of variance (ANOVA) was performed to investigate the response to browsing impact on total invertebrate macrofauna abundance and density of individual arthropod taxa. Additionally, the proportion of overall abundance characterized as non-native taxa was analyzed separately using ANOVA. Density data were log-transformed,  $\log_{10}(X+1)$ , and proportions were arcsine-square root transformed prior to analysis to improve conformance to normality.

## RESULTS

Total invertebrate macrofauna abundance did not differ between areas of high and low deer impact (ANOVA,  $F_{(1, 1125)} = 0.318, p = 0.57$ ); however, a significant year-to-year interaction was observed (ANOVA,  $F_{(1, 1125)} = 4.198, p = 0.04$ ; Figure 4.1a). Although total numbers did not differ between areas of high and low impact, a significant shift in overall community composition between areas of high and low impact was evident (MANOVA, Pillai's Trace = 0.078,  $F_{(11, 1111)} = 6.254, p \leq 0.001$ ; Table 4.1) and the magnitude of these effects varied among years (MANOVA, Pillai's Trace = 0.116,  $F_{(11, 1111)} = 9.738, p \leq 0.001$ ; Table 4.1), an effect largely by the orders Diplopoda, Hemiptera, Isopoda, and Opiliones (Figure 4.2). According to the Bernoulli process equation, the probability of finding 6 significant results among 12 possible tests (Table 4.1), at  $p > 0.05$ , by chance alone is  $p = 0.00001$ . The most notable change in community composition was a significantly higher assemblage of non-native arthropods at high impact sites (ANOVA,  $F_{(1, 835)} = 22.614, p \leq 0.001$ ; Figure 4.3a).

No difference was found in invertebrate mesofauna density (#/gram leaf litter) between areas of high and low impact (ANOVA,  $F_{(1, 282)} = 0.027, p = 0.869$ ; Figure

4.1b). However, an overall shift in community composition between areas of high and low impact was observed for small litter-dwelling invertebrates (MANOVA, Pillai's Trace = 0.070,  $F_{(11, 479)} = 3.007$ ,  $p \leq 0.001$ ; Table 4.2). This shift was driven largely by the orders Acari, Coleoptera, Psocoptera, Gastropoda, Chilopoda, and Diplopoda (Figure 4.4). Using the Bernoulli process the probability of finding 6 significant results out of 11 possible tests (Table 4.2), at  $p > 0.05$ , by chance alone is  $p = 5.58 \times 10^{-6}$ . The overall degree of change in community composition did, however, vary among years (MANOVA, Pillai's Trace = 0.166,  $F_{(11, 479)} = 7.924$ ,  $p = 0.001$ ; Table 4.2). Again, the most notable community level response by litter-dwelling invertebrates to the browsing activities of deer was an increase in non-native taxa in areas of high impact (ANOVA,  $F_{(1, 904)} = 9.727$ ,  $p = 0.002$ ; Figure 4.3b).

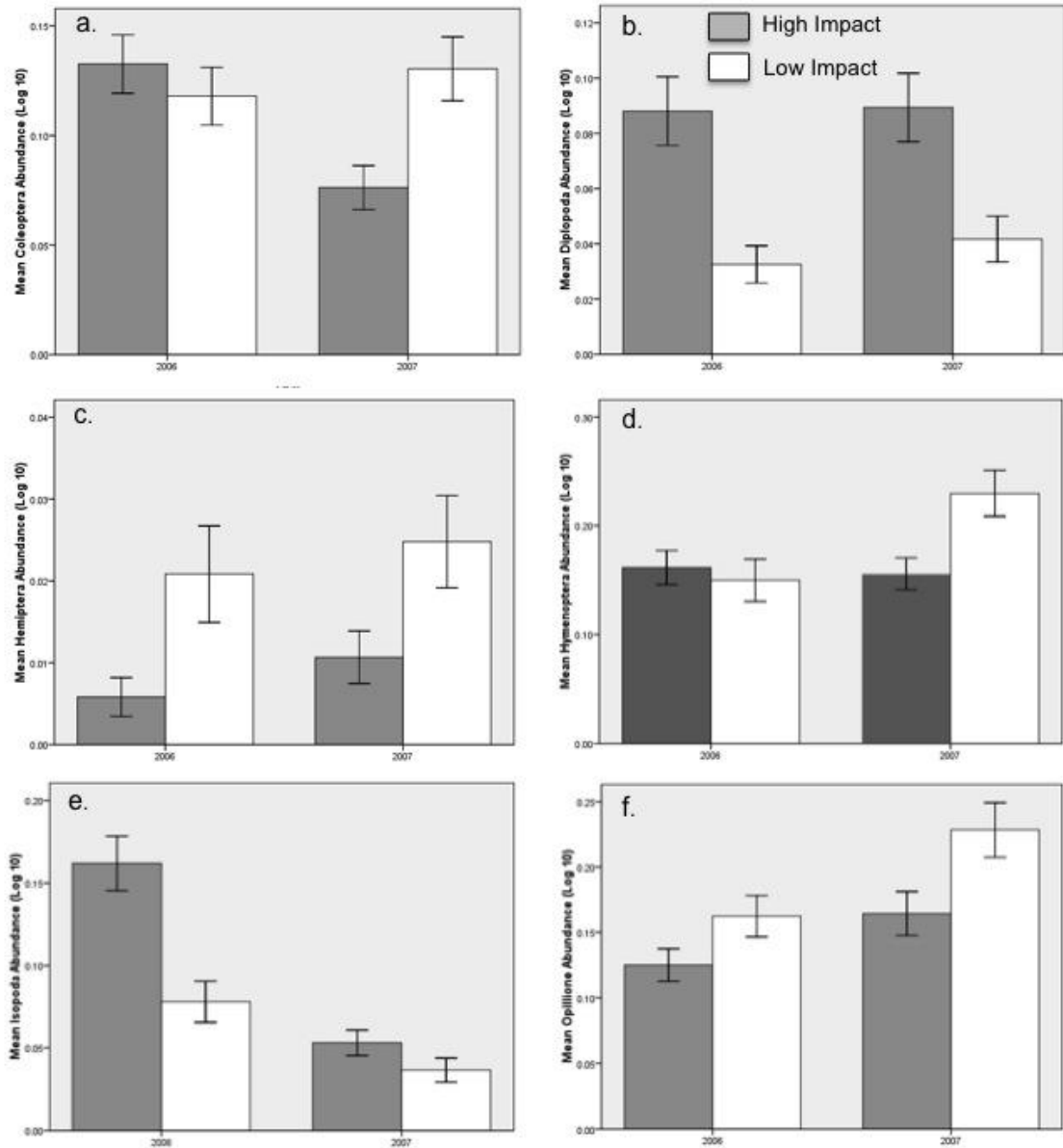


**Figure 4.1. Litter-dwelling arthropod response to browsing.** Total litter-dwelling a) macrofauna arthropod abundance sampled by pitfall traps and b) mesofauna arthropod taxonomic density (#/gram leaf litter) sampled by Berlese litter extraction in areas of high and low deer impact in 2006 & 2007.

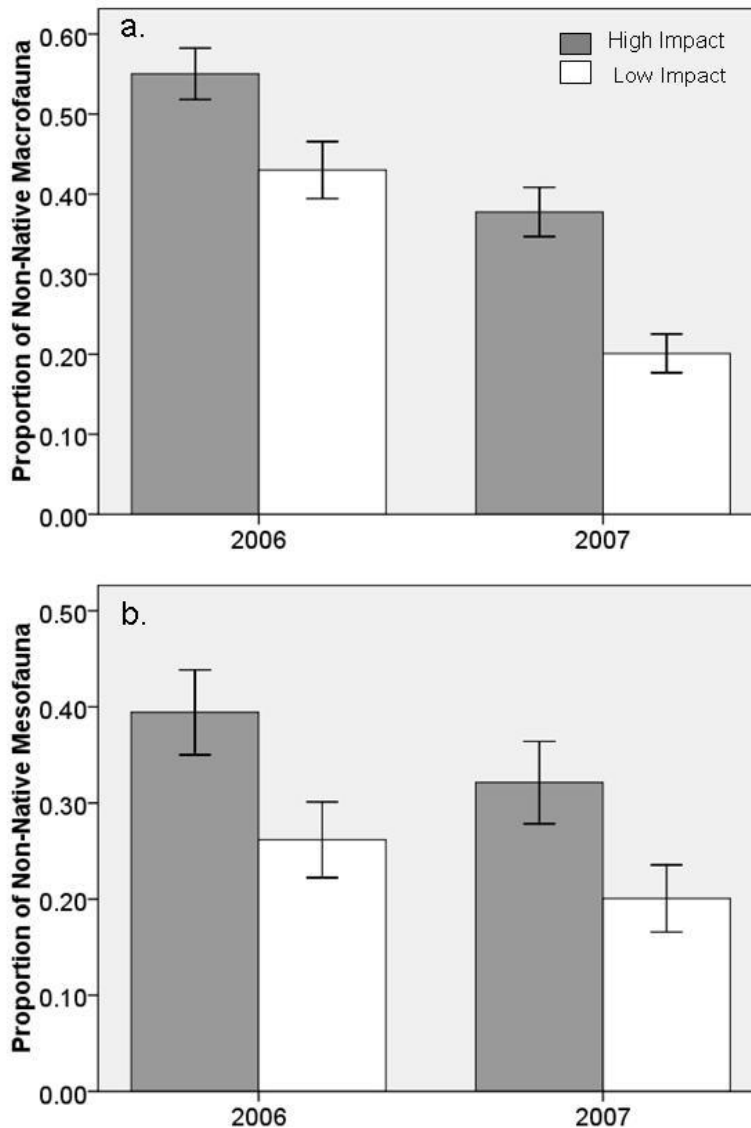
**Table 4.1 Community level response by macrofauna to browsing.** Below show results of community level responses by large active litter-dwelling arthropods to the browsing activities in 2006 & 2007. A MANOVA was performed to determine the effect of deer impact, year and impact x year interactions on the taxonomic abundance of litter-dwelling arthropods between areas of high and low impact.

<b>Taxa</b>	<b>Impact</b>	<b>Year</b>	<b>Impact x Year</b>
Annelid	$F = 1.26$ ( $p = 0.261$ )	$F = 4.91$ ( $p = 0.027$ )	$F = 0.21$ ( $p = 0.647$ )
Gastropoda	$F = 0.60$ ( $p = 0.438$ )	$F = 19.90$ ( $p \leq 0.001$ )***	$F = 2.83$ ( $p = 0.093$ )
Opiliones	$F = 9.26$ ( $p = 0.002$ ) *	$F = 10.01$ ( $p = 0.002$ ) *	$F = 0.65$ ( $p = 0.420$ )
Formicidae	$F = 3.14$ ( $p = 0.077$ )	$F = 4.43$ ( $p = 0.035$ ) *	$F = 5.91$ ( $p = 0.015$ ) *
Coleoptera	$F = 2.39$ ( $p = 0.122$ )	$F = 2.94$ ( $p = 0.087$ )	$F = 7.25$ ( $p = 0.007$ ) **
Araneae	$F = 3.45$ ( $p = 0.064$ )	$F = 11.54$ ( $p \leq 0.001$ ) *	$F = 0.61$ ( $p = 0.434$ )
Orthoptera	$F = 3.41$ ( $p = 0.065$ )	$F = 0.56$ ( $p = 0.453$ )	$F = 0.24$ ( $p = 0.626$ )
Hemiptera	$F = 11.76$ ( $p \leq 0.001$ ) *	$F = 1.07$ ( $p = 0.302$ )	$F = 0.01$ ( $p = 0.916$ )
Isopoda	$F = 17.66$ ( $p \leq 0.001$ ) ***	$F = 39.34$ ( $p \leq 0.001$ ) ***	$F = 7.96$ ( $p = 0.005$ ) *
Diplopoda	$F = 21.80$ ( $p \leq 0.001$ ) ***	$F = 0.23$ ( $p = 0.634$ )	$F = 0.13$ ( $p = 0.722$ )
Chilopoda	$F = 0.02$ ( $p = 0.903$ )	$F = 0.24$ ( $p = 0.621$ )	$F = 0.20$ ( $p = 0.654$ )
Thysanoptera	$F = 0.60$ ( $p = 0.441$ )	$F = 0.01$ ( $p = 0.932$ )	$F = 1.07$ ( $p = 0.301$ )

\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$



**Figure 4.2 Yearly taxonomic shifts in macrofauna.** Yearly taxonomic shifts in abundance of large litter-dwelling arthropods in areas of high and low deer impact. A significant overall negative effect of impact was evident for c) Hemiptera ( $p < 0.05$ ) and f) Opiliones ( $p < 0.05$ ). A significant overall positive effect of impact was evident for e) Isopoda ( $p < 0.001$ ) and b) Diplopoda ( $p < 0.001$ ). A significant impact x year interaction was evident for d) Hymenoptera ( $p < 0.05$ ) and a) Coleoptera ( $p < 0.05$ ). Error bars represent  $\pm 1$  SE.

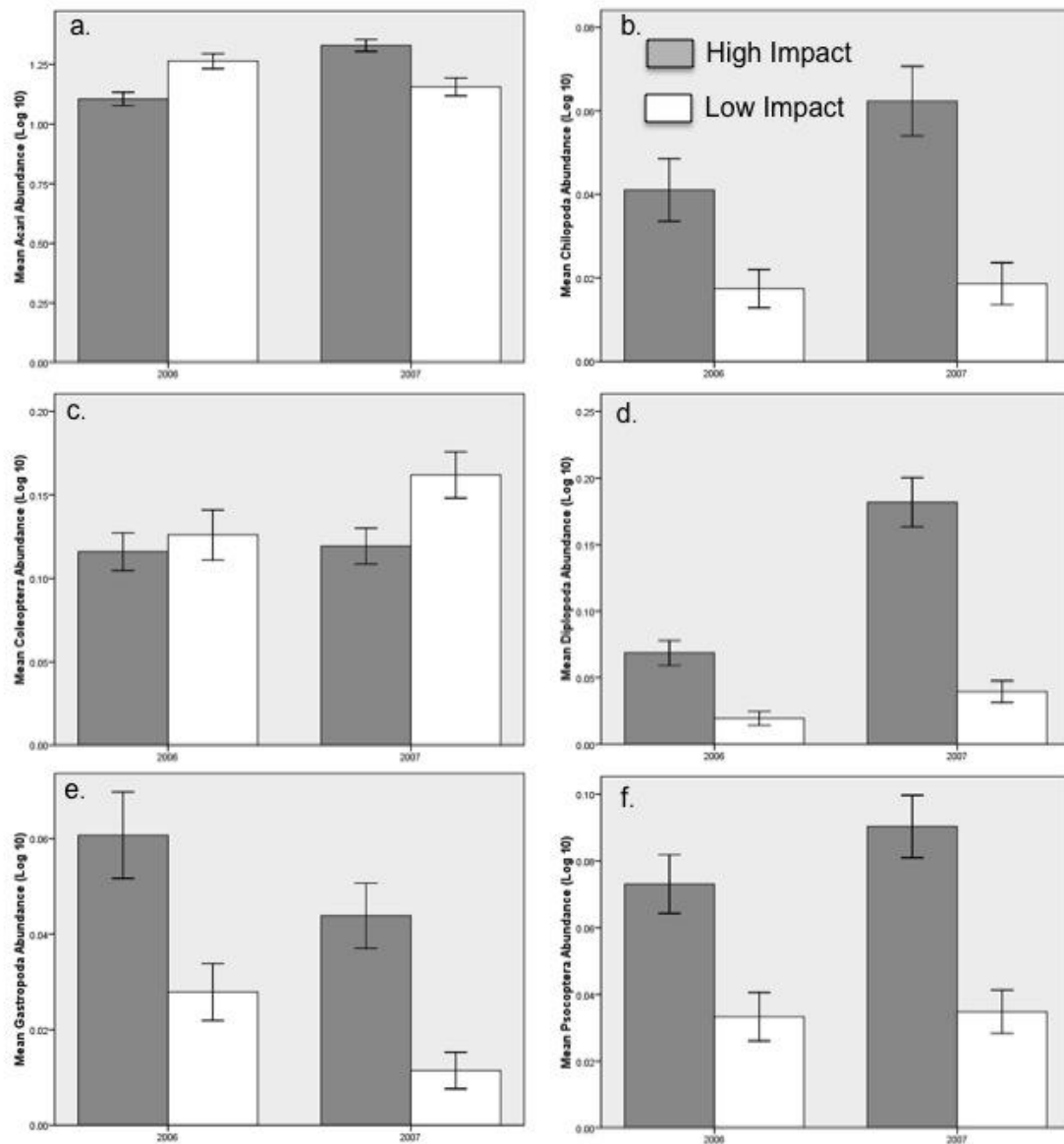


**Figure 4.3 Proportion of native vs. non-native taxa.** Overall taxonomic shift favoring non-native species in areas of high impact for a) larger mobile litter-dwelling arthropods sampled by pitfall traps (ANOVA,  $p < 0.001$ ) and b) mesofauna litter-dwelling arthropods (ANOVA,  $p < 0.01$ ). Non-native taxa included those arthropods classified as Isopoda, Diplopoda, Chilopoda and Gastropoda. Error bars represent  $\pm 1$  SE.

**Table 4.2 Community level response by mesofauna to browsing.** Below are results of community level responses by small litter-dwelling arthropods to browsing activities in 2006 & 2007. A MANOVA was performed to determine the effect of deer impact, year and impact x year interactions on the species density (#/gram leaf litter) of the litter-dwelling mesofauna between areas of high and low impact.

<b>Taxa</b>	<b>Impact</b>	<b>Year</b>	<b>Impact x Year</b>
Collembola	$F = 2.36 (p = 0.125)$	$F = 18.31 (p = 0.001) *$	$F = 3.65 (p = 0.06)$
Acari	$F = 3.77 (p = 0.539)$	$F = 3.72 (p = 0.05) *$	$F = 14.47 (p \leq 0.001) **$
Coleoptera	$F = 0.21 (p = 0.643)$	$F = 0.03 (p = 0.868)$	$F = 8.63 (p = 0.003) *$
Araneae	$F = 3.13 (p = 0.077)$	$F = 31.36 (p \leq 0.001) **$	$F = 2.53 (p = 0.112)$
Isopoda	$F = 0.72 (p = 0.395)$	$F = 0.69 (p = 0.406)$	$F = 0.17 (p = 0.683)$
Formicidae	$F = 0.06 (p = 0.809)$	$F = 6.20 (p = 0.013) *$	$F = 0.11 (p = 0.746)$
Chilopoda	$F = 6.33 (p = 0.012) *$	$F = 0.05 (p = 0.817)$	$F = 1.31 (p = 0.253)$
Diplopoda	$F = 5.57 (p = 0.019) *$	$F = 4.32 (p = 0.04) *$	$F = 1.60 (p = 0.206)$
Pseudoscorpiones	$F = 2.22 (p = 0.137)$	$F = 0.82 (p = 0.366)$	$F = 1.24 (p = 0.270)$
Psocoptera	$F = 18.17 (p \leq 0.001) **$	$F = 17.13 (p \leq 0.001) **$	$F = 0.023 (p = 0.866)$
Gastropoda	$F = 4.18 (p = 0.04) *$	$F = 3.37 (p = 0.067)$	$F = 1.76 (p = 0.185)$

\* =  $p < 0.05$ , \*\* =  $p < 0.001$



**Figure 4.4 Yearly taxonomic shifts in mesofauna.** Yearly taxonomic shifts in abundance of litter-dwelling mesofauna in areas of high and low deer impact. A significant overall negative effect of impact was evident for f) Psocoptera ( $p < 0.001$ ). A significant overall positive effect of impact was evident for e) Gastropoda ( $p < 0.05$ ), b) Chilopoda ( $p < 0.05$ ), and d) Diplopoda ( $p < 0.05$ ). A significant impact x year interaction was evident for a) Acari ( $p < 0.001$ ) and c) Coleoptera ( $p < 0.05$ ). Error bars represent  $\pm 1$  SE.



## DISCUSSION

The response of litter-dwelling arthropods to the browsing activities of deer is complex, varying significantly between years and among taxa. Despite clearly observable changes to the forest understory and leaf litter microhabitat between areas of high and low deer impact (see Chapter 2), the expected response in overall abundance by litter-dwelling arthropods was not evident. However, community composition differed significantly between high and low deer impact sites, and several major forest floor invertebrate taxa varied substantially with deer impact as well, indicating that deer may have important effects on species composition, activity, and species interactions within the forest floor.

The response by individual taxa to the browsing activities of deer was highly variable. Of the larger more mobile taxa, the abundance of Hemiptera and Opiliones were consistently higher in areas of low impact. This makes sense, because members of the order Hemiptera, i.e leafhoppers and shield bugs, generally rely on the structural diversity and abundance of understory vegetation for food and reproduction (Korösi 2012). Other taxa showing a significant response to browsing were the Coleoptera and Formicidae, although the response varied between years (Figure 4.2). Members of the order Diplopoda and Isopoda, generally considered to be non-native to Northeast Ohio, were found more often in areas of high deer impact (Figure 4.2). Of the arthropods sampled by litter extraction, litter-dwelling psocids were more abundant in areas of low impact, while the abundance of Acari and Coleoptera varied among years. Similar to the macrofauna, more non-native taxa (Gastropoda, Chilipoda and Diplopoda) were found in areas of high impact.

Although the response by Coleoptera varied between years, a general trend of more beetles in areas of low impact is evident. Of the beetles sampled, the family Carabidae was most abundant. Carabid beetles are a relatively abundant ecologically diverse group of taxa filling multiple niches on the forest floor, and they are considered ecological indicators of overall ecosystem health and functioning (Niemelä 2001; Rainio and Niemelä 2003; see also Work et al. 2008). Factors important to carabid abundance include percent ground cover, soil moisture, and overall habitat heterogeneity (Work et al. 2008). The finding of more carabids at low impact sites characterized by a more structurally diverse habitat (i.e., increased ground & herbaceous cover, deeper leaf litter layer and more moist soils) relative to areas of high impact (see Chapter 2) suggests that carabid beetles prefer more structurally complex litter habitat and may be sensitive to reduced litter habitat caused by the indirect impacts of browsing by deer. Similar results were also observed in an enclosure study at nearby sites in Lake County, Ohio (see Chapter 3). That more beetles, specifically more carabid beetles, were found inside relative to outside deer enclosures (see Chapter 3).

Most notable is the response by non-native species to the browsing activities of deer. Areas of high impact supported a greater proportion of non-native species relative to areas of low impact. Nearly 30% of all invertebrate taxa present in areas of high impact are considered non-native. Invasion by non-native invertebrate species are among the most important global-scale problems facing natural ecosystems today (Vitousek 1990; Vitousek et al. 1996; Walker and Steffen 1997; Mack 2000). Invading species can alter fundamental ecological properties by altering species dominance in a community, including extinctions of native species, alter plant productivity and diversity and disrupt

nutrient cycling regimes (Vitousek 1990). Evidence in support of the direct impacts of non-native species on the structure of ecosystems is well documented (Table 4.3), but less understood are the factors facilitating such invasions (Levine and D'Antonio 1999). The ability to predict and identify habitats vulnerable to invasions and identify factors facilitating such invasions is critical to managing and/or mitigating the impact of biological invasions. Six general hypotheses have been proposed to explain and predict biological invasions based on ecosystem susceptibility, biotic potential of the invading species, and invader-ecosystem interactions (Table 4.3). Of the hypotheses outlined here, the invasional meltdown hypothesis best suits the mechanism by which deer may facilitate biological invasions of non-native species (Simberloff and VonHolle 1999).

Through selective browsing, deer alter plant species composition in favor of browse tolerant, unpalatable species. This in combination with a reduction in native plant biomass, may facilitate the invasion non-native plant species. Through competitive interactions or allelopathic effects, for example, non-native species may further degrade habitat for native species while improving conditions for non-natives. This sequence of events supports the invasional meltdown hypothesis, which states the presence of non-native species in an ecosystem may facilitate invasions by additional non-native species, increasing their likelihood of survival or ecological impact (Simberloff and Von Holle 1999). Figure 4.5 proposes a series of mechanisms by which deer can facilitate biological invasions of plants and other taxa under the invasional meltdown hypothesis. By increasing the likelihood of survival and ecological impact of non-native taxa, the browsing activities of overabundant deer amplify the impact of biological invasions by

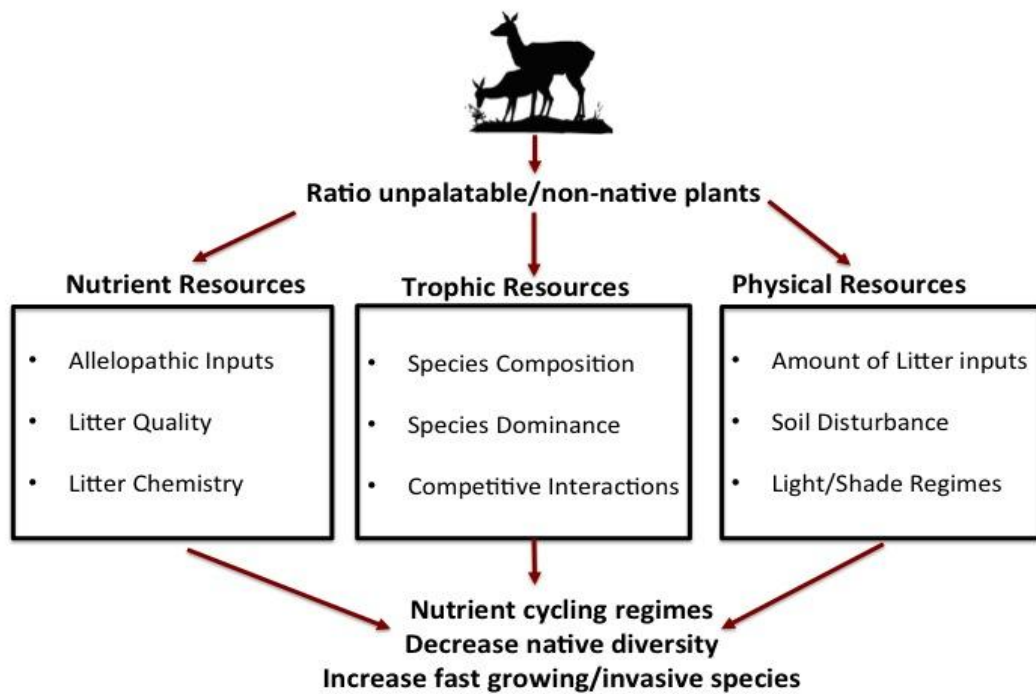
further altering local species diversity and thus further degrading overall ecosystem functioning.

### **Management implications**

Threats to overall species diversity and ecosystem functioning as a result of deer overabundance are often felt at local or regional scales. However, when linked with the global threat of biological invasions, the threat of overabundant deer to global biodiversity becomes more apparent. Ways to mitigate biological invasions and improve habitat vulnerability should be part of all management regimes. Success of such regimes should be measured in terms of overall species composition rather than the maintenance of deer numbers at or below the ecological carrying capacity based on plant species responses alone. Restoration efforts and current management regimes aimed to maintain or increase species diversity and the ecological integrity of a system are most effective when they employ long-term ecosystem wide strategies. Therefore, any efforts to improve the overall quality of an ecosystem should acknowledge the interconnection between deer overabundance and the invasion of non-native and potentially invasive arthropod species.

**Table 4.3 Major hypotheses proposed to explain biological invasions.** Review of the six major hypotheses proposed to explain biological invasions. Level of empirical support defined by a meta-analysis study by Jeschke et al. 2012. General support of presented hypotheses is based 371 empirical studies across taxonomic groups and habitats that tested each of the six hypothesis outlined below.

<b>Biological Invasion Hypothesis</b>	<b>Description</b>	<b>Evidence</b>	<b>General Empirical Support</b>	<b>Support Invertebrates Only</b>
<b>Ecosystem Susceptibility</b>				
Biotic Resistance	Ecosystems with high biodiversity are more resistant against invaders than ecosystems to low biodiversity	Elton 1958, Levine and D'Antonio 1999, Mack et al. 2000, Levine et al. 2004, & Jeschke and Genovesi 2011	moderate; <30% literature support	moderate; <30% literature support
Island Susceptibility	Invasive species are more likely to become established and have major ecological impacts on islands than continents	Elton 1958, Simberloff 1995, Shea and Chesson 2002 & Jeschke 2008	low; <20% literature support	N/A
<b>Biotic Potential of Invaders</b>				
Tens Rule	Approximately 10% of species transported beyond their range will escape in the wild; about 10% of those species will establish themselves in the wild and 10% of those species will become invasive	Williamson and Brown 1986, Jeschke and Strayer 2005 & Jeschke	moderate; <30% literature support	moderate; <40% literature support
<b>Invader-Ecosystem Interactions</b>				
Invasional Meltdown	The presence of invasive species in an ecosystem facilitates the invasion of additional species, increasing their likelihood of survival and ecological impact	Simberloff and Von Holle 1999	high >50% literature support	high >50% literature support
Novel Weapons	In the exotic habitat, invasive species can have a competitive advantage against native species because they possess a novel weapon which negatively affects native species	Callaway and Aschehoug 2000 & Callaway and Ridenour 2004	high >50% literature support	N/A
Enemy Release	The absence of enemies in the exotic range is a cause of invasion success	Maron and Vila 2001, Keane and Crawley 2002 & Blumenthal et al. 2009	high >50% literature support	moderate; <40% literature support



**Figure 4.5 The role of deer in facilitating biological invasions.** Suggested mechanisms derived from the invasional meltdown hypothesis (Simberloff and Von Hollee 1999) explaining the role of deer in facilitating biological invasions. Changes in plant species composition as a result of browsing favors browse tolerant/unpalatable species, which may further influence biological invasions through changes in resource acquisition, trophic resources, and physical disturbance.

## LITERATURE CITED

- Allombert, S., Stockton, S., Martin, J. L. (2005) A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology* 19(6), 1917- 1929.
- Baines, D., Sage, R. B., and Baines, M. M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology* 31, 776-783.
- Bartuszevige, A., and B. A. Endress. (2008) Do ungulates facilitate native and exotic plant spreads? Seed dispersal by cattle, elk, and deer in northeastern Oregon. *Journal of Arid Environments* 72, 904- 913
- Blumenthal D, Mitchell C. E., Pyšek P., and Jarošík V. (2009) Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences USA* 106, 7899–7904.
- Callaway, R. M., Aschehoug, E. T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290, 521–523.
- Callaway, R. M. and Ridenour, W. M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2, 436–443.
- Côté, S. D., Rooney, T. P., Tremblay, J., Dussault, C., and Waller, D. M. (2004) Ecological impact of deer overabundance. *Annual Review of Ecology and Systematics* 35,113-147.
- D’Antonio, C. M. and Vitousek, P. M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23, 63–87
- deCalesta, D. S. (1994) Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58, 711-718.
- Dennis, P., Young, M. R., and Gordon, I. J. (1997) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 23, 253-264.
- Elton, C. S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Eschtruth, A. K. and Battles, J. J. (2009) A generalist herbivore accelerates exotic plant invasion in a forested ecosystem. *Conservation Biology* 23(2), 388-399.
- Facelli, J. M. (1994) Multiple indirect effects on plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75, 1727-1735.

- Flowerdew, J. R. and Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry* 74, 277-287.
- Fuller, R. J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanism. *Forestry* 74, 289-298.
- García, L.V. (2003) Controlling the false discovery rate in ecological research. *Trends in Ecology and Evolution* 18, 553–554.
- Greenwald, K.R., Petit, L.J., and Waite, T.A. 2008. Indirect effects of a keystone herbivore elevate local animal diversity. *The Journal of Wildlife Management* 72(6), 1318-1321.
- Hartley, S. E., Gardner, S. M., and Mitchell, R. J. (2003) Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. *Journal of Applied Ecology* 40, 793-803.
- Jeschke, J. M. and Genovesi, P. (2011) Do biodiversity and human impact influence the introduction or establishment of alien mammals? *Oikos* 120, 57–64.
- Jeschke, J. M., Strayer, D. L. (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences USA* 102, 7198–7202
- Jeschke, J. M. (2008) Across islands and continents, mammals are more successful invaders than birds. *Diversity and Distributions* 14, 913–916.
- Jeschke, J. M., Aparicio, L. G., Haider, S., Heger, T., Lortie, C. J. Pyšek, P. and Strayer, D.L. (2012) Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14, 1-20.
- Keane, R. M. and Crawley, M. J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17, 164–170.
- Korosi, A., Batary P., Orosz, A., Redel, D., and Baldi, A. Effects of grazing, vegetation structure and landscape complexity on grassland leafhopper (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary. *Insect Conservation & Diversity*. 5(1), 57-66.
- Lessard, J. P., Reynolds, W. N., Bunn, W. A., Genung, M. A., Gregger, M. A., Felker-Quinn, E., Barrios-Garcia, M.N., Stevenson, M. L., Brown, C. B., Patrick, M., Rock, J.H., Jenkins, M. A., Bailey, J. K., and Schweitzer, J. A. (2012) Equivalence in the strength of deer herbivory on and above and below ground communities. *Basic and Applied Ecology*. 13, 59-66.
- Levine, J. M. and D'Antonio, C. M. (1999) Elton revisited: a review of evidence linking diversity and invisibility. *Oikos* 87, 15-26.



- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and Bazzaz, F. A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3), 689-710.
- Maron, J. L. and Vilà, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95, 361–373.
- McShea, W. J., Underwood, H. B., and Rappole, J. H. (1997) The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.
- McShea, W. J., and Rappole, J. H. (1992) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology* 14 (4), 1161-1170.
- Melis, C. (2007). The role of moose *Alces alces* L. in boreal forests—the effect on ground beetles (Coleoptera, Carabidae) abundance and diversity. *Biodiversity Conservation* 16, 1321-1335.
- Miyashita, T., Takada, M., and Shimazaki, A. (2004) Indirect effects of herbivory by deer reduce abundance and species richness of web-building spiders. *Ecoscience* 11, 74-79.
- Moran, M. D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100(2), 403-405.
- Nakagawa, S (2004) A farewell to Bonferroni: the problem of low statistical power and publication bias. *Behavioral Ecology* 15(6), 1044-1045.
- Pastor, J., Dewey, B., Naiman, R. J., McInnes, P., and Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74, 467-480.
- Rambo, J. L. and Faeth, S. H. (1999) Effects of vertebrate grazing on plant and insect community structure. *Conservation Biology* 13, 1047-1054.
- Rooney, T. P. and Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181, 165-176.
- Russell, F. L., Zippin, D. B., and Fowler, N. L. (2001) Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations, and communities: A review. *American Midland Naturalist* 146, 1-26.
- Smit, R., Bokdam, J., den Ouden, J., Olf, H., Schot-Opschoor, H., and Schrijver, M. (2001) Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology* 155, 119-127.

- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17, 170–176.
- Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49, 87–97.
- Simberloff, D. and VonHolle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1, 21-32.
- Suominen, O., Danell, K., and Bergstrom, R. (1999a) Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests *Oikos* 84, 215-226.
- Suominen, O., Danell, K., and Bryant, J. P. (1999b) Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. *Ecoscience* 6, 505-510.
- Suominen, O., Niemelä, J., Martikainen, P., Niemelä, P., and Kojola, I. (2003) Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidea assemblages in Lapland. *Ecography* 26, 503-513.
- Suominen, O., Persson, I., Danell, K., Bergström, R. and Pastor, J. (2008) Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. *Ecography* 31, 636-645.
- Underwood, H. B and Coffey, M. A. (1999) Evaluation of distance sampling for deer density estimation at Cuyahoga Valley National Recreation Area (CUVA): part II. National Park Service, Brecksville, Ohio, USA.
- Vitousek, P. M. (1990) Biological invasions and ecosystems process—towards an integration of population biology and ecosystem studies. *Oikos* 57, 7-13.
- Vitousek, P. M., D;Antonio, C. M., Loope, L. L., and Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist* 84, 468-478.
- Wagner, J. D., Toft, S. and Wise, D. H. (2003) Spatial Stratification in litter depth by f forest-floor spiders. *The Journal of Arachnology* 31, 28-39.
- Walker, B. H. and Steffen, W. (1997) An overview of the implications of global change for natural and managed terrestrial ecosystems. *Conservation Ecology* 2(2), 112-116.
- Wardle, D. A. 2002. *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton, NJ: Princeton University Press.
- Williamson, M. and Brown, K. C. (1986) The analysis and modeling of British invasions. *Philosophical Transactions of the Royal Society London Series B* 314: 505–522.

## CHAPTER V

### THE EFFECT OF OVER-BROWSING BY WHITE-TAILED DEER ON SMALL MAMMAL POPULATIONS INHABITING THE FOREST FLOOR

#### ABSTRACT

Sustained over-browsing in forest ecosystems has important consequences on small mammal population dynamics; the loss of vegetative cover and reduction in leaf litter biomass reduces resource availability and habitat suitability for small mammals, affecting survivorship and foraging success. Additionally, changes to the forest floor microhabitat may negatively affect important food sources for small mammals such as litter-dwelling arthropod populations, thus further influencing small mammal responses to deer browse, especially insectivorous small mammals. A combination of Sherman live traps and pitfall arrays were used to assess differences in small mammal abundance and diversity between areas of low and high deer impact. Data collected over three field seasons suggest overall species diversity was slightly higher at low impact ( $H' = 1.40$ ) relative to high impact sites ( $H' = 0.99$ ). Additionally, significantly more animals were captured in areas of low impact relative to areas high impact (Pillai's Trace = 0.874,  $F_{(5,10)} = 11.562$ ,  $p \leq 0.001$ ), driven largely by two insectivores: masked (*Sorex cinereus*) and short-tailed shrews (*Blarina brevicauda*; Pillai's Trace = 0.812,  $F_{(2,13)} = 28.148$ ,  $p \leq 0.001$ ). The

potential indirect effects of deer on small mammal population abundance and species diversity are important because the activities of these species increase the functional diversity of ecosystems. Further research will determine if the lack of forest microhabitat or changes in invertebrate availability are more important in determining small mammal response to deer browse.

## INTRODUCTION

Perhaps one of the largest threats to biodiversity in eastern deciduous forest is the overabundance of white-tailed deer (*Odocoileus virginianus*). White-tailed deer are keystone herbivores within forest ecosystems (Waller and Alverson 1997) and therefore, play an integral role in forest ecosystem dynamics. However, where overabundant, sustained browsing can reduce plant cover and diversity, alter nutrient and carbon cycling, and redirect succession and future canopy composition (Rooney and Waller 2003). An important but poorly understood deer-induced change to forest ecosystems is the initiation of a cascade of effects on small mammal diversity and abundance (Flowerdew and Ellwood 2001). Sustained over-browsing in forest ecosystems has important consequences on small mammal population dynamics; the loss of vegetative cover and reduction in leaf litter biomass reduces resource availability and habitat suitability for small mammals, affecting survivorship and foraging success (Miller and Getz 1977; Geier and Best 1980; Putman 1986; Smit et al. 2001). The forest floor microhabitat provides not only shelter and nesting sites for small mammals, but provides important food resources, such as seeds and invertebrates, both of which may respond negatively to the direct and indirect impact of browsing (Flowerdew and Ellwood 2001, see Chapter 3 & 4).

In woodlands of Northeast Ohio, the small mammal community can be grouped broadly into rodents and insectivores. The rodent community consists largely of white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), and woodland voles (*Microtus pinetorum*), and that feed primarily on vegetation and mast crop produced within the canopy and forest understory. These species may compete directly with deer for food resources (i.e., acorns) or may face reduced food biomass as a result of reduced abundance and diversity of understory vegetation (McShea 2000).

Common insectivores in Northeast Ohio include the short-tailed shrew (*Blarina brevicauda*), masked-shrew (*Sorex cinereus*), hairy tailed mole (*Parascalops breweri*) and star-nosed mole (*Condylura cristata*). The impact of deer on the forest floor microhabitat may be especially detrimental to shrews, and changes in shrew abundance in relation to browsing by deer are of particular interest in this study. Shrews have a high metabolism, and as such require ample invertebrate prey, which may be reduced in areas of decreased litter and understory cover. In addition, and related to their high metabolism, shrews require moist habitats with adequate cover to maintain homeostasis and to provide protection from predators (Churchfield 1990). A reduced understory, increased light penetration to the forest floor, and decreased litter accumulation are likely to result in drier soils and a xeric microclimate within the litter layer, thereby degrading the suitability of habitat for shrews and their invertebrate prey.

The evidence cited above suggests that deer-mediated changes to the forest understory and forest floor microhabitat can influence habitat suitability and survivorship of small mammals, ultimately impacting community composition and diversity. Evaluating these interactions is important because small mammals represent a large component of

biodiversity in forest ecosystems and their activities help maintain forest ecosystem function (Wardle 2002). The objective of this study is to document differences in small mammal community abundance and diversity in areas of high and low deer impact. If over-browsing by deer reduces habitat quality within the forest floor microhabitat, then those species living within these areas may show reduced abundance and diversity. More specifically, I expect litter-dwelling insectivores, such as shrews, to have reduced abundance in areas of high deer impact. The rodents, mice and chipmunks, are broadly characterized as habitat generalists, may show little response to deer overabundance and may even increase in abundance as a result of reduced competition with habitat specialists and/or habitat modification to a more open understory.

## METHODS

### **Study Site**

This research was conducted within Cleveland Metroparks (CMP) and Cuyahoga Valley National Park (CVNP) in Northeast Ohio. Cleveland Metroparks was founded in 1917 and currently manages 18 reservations encompassing 8,498 ha of interconnected parks and reserves located primarily along riparian corridors. Cuyahoga Valley National park consists of 8,230 ha of intermingled federal, municipal and private land surrounded by the suburban communities of Akron and Cleveland, Ohio. Hunting is prohibited in both park systems. However, CMP has been culling deer herds since 1998. Cuyahoga Valley National Park, on the other hand, monitors the size and health of its deer herd but does not cull or employ any other method of herd reduction. Such management regimes have resulted in densities ranging between 8 and 30 deer/ km<sup>2</sup> in CMP to densities > 52 deer/km<sup>2</sup> at CVNP (Underwood and Coffey 1999). As a result, I was able to undertake a

comparative assessment of the ecological impacts of deer browsing activities in a natural, biologically-relevant setting without the use of exclosures. Within these park systems, seven field sites were chosen based on several measures of deer impact. Because the current structure and species diversity within the forest understory is most likely influenced by past browsing events, browse estimates from the years leading up to the study were more heavily weighted than current estimates of browse intensity that may have fluctuated as a result of current management efforts. Pellet count, aerial infrared and spotlight surveys and numbers obtained through culling efforts conducted between 1997 and 2003 were used to obtain estimates of deer density and impact for each study site.

### **Data Collection**

I used a series of replicated Sherman live and pitfall trap grids to estimate population size and small mammal diversity at each field site using mark-recapture techniques. I established a 7 X 7 grid of Sherman live traps (7.5 x 9.0 x 23.0 cm, H.B. Sherman Trap, Inc.) consisting of 49 trapping stations (two traps per station) placed at 10-m intervals to target larger rodent species active on the forest floor. I used two baited traps at each station to increase capture probability by preventing trap saturation from “trap happy” animals. Prior to each trapping session, all Sherman traps were locked open and pre-baited with oats and carrot slices for 36 hrs. A simple bait of oats and carrot were used instead of the traditional peanut butter and oats because of a high rate of raccoons (*Procyon lotor*) tampering with traps. In addition, I established a 4 x 5 grid of pitfall arrays at each site targeting smaller insectivorous species foraging on the forest floor. Each pit-fall grid consisted of 20 pitfall arrays (4 rows of 5 arrays placed at 25-m

intervals totaling 120 pitfalls where each array was composed of 6 pitfall traps (6.4 liter buckets) arranged in a Y-formation connected by a drift fence. A drift fence was used to help guide animals foraging in the leaf litter into a trap. Each drift fence was partially buried within the soil/leaf litter layer to prevent animals from burrowing beneath the drift fence to increase trap effectiveness. During periods of non-trapping each pitfall was filled with leaf litter and twigs and covered with a wood cover to prevent unwanted captures and decrease trap mortality. During periods of trapping each pitfall was cleaned out and covers raised to 10 cm above the ground to protect captured animals from sun and rain and help discourage predation.

All traps (Sherman and pitfall) were active for 2 four-night sessions separated by a 12-14 day period of no trapping from May through September in 2005 and for 3 four-night sessions separated by 12-14 days of no trapping during the 2006 & 2007 field seasons. Traps were checked frequently during each period of active trapping to decrease stress to the animal and reduce trap mortality. Sherman traps were checked at least twice per day (dawn and dusk). Because shrews have a high metabolism and require a constant supply of food, each pitfall trap was checked frequently, every 2-4 hours, and supplied with an adequate food supply (local insects) between check points to increase survival rates of captures.

Each animal captured was identified to species, weighed, measured and marked before release back into the population. All rodents received a 0.5 cm self-piercing numbered ear tag (National Band & Tag Company, [www.nationalband.com](http://www.nationalband.com)). Because shrews and moles lack external ear features, numbered ear tags could not be used. Instead, we used a combination of permanent ink marks and pink, blue, yellow or green



fluorescent powder to mark these species. Each mark was assumed to last for the duration of each trapping session. Upon recapture each animal was examined for either an existing ear tag or mark. All trapping and handling procedures were approved by the Cleveland State University Animal Care and Use Committee (IACUC # 2601-WAL-AS).

### **Statistical Analysis**

I compared capture rate between areas of high and low deer impact using multivariate analysis of variance (MANOVA) for those species representing the most captures. Those species included *P. leucopus*, *M. pinetorum*, *T. striatus*, *S. cinereus*, and *B. brevicauda*. The three other species captured; the star-nosed mole, the hairy-tailed mole and least weasel (*Mustela nivalis*), were caught on occasion and considered incidental catches (Table 5.1). To adjust for differences in trapping effort between sites (because of flooded or traps sprung accidentally) I standardized the data using a trap-night index, number of animals captured per 100 trap-nights. A trap-night was calculated as the number of traps open per 24-hr period. The Shannon-Wiener diversity index ( $H'$ ) was calculated to measure species diversity between areas of high and low impact.

### **RESULTS**

Eight species were captured totaling 794 individuals (432 in high deer impact areas; 362 in low deer impact areas) in 67,720 trap-nights (38,132 in high deer impact areas; 31,414 in low deer impact areas) between the years of 2005-2007 (Table 5.1). Although species diversity was slightly higher at low impact ( $H' = 1.40$ ) relative to high impact sites ( $H' = 0.99$ ) species diversity was low at all sites, using these trapping methods. Seven of the 8 species captured were observed both in areas of high and low impact. The only species not captured in any of the high impact sites was *C. cristata*, which was only

seen at Hinckley Reservation (CMP) on one occasion during the 2005 field season (Table 5.1). When adjusted for trapping effort, significantly more animals were captured in areas of low impact relative to areas high impact (Pillai's Trace = 0.874,  $F_{(5,10)} = 11.562$ ,  $p \leq 0.001$ ).

Differences in rodent versus insectivore communities also varied significantly between areas of high and low impact (Pillai's Trace = 0.812,  $F_{(2,13)} = 28.148$ ,  $p \leq 0.001$ ; Figure 5.1). Significantly more insectivores were captured in areas of low impact ( $F_{(2,13)} = 53.608$ ,  $p \leq 0.001$ ) while significantly more rodents were captured in areas of high impact ( $F_{(2,13)} = 5.232$ ,  $p = 0.04$ ; Figure 5.1). Of the species analyzed separately, *S. cinereus* and *B. brevicauda*, were significantly more abundant in areas of low impact relative to areas of high impact (*S. cinereus*  $F_{(1,14)} = 16.785$ ,  $p = 0.001$ ; *B. brevicauda*  $F_{(1,14)} = 23.586$ ,  $p \leq 0.001$ ; Table 5.1). Although the overall trend was to capture more *T. striatus* and *P. leucopus* in areas of high impact relative to areas of low impact, these differences were only significant for *P. leucopus* ( $F_{(1,14)} = 4.609$ ,  $p = 0.05$ ; Table 5.1). Similarly, more *M. pinetorum* were observed in areas of low impact but these differences were not significant ( $F_{(1,14)} = 2.990$ ,  $p = 0.106$ ; Table 5.1).

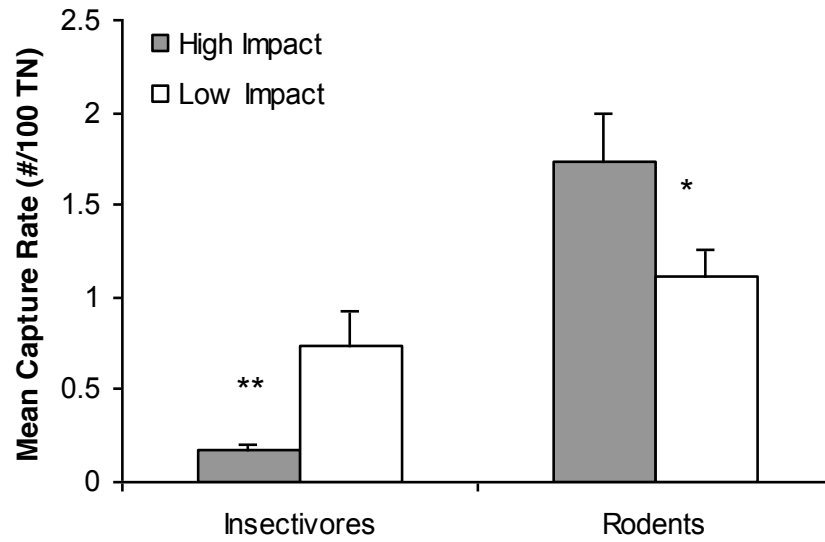
Further analysis revealed differences in species specific capture rates between years (Pillai's Trace = 1.044,  $F_{(10,22)} = 2.404$ ,  $p = 0.04$ ; Figures 5.2 & 5.3). Significantly more *P. leucopus* were captured in areas of high impact during the 2006 field season (2005:  $F_{(1,4)} = 1.984$ ,  $p = 0.232$ , 2006:  $F_{(1,4)} = 6.647$ ,  $p = 0.05$ , 2007:  $F_{(1,4)} = 0.014$ ,  $p = 0.911$ ; Figure 5.2a). More *S. cinereus* were captured in areas of low impact in years 2005 & 2006 but not 2007 (2005:  $F_{(1,4)} = 14.404$ ,  $p = 0.019$ , 2006:  $F_{(1,4)} = 10.353$ ,  $p = 0.024$ , 2007:  $F_{(1,4)} = 0.526$ ,  $p = 0.501$ ; Figure 5.3a) and more *B. brevicauda* were captured in

areas of low impact in 2005 and 2007 (2005:  $F_{(1,4)} = 38.386, p = 0.003$ , 2006:  $F_{(1,4)} = 0.145, p = 0.719$ , 2007:  $F_{(1,4)} = 5.075, p = 0.055$ ; Figure 5.3b).

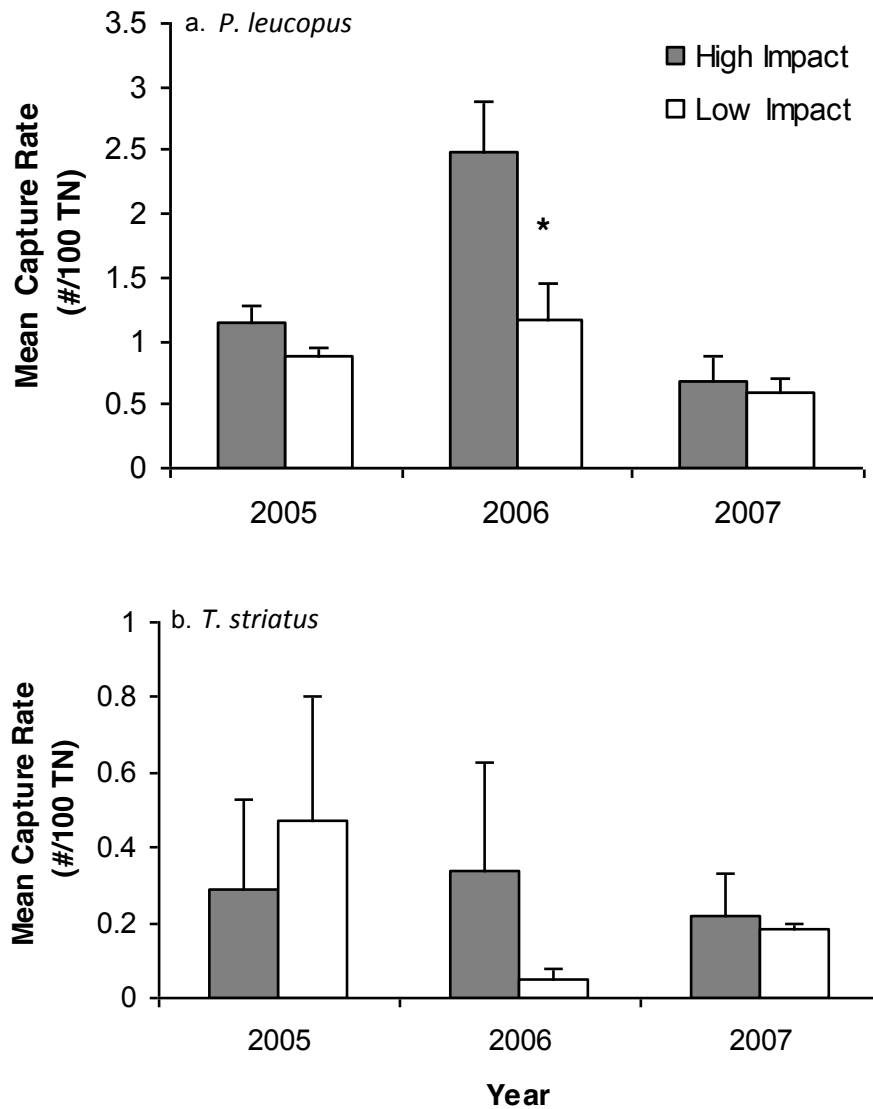
**Table 5.1 Total mammalian species captured.** Total species captured, represented by overall capture rate (number caught per 100 trap nights), in areas of high and low impact from May through September 2005-2007.

Species	High Impact		Low Impact		<i>p</i>
	N	#/100 TN	N	#/100 TN	
<i>P. leucopus</i>	297	1.476	124	0.880	0.05
<i>T. striatus</i>	59	0.293	26	0.184	0.847
<i>M. pinetorum</i>	2	0.005	11	0.038	0.106
<i>S. cinereus</i>	22	0.058	55	0.190	0.001 *
<i>B. brevicauda</i>	49	0.129	140	0.483	0.001*
<i>P. breweri</i>	1	0.003	2	0.007	n/a
<i>C. cristata</i>	0	0.000	3	0.010	n/a
<i>M. nivalis</i>	2	0.010	1	0.007	n/a

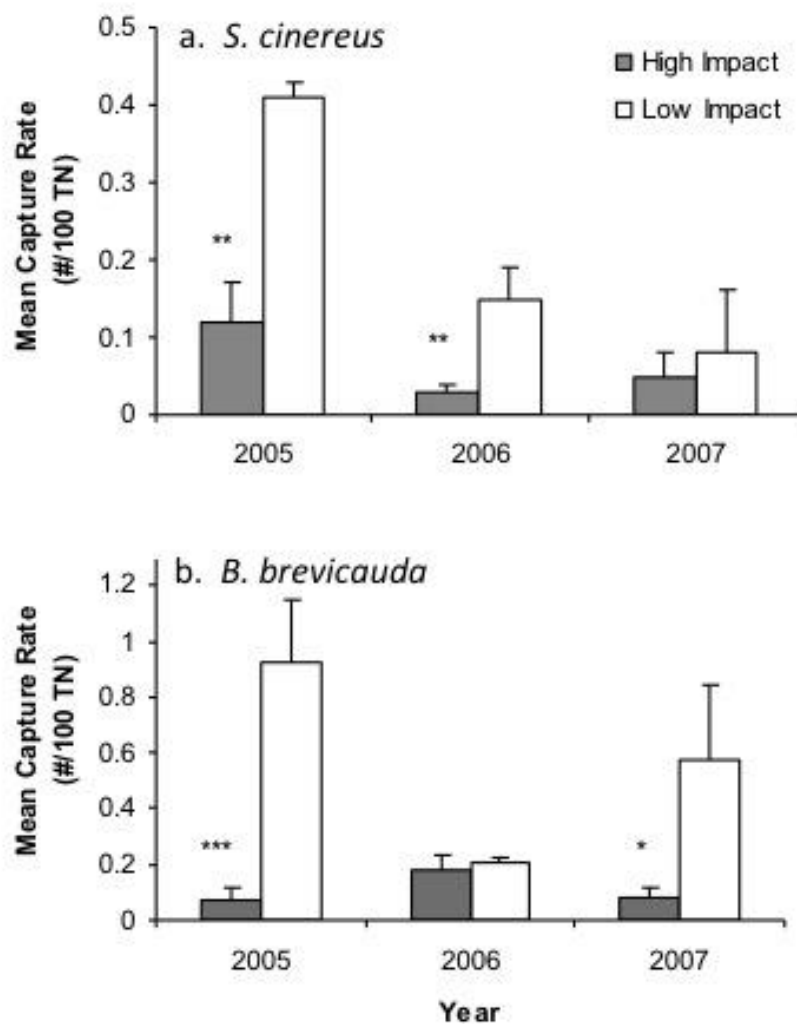
*n/a = statistical analysis not warranted due to low capture rates*



**Figure 5.1 Mean captures of insectivores and rodents.** Total combined captures standardized per 100 trap-nights for the years 2005-2007 grouped as insectivores (shrews and moles) and rodents (mice, voles, and chipmunks) in areas of high and low deer impact within Cleveland Metroparks and Cuyahoga Valley National Park. Error bars represent 1 SE. \*\* =  $p \leq 0.001$  \*  $p \leq 0.05$



**Figure 5.2 Mean rodent capture rate.** Mean capture rate for a) *P. leucopus* and b) *T. striatus* between the years of 2005-2007 in areas of high and low deer impact within Cleveland Metroparks and Cuyahoga Valley National Park. \*  $p = 0.05$



**Figure 5.3. Mean insectivore capture rate.** Mean yearly capture rate for a) *S. cinereus* and b) *B. brevicauda* between the years of 2005-2007 in areas of high and low deer impact within the Cleveland Metroparks and Cuyahoga Valley National Park. Error bars represent 1 SE. \*\*\*  $p \leq 0.01$ , \*\*  $p \leq 0.02$ , and \*  $p = 0.05$

## DISCUSSION

The potential indirect effects of deer on small mammal population abundance and species diversity are important because the activities of these species increase the functional diversity of ecosystems. They serve as a vital prey base for many species including raptors, reptiles and other mammals, and they play a key role in the dispersal of seeds and distribution of plant species within forest ecosystems. Previous research at these sites has documented an indirect relationship between the browsing activities of deer and the quality of forest floor microhabitat (see Chapter 2). As the browsing activities of deer increase, herbaceous cover within the forest understory decreases causing a decline in leaf litter depth, litter biomass, and soil moisture of the forest floor (see Chapter 2). These changes have contributed to significant but contrasting responses by rodents and insectivores to the browsing activities of deer.

In general, the most common rodent species, *P. leucopus* and *T. striatus*, responded positively to deer induced changes to the forest understory and forest floor microhabitat, while *M. pinetorum* responded negatively to these changes. Although, *P. leucopus* showed the strongest response to browsing, the overall positive response of both *P. leucopus* and *T. striatus* to increased browsing can be explained by the generalist nature of these two species. *Peromyscus leucopus* generally prefer late successional forests with increased canopy cover; however, they are behaviorally flexible and are quick to colonize disturbed sites and exploit various food resources dependent on availability (Ivan and Swihart 2000). *Tamias striatus* prefer early successional forests (Urban and Swihart 2011) with a more open forest canopy and low leaf litter accumulation and may respond favorably to moderate habitat disturbance (Kaminski et al. 2007). *Microtus pinetorum*,

on the other hand behaves as a habitat specialist, and prefer habitats with thick litter accumulation and increased herbaceous cover and are generally thought to respond negatively to habitat disturbance (Miller and Getz 1969; Smolen 1981; Fuller et al. 2004; Byman 2011). The breadth of diet and ability to exploit a wide range of niches may allow habitat generalists such as *P. leucopus* and *T. striatus* to tolerate local habitat disturbance and even thrive because of a lack of competition with more sensitive specialist species such as *M. pinetorum*, deer mouse (*Peromyscus maniculatus*) and woodland jumping mice (*Napaeozapus insignis*).

*Sorex cinereus* and *B. brevicauda* exploit a wide range of habitats; however, both species prefer mesic hardwood forests with abundant understory vegetation and deep leaf litter accumulation (Pruitt 1953; Getz 1961; Miller and Getz 1977; Yahner 1982; George et al. 1986; Whitaker 2004). Although a direct correlation between shrew abundance and herbaceous cover has not been documented, components of the forest floor microhabitat associated with herbaceous cover, such as shade and leaf litter accumulation, may influence shrew abundance through indirect effects on moisture content of the litter layer (Getz 1961; Pagels et al. 1994; Laerm et al. 1999; McCay et al. 1998). Litter moisture is important in determining the distribution of shrews (Wrigley et al. 1979; Kirkland 1979; Pagels et al. 1994; Parmley and Harley 1995). Because of their high metabolic rates shrews experience high rates of respiratory water loss, and may be unable to regulate such losses in xeric environments (Getz 1961).

In addition to metabolic regulation, moisture within the forest floor microhabitat is important in supporting a diverse and abundant assemblage of litter-dwelling invertebrate fauna (Gist and Crossley 1975; Kirkland 1991). Because invertebrates have been



positively associated with moist sites and shrews have been positively correlated with invertebrate abundance, both the direct and indirect effect of moist habitats has proven influential in determining overall shrew abundance and diversity (Churchfield 1990; Getz 2004).

Even though the overall trend in capture rate was an increase in rodents and decrease in insectivores, significant interannual variation was observed. Small mammal populations are regulated by several density dependent and independent factors, and often cycle in response to annual variation in precipitation, temperature and seasonal food availability (Hestbeck 1982, Sibley et al. 2005) . In an attempt to explain yearly variation, I looked at annual precipitation and temperature variation, and also for evidence of seasonal pulses in food crop availability. Annual rainfall and temperature may impact the availability of seasonal food crop production and insectivore abundance, as well as influence the activity and capture rate of animals. However, over the course of this study the average temperature remained constant from year to year and annual rainfall was consistently above normal during all sampling periods between the years of 2005-2007 ([www.nws.noaa.gov](http://www.nws.noaa.gov)). This suggests that local temperature and precipitation variation were not a significant factor influencing yearly fluctuation of population numbers in this study. However, local temperature and precipitation variation may have affected overall capture success and mortality rates. Animals may have been less mobile during periods of heavy rain and therefore less active during periods of trapping. Additionally, several pitfall traps flooded rendering them inactive or causing increased mortality. Although every attempt was made to increase shrew survival, the gradual

decline in numbers over the years may have resulted from stress- induced mortality during the previous year's sampling effort.

An important resource for rodents is the production of mast crop, a highly variable and cyclic resource. Oak (*Quercus spp.*) & hickory (*Carya spp.*) mast exerts significant impacts on animal communities, especially *P. leucopus* and *T. striatus*, which rely on mast crop as winter food (Healy 1997; Ivan and Swihart 2000; Elias et al. 2004). Competition for mast crop may also increase the interaction between rodents and deer (Ostfeld et al. 1996). Peak abundance for both *P. leucopus* and *T. striatus* is positively related to the previous year's mast production (Ostfeld et al. 1996; McShea 2000). However, *P. leucopus* and *T. striatus* are often in direct competition with deer for mast crop (Ostfeld et al. 1996; McShea 2000). The increase in relative abundance of rodent species, in areas of high deer impact, despite potential for direct competition between deer and rodents for mast crop (i.e. acorns) suggest competition was low between these species at the time of the study. Survey data across the state documented relatively high overall mast crop production (white and red oak) between the years of 2005-2007. On average 67% of red oak and 41% of white oak bore fruit between the years of 2005-2007 (Wildlife Population Status Report, ODNR, 2011). A slight decline of white oak production was seen during 2006 (Wildlife Population Status Report, ODNR, 2011), which may partially explain a decline in abundance for both *P. leucopus* and *T. striatus* between 2006 & 2007. However, the general trend toward high mast crop production throughout the duration of the study may indicate that direct competition between rodents and deer was low during this study.

## **Management Implications**

This study does not allow me to determine a cause and effect relationship between the browsing activities of deer and small mammal community dynamics; however, it does allow me to relate browsing intensity to small mammal community dynamics. Areas heavily impacted by deer support a less structurally complex forest floor microhabitat. These changes negatively impact insectivorous species, and reduced insectivorous species may relieve predation pressure on litter-dwelling arthropods thus altering trophic interactions on the forest floor. These results are important, as resource managers are increasingly interested in trophic interactions within forest ecosystems, moving away from species specific responses to browsing toward a more complete ecosystem management approach (Thomas 1994; Grumbine 1994, Fontaine 2011). Understanding how deer may potentially impact the species composition and abundance of local mammal communities may lead to a more complete understanding of the community dynamics within forest ecosystems. This understanding has important implications for invasive species management. Many species of small mammals are known to regulate the abundance and occurrence of invasive species outbreaks (Ostfeld et al. 1996), understanding how deer play a role in regulating these small mammal populations may lead to a more integrated ecosystem approach to regulating and mitigating the impact of invasive species.

## LITERATURE CITED

- Byman, D. (2011) The effects of deer exclosures on voles and shrews in two forest habitats. *Northeastern Naturalist* 18(4): 509-520.
- Churchfield, S. (1990) The natural history of shrews. Comstock Publishing Associates, Ithaca, N.Y.
- Elias, S. P., Witham, J. W., and Hunter, M. L., Jr. (2004) *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. *Journal of Mammalogy* 85(4), 743–747.
- Fontaine, J. J. (2011) Improving our legacy: Incorporation of adaptive management into state wildlife action plans. *Journal of Environmental Management*. 92(5), 403-1408.
- Flowerdew, J. R. and Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry* 74, 277-287.
- Fuller, R. J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanism. *Forestry* 74, 289-298.
- Fuller, A. K., Harrison, D. J., and Lachowski, H. J. (2004) Stand scale effects of partial harvesting and clearcutting on small mammals and forest structure. *Forest Ecology and Management* 191, 373–386.
- Gist, C. S. and Crossley, D. A., Jr. (1975) The litter arthropod community in a southern Appalachian hardwood forest: numbers, biomass and mineral element content. *The American Midland Naturalist* 93,107-122.
- Geier, A. R. and Best, L. B. (1980) Habitat selection by small mammals of riparian communities: evaluating effects of habitat relations. *Journal of Wildlife Management* 44, 16-24.
- George, S. B., Choate, J. R., and Genoways, H. H. (1986) *Blarina brevicauda*. *Mammalian Species* 261, 1–9.
- Getz, L. L. (1961) Factors influencing the local distribution of shrews. *American Midland Naturalist* 65, 67-88.
- Getz, L. L., Hofmann, J. E., McGuire, B. and Madan, K. (2004) Population dynamics of the northern short-tailed shrew, *Blarina brevicauda*: insight from a 25 year study. *Canadian Journal of Zoology* 82, 1679-1686.
- Grumbine, R. (1994) What is ecosystem management? *Conservation Biology* 8(1), 27-38.

- Healy, W. M. (1997) Influence of deer on the structure and composition of oak forests in central Massachusetts. Pp. 249–266, *In* W.J. McShea, H.B. Underwood, and J.H. Rap-pole (Eds.). *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington DC. 402 pp.
- Hestbeck, J. B. (1982) Population regulation of cyclic mammals: the social fence hypothesis. *Oikos* 39, 157–163.
- Ivan, J. S. and Swihart, R. K. (2000) Selection of mast by granivorous rodents of the central hardwood forest region. *Journal of Mammalogy* 81(2), 549-562.
- Kaminski, J. A., Davis, M. L., Kelly, M. and Keyser, P. D. (2007) Disturbance effects on small mammal species in a managed Appalachian forest. *American Midland Naturalist* 157, 285-297.
- Kirkland, G. L., Jr., and R. J. Griffin. (1974) Microdistribution of small mammals at the coniferous-deciduous forest ecotone in northern New York. *Journal of Mammalogy* 55, 417–427.
- Laerm, J., Ford, W. M., McCay, T. S., Menzel, M. A., Lepardo, L. T., and Boone, J. L. (1999) Soricid communities in the southern Appalachians. Pages 177-193 in R. O. Eckerlin, Ed. *Proceedings of the Appalachian biogeography symposium*. Virginia Museum of Natural History Special Publication No. 7.
- McCay, T. S., Laerm, J., Menzel, M. A., and Ford, W. M. (1998) Methods used to survey shrews (Insectivora: Soricidae) and the importance of forest-floor structure. *Brimleyana* 25, 110-119.
- McShea, W. J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 81(1), 228-238.
- Miller, D. H. and Getz, L. L. (1977) Factors influencing local distribution and species diversity of forest small mammals in New England. *Canadian Journal of Zoology* 55, 806-814.
- Otsfeld, R. S., Jones, C. G. and Wolff, J. O. (1996) Of mice and mast: ecological connections in eastern deciduous forests. *BioScience* 46, 323–30.
- Pagels, J. F., Uthus, K. L., and Duval, H. E. (1994) The masked shrew, *Sorex cinereus*, in a relictual habitat of the southern Appalachian Mountains. Pages 103-110 in J. F. Merritt, G. L. Kirkland, and R. K. Rose, eds. *Advances in the biology of shrews*. Carnegie Museum Natural History Special Publication 18.
- Parmley, D. and Harley, D. (1995) The relative seasonal abundance of shrews in two central Georgia deciduous woodlots. *Georgia Journal of Science* 53, 83-8.

- Pruitt, W. O., Jr. (1953) An analysis of some physical factors affecting the local distribution of the Shorttail Shrew (*Blarina brevicauda*) in the northern part of the Lower Peninsula of Michigan. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 79, 1–39.
- Putman, R. J. (1986) Foraging by roe deer in agricultural areas and impact on arable crops. *Journal of Applied Ecology*. 23, 91–99.
- Rooney, T. P. and Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181, 165-176.
- Sibly, R. M., Barker, D., Denham, M.C., Hone, J., and Pagel, M. (2005) On the regulation of populations of mammals, birds, fish, and insects. *Science* 309, 607– 610
- Smit, R., Bokdam, J., den Ouden, J., Olf, H., Schot-Opschoor, H., and Schrijver, M. (2001) Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology* 155, 119-127.
- Smolen, M. J. (1981) *Microtus pinetorum*. *Mammalian Species* 147, 1–7.
- Thomas, J. W. (1994) Trends in forest management in the United States. *The Forestry Chronicle* 70(5), 546-548.
- Urban, N. A. and Swihart, R. K. (2011) Small mammal responses to forest management for oak regeneration in southern Indiana. *Forest Ecology and Management* 261, 353-361.
- Underwood, H. B and Coffey, M. A. (1999) Evaluation of distance sampling for deer density estimation at Cuyahoga Valley National Recreation Area (CUVA): part II. National Park Service, Brecksville, Ohio, USA.
- Waller, D. M. and W. S. Alverson. (1997) The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25, 217–226.
- Wardle, D. A. (2002) *Communities and ecosystems: linking the aboveground and belowground components*. Princeton University Press, Princeton, New Jersey.
- Whitaker, J. O. (2004) *Sorex cinereus*. *Mammalian Species* 74, 1-9.
- Wrigley, R. E., Dubois, J. E., and Copland, H. W. R. (1979) Habitat abundance and distribution of six species of shrews in Manitoba, Canada. *Journal of Mammalogy* 60, 505-520.
- Yahner, R. H. (1982) Microhabitat use by small mammals in farmstead shelterbelts. *Journal of Mammalogy* 64, 440–445.

## CHAPTER VI

### HABITAT AND PREY ASSOCIATIONS FOR TWO SPECIES OF SHREW IN NORTHEAST OHIO

#### ABSTRACT

Previous research suggests shrew populations respond negatively to the indirect effect of browsing by deer on the habitat quality of the forest floor. This study aims to determine which factors, habitat or prey availability, are most important in determining the abundance of shrews. I approached this project from two different scales: 1) microhabitat, defined as the habitat immediately surrounding a trap site and 2) macrohabitat, defined as the collective quality of habitat across the broader study site over several years (2005-2007) including the availability of invertebrate prey. In general, traps successful in capturing shrews had a significantly deeper litter layer ( $U = 535.5$   $p \leq 0.001$ ), wetter soils ( $U = 815.5$ ,  $p = 0.028$ ) and more downed-woody debris (DWD), in terms of both number ( $U = 834.0$ ,  $p = 0.036$ ), volume ( $U = 796.5$ ,  $p = 0.019$ ), and proximity to trap site ( $U = 779.0$   $p = 0.014$ ) compared to non-successful trap sites. Spearman's correlation analysis suggests total capture rate was positively correlated with average leaf litter depth across the larger macrohabitat for both *Blarina* ( $r_s = 0.786$ ,  $p = 0.036$ ) and *Sorex* ( $r_s = 0.750$ ,  $p = 0.052$ ). No relationship was found between overall

shrew capture rate and invertebrate abundance (*Blarina*,  $r_s = -0.107$ ,  $p = 0.819$ ; *Sorex*,  $r_s = 0.464$ ,  $p = 0.294$ ) or biomass (*Blarina*,  $r_s = 0.36$ ,  $p = 0.939$ ; *Sorex*,  $r_s = 0.286$ ,  $p = 0.535$ ). However, a significant relationship between invertebrate biomass in 2006 and *Sorex* abundance in 2007 ( $r_s = 0.852$ ,  $p = 0.015$ ) was observed, suggesting that previous years prey availability influenced reproductive success and/or overwintering ability, and therefore, higher numbers in subsequent years. The structural composition of the forest microhabitat is more important in determining soricid presence than the overall characterization of the macro-habitat and abundance of invertebrate prey.

## INTRODUCTION

Across much of Northeast Ohio, the browsing activities of overabundant deer populations have altered forest habitat, potentially threatening species diversity and abundance of small mammals. Particularly vulnerable to the threats of deer browsing are the masked (*Sorex cinereus*) and short-tailed shrews (*Blarina brevicauda*; see Chapter 5). *Sorex cinereus* and *B. brevicauda* are common species belonging to the family Soricidae and found in the forests of Northeast Ohio. They prefer mesic forest habitats with considerable structural microhabitat and adequate vegetation cover (Yahner 1982; Getz 1961; Mitchell et al. 1997; McCay et al. 1998; Brannon 2000). Canopy and understory vegetation supplies the forest floor microhabitat with leaf litter, which provides protective cover from predators, supports a diverse and abundant prey base, and helps to mediate moisture and humidity levels within the forest microhabitat (Getz 1961; Pagels et al. 1994; McCay et al. 1998; Laerm et al. 1999). Environmental moisture is also important in determining the distribution of shrews (Spencer and Pettus 1966; Wrigley et al. 1979; Kirkland 1979; Pagels et al. 1994; Parmley and Harley 1995). Shrews experience



relatively high respiratory water loss because of their high metabolism and may be unable to regulate such losses in xeric environments (Getz 1961).

Habitat moisture is also likely to have an indirect effect on shrews by influencing the abundance and behavior of invertebrate prey (Getz 1961; Wrigley et al. 1979; Churchfield 1990; McCay and Storm 1997). Many litter-dwelling invertebrates are influenced by environmental moisture, which may not simply affect their presence or absence in an area but also their distribution within the litter profile and thus their availability to shrews (Churchfield 1990; McCay and Storm 1997; Tauber et al. 1998; Getz 2004; Jabin et al. 2004). Shrews are opportunistic predators that feed on a variety of common litter-dwelling invertebrates, particularly beetles, earthworms, isopods, spiders and insect larvae. However, shrews may show preference or specialization based upon prey type, size or availability (Getz 1961; McCay and Storm 1997). For example, isopods are a common prey choice for many shrew species, but species belonging to the isopod genus *Armadillidium* are rarely eaten because of their thick exoskeleton (Churchfield 1990). Additionally, millipedes, which are among the most common large invertebrates on the forest-floor, are rarely eaten because they secrete distasteful and noxious substances (Churchfield 1990; McCay and Storm 1997).

In a study on the effects of forest floor microhabitat and invertebrate abundance on the distribution and abundance of *B. brevicauda* and *S. cinereus*, Getz (1961) found food availability to be the most important factor determining the distribution of these shrews. Moreover, the availability of food was largely determined by moisture and vegetative cover. Getz found that both *B. brevicauda* and *S. cinereus* avoided dry upland sites in favor of more moist sites with abundant invertebrate food resources. Because

invertebrates have been positively associated with moist sites and shrews have been positively correlated with invertebrate abundance, it follows that both direct and indirect effects of moist habitats influences Soricid abundance and diversity (Churchfield 1990; McCay and Storm 1997; Getz 2004).

This study aims to define associations between habitat quality and the abundance of shrews. I approached this aim at two different scales: 1) microhabitat, defined as the habitat immediately surrounding a trap site and 2) macro-habitat, defined as the collective quality of habitat across the broader study site over several years (2005-2007) including food availability. At the microhabitat scale, I hypothesize an increase in shrew capture rate in areas with available refugia defined as sites with increased soil moisture, leaf litter accumulation, downed woody debris and understory cover. At the macro-habitat scale, I predict an increase in the presence of shrews at sites characterized by increased leaf litter and herbaceous cover supported by more abundant invertebrate populations.

Understanding the relationship between shrew populations, habitat preference and invertebrate abundance will help provide insight to the larger question at hand: how do the browsing activities of deer indirectly influence the faunal diversity of the forest floor?

## METHODS

I used a series of replicated Sherman live and pitfall trap grids to estimate population size and small mammal diversity at each field site using mark-recapture techniques. I established a 7 X 7 grid of Sherman live traps (7.5 x 9.0 x 23.0 cm, H.B. Sherman Trap, Inc.) consisting of 49 trapping stations (two traps per station) placed at 10-m intervals to target larger rodent species active on the forest floor. I used two baited traps at each station to increase capture probability by preventing trap saturation from “trap happy”

animals. Prior to each trapping session, all Sherman traps were locked open and pre-baited with oats and carrot slices for 36 hrs. A simple bait of oats and carrot were used instead of the traditional peanut butter and oats due to the high rate of raccoons tampering with traps. In addition, I established a 4 x 5 grid of pitfall arrays at each site targeting smaller insectivorous species foraging on the forest floor. Each pit-fall grid consisted of 20 pitfall arrays (4 rows of 5 arrays placed at 25-m intervals totaling 120 pitfalls) where each array was composed of 6 pitfall traps (6.4 liter buckets) arranged in a Y-formation connected by a drift fence. A drift fence was used to help guide animals foraging in the leaf litter into each trap. Each drift fence was partially buried within the soil/leaf litter layer to prevent animals from burrowing beneath the drift fence to increase trap effectiveness. During periods of non-trapping each pitfall was filed with leaf litter and twigs and covered with a wood cover to prevent unwanted captures and decrease trap mortality. During periods of trapping each pitfall was cleaned out and covers raised to 10 cm above the ground to protect captured animals from sun and rain and help discourage predation.

All traps (Sherman and pitfall) were active for 2 four-night sessions separated by a 12-14 day period of no trapping from May through September in 2005 and for 3 four-night sessions separated by 12-14 days of no trapping during the 2006 & 2007 field seasons. Because shrews have a high metabolism and require a constant supply of food, each pitfall trap was checked frequently, every two-four hours, and supplied with an adequate food supply (local insects) between check points to increase survival rates of captures.

Each animal captured was identified to species, weighed, measured and marked before release back into the population. Because shrews lack external ear features, numbered ear tags could not be used; instead we used a combination of permanent ink marks and pink, blue, yellow or green fluorescent powder to mark these species. Each mark was assumed to last for the duration of each trapping session. Upon recapture each animal was examined for an existing mark or scanned with a black light for evidence of fluorescent powder. All trapping and handling procedures were approved by the Cleveland State University Animal Care and Use Committee (IACUC # is 2601-WAL-AS).

Data on a suite of microhabitat variables were collected at each successful and non-successful trap during the 2007 field season. A successful trap was defined as a Sherman or pitfall trap, which was successful in trapping *Sorex* or *Blarina*, while a non-successful trap had never captured a shrew between the years of 2005-2007. Each non-successful trap site was chosen at random from a list of trap locations that had never previously captured a shrew. Immediately following capture, data were collected at each successful and corresponding non-successful trap site. A 1-m circular sampling frame was centered over each trap site to estimate percent ground and herbaceous cover and measure leaf litter depth, % soil moisture and soil pH. I visually estimated ground cover including, % herbaceous cover, % leaf litter cover and % cover of downed woody debris (DWD). I counted number of seedlings ( $\leq 15$  cm in height) and saplings (trunk DBH  $< 10$ cm) and mature trees within each sampling frame. Percent canopy cover was estimated using a spherical crown densiometer at the center of each circular plot. Estimates of canopy cover were taken in each of the four cardinal directions at the center of each sampling

grid and averaged to come up with an overall estimate for each sampling frame. Measurements on leaf litter depth to the nearest 0.5 cm and soil moisture using a Kelway® soil pH and moisture meter (at 15cm depth) were also collected at 4 points along the perimeter of each sampling grid. In addition, the amount and decay state of downed woody debris (DWD) was estimated using line-transect method. Two 10-m transects placed along the north-south and east-west axis centered over each successful and non-successful trap site were used to estimate total amount and size of DWD. The length and width of any DWD  $\geq 10$ cm in diameter touching the transect line were recorded as well as the decay class. Decay class was estimated based on a 6 point scale: 1) freshly fallen, 2) slight decay, 3) moderate decay, 4) slight fragmentation, 5) heavy fragmentation, and 6) complete decomposition (Maser et al. 1979). Distance of downed wood to trap site was also measured to the nearest centimeter. These measurements were then used to estimate total volume and mean decay state of DWD within close proximity to trap sites. Similar habitat data were collected across each site the 2005-2007 field season to evaluate habitat across a broader macro-habitat scale (see Chapter 2).

Invertebrates were sampled by pitfall trapping three times, June, August & October, between the years of 2006-2007. Twenty nine pitfall traps (16 oz double stacked plastic cups) were placed at each field site; 9 were overlaid within the 7 X 7 Sherman trap grid at 20 m intervals and 20 were interspersed with the 4 X 5 grid of pitfall arrays (1 in the center of each pitfall array). After a 36 hr sampling period all invertebrates were collected and transferred to a vial containing 70% ethanol. All sampled invertebrates were separated from ethanol by filtration and identified to order or further if possible. Analyses of individual taxa were then confined to those taxa accounting for  $\geq 1$  % of the

total invertebrates collected. This resulted in a total of 14 orders and one morphogroup (larvae) being analyzed including: Acari, Araneae, Chilopoda, Coleoptera, Collembola, Diplopoda, Diptera Hemiptera, Hymenoptera, Isopoda, Oligocheata, Opiliones, Orthoptera, Pseudoscorpiones, and Thysanoptera. Once identified all invertebrates were sorted by taxa and placed in a drying oven for 36 hrs to obtain data on biomass of available prey items for shrews.

### **Statistical analyses**

The Mann-Whitney *U*-test was used to determine differences in microhabitat between successful and non-successful trap sites. Shrew abundance was determined by calculating overall capture rate; this accounts for sprung traps and differences in trapping effort across sites. To adjust for differences in trapping effort I standardized the data using a trap-night index or number of animals captured per 100 trap-nights. A trap-night was calculated as the number of traps open per 24-hour period. The relationship between *Blarina* and *Sorex* capture rate and available microhabitat were examined using Spearman's correlation coefficient ( $r_s$ ). Spearman's correlation coefficient was also used to identify any relationship between overall capture rate and invertebrate abundance and biomass. Because fecundity often depends on the previous year's food crop, Spearman's correlation coefficient was also used to determine any relationship between shrew abundance and the previous year's food availability in terms of invertebrate abundance and biomass.

### **RESULTS**

A total of 89 (70 *Blarina* and 19 *Sorex*) shrews were caught at 47 trap sites across all field sites in 2007. Thirty-six trap sites were successful at capturing *Blarina* and 11 trap

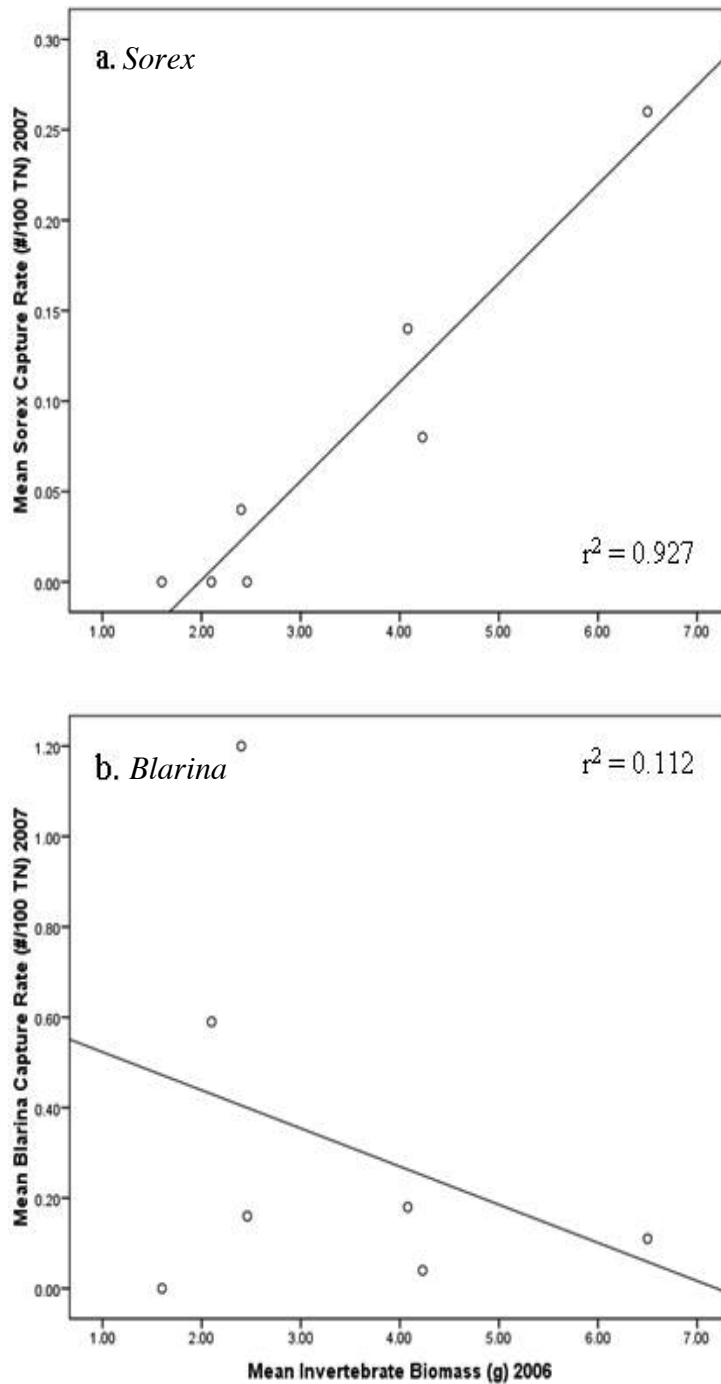
sites were successful at capturing *Sorex*. In general, traps successful in capturing shrews had a significantly deeper litter layer ( $U = 535.5$ ,  $p \leq 0.001$ ), wetter soils ( $U = 815.5$ ,  $p = 0.028$ ) and more DWD, in terms of both number ( $U = 834.0$ ,  $p = 0.036$ ) and volume ( $U = 796.5$ ,  $p = 0.019$ ), and DWD was closer to the trap site ( $U = 779.0$ ,  $p = 0.014$ ) compared to non-successful trap sites (Table 6.1). *Sorex* tended to be caught more often at traps with greater litter depth ( $U = 29.0$ ,  $p = 0.038$ ) and number of DWD ( $U = 26.0$ ,  $p = 0.016$ ), while *Blarina* were caught more often at traps with greater litter depth ( $U = 304.5$ ,  $p \leq 0.001$ ), increased soil moisture ( $U = 447$ ,  $p = 0.023$ ) and at traps located closer to DWD ( $U = 421.5$ ,  $p = 0.01$ ). Spearman's correlation analysis suggests total capture rate was positively correlated with average leaf litter depth across the larger macrohabitat for both *Blarina* ( $r_s = 0.786$ ,  $p = 0.036$ ) and *Sorex* ( $r_s = 0.750$ ,  $p = 0.052$ ). No relationship was found between overall shrew capture rate and invertebrate abundance (*Blarina*,  $r_s = 0.107$ ,  $p = 0.819$ ; *Sorex*,  $r_s = 0.464$ ,  $p = 0.294$ ) or biomass (*Blarina*,  $r_s = 0.36$ ,  $p = 0.939$ ; *Sorex*,  $r_s = 0.286$ ,  $p = 0.535$ ).

However, a significant relationship between invertebrate biomass in 2006 and *Sorex* abundance in 2007 ( $r_s = 0.852$ ,  $p = 0.015$ ; Figure 6.1a) was observed, suggesting that previous years prey availability influenced reproductive success and/or overwintering ability, and, therefore, higher numbers in subsequent years. No significant relationship between the invertebrate biomass in the previous and subsequent year abundance of *Blarina* was observed ( $r_s = -0.143$ ,  $p = 0.76$ ; Figure 6.1b).

**Table 6.1. Microhabitat variables measured at successful and non-successful traps.** Microhabitat variables measured at all successful and non-successful (n = 47) soricid trap sites across seven field sites in 2007.

Habitat Variable	Mean (+/- SE)		Mann-Whitney U-Test	
	Successful	Non-Successful	U	p
<i>Ground Cover (%)</i>				
Leaf Litter	48 (6.8)	84 (2.4)	1022	0.519
Bare Ground	.24 (.23)	.85 (2.39)	1057.5	0.401
Herbaceous	3.5 (1.7)	2 (1.1)	1046.5	0.503
<i>Downed Woody Debris</i>				
Distance to trap (m)	3.3 (.28)	4.21 (.55)	779	0.014
Volume (m <sup>3</sup> )	53.98 (5.7)	53.76 (10.3)	796.5	0.019
Number	2.1 (1.4)	1.5 (1.3)	834	0.036
Length (m)	11.4 (.73)	11.94 (1.68)	1010.5	0.476
Decay State	2	2	927.5	0.174
Canopy Cover (%)	86 (2.08)	85 (2.05)	1021.5	0.528
Leaf Litter Depth (cm)	3.15 (.16)	2.13 (.20)	535.5	≤ 0.001
Soil Moisture (%)	51 (3.8)	42 (.55)	815.5	0.028





**Figure 6.1 Relationship between soricid captures and invertebrate biomass.** Linear relationship between mean soricid captures rates in 2007 across seven field sites within the Cleveland Metroparks and Cuyahoga National Park and available invertebrate biomass in 2006, estimated using pitfall traps.

## DISCUSSION

The structural composition of the forest microhabitat is more important in determining soricid presence than the overall characterization of the macro-habitat and abundance of invertebrate prey. In general, shrews preferred sites characterized by deep litter, moist soils and high density of DWD, and these variables were more influential in determining the presence of shrews than availability of invertebrate prey. The observed correlation between shrew presence and microhabitat, specifically DWD, are consistent with other studies (Bellows et al. 2001). Downed woody debris not only provides a refuge for invertebrates but also travel routes, important for protection from predators (Miller and Getz 1977). In addition, DWD traps environmental moisture (Morris 1984; Carey and Johnson 1995) and promotes hydric conditions necessary to maintain homeostasis between shrews and their environment (Churchfield 1990; Bellows et al. 2001).

Although DWD plays an important role in the presence of both *Sorex* and *Blarina*, the distance between DWD and capture sites was more important for the capture of *Blarina* than for *Sorex*, whereas the number of available DWD was more important for *Sorex*. Because *Blarina* is nearly 3 times larger than *Sorex*, and presumably more easily detected by predators, proximity to cover may be more important in determining travel routes within a larger habitat than it is for *Sorex*. On the other hand, the smaller more cryptic *Sorex* may be less influenced by the proximity to DWD, relying instead upon simple availability of adequate cover within the larger habitat.

The lack of obvious correlation between shrews and invertebrate abundance should not be overlooked in this study. Interestingly, the abundance of *Sorex* in 2007 was related to biomass of invertebrates in the preceding year. This correlation suggests that

the abundance of food influences overwintering success and, therefore, the number of reproductive animals entering the population the following spring. Northern climate shrews, such as *Sorex* and *Blarina*, overwinter as immatures and remain active overwinter while undergoing sexual maturation (Pasanen and Hyvarinen 1970; Churchfield 1981). Merritt (1986) has shown an increased rate of thermogenesis, basal and resting metabolic rates as well as increased brown fat deposits (Churchfield 1981) in these species during the winter months. These energetically demanding physiological changes, necessary for winter survival, require ample food resources prior to the onset of winter. Therefore, food availability is an essential component of annual recruitment and as such affect estimates of population density and abundance. These constraints may be especially significant for *Sorex* which, because of its smaller size, has a mass-specific basal metabolic rate nearly three-times that of *Blarina* (Tacutu et al. 2013). Indeed, the genus *Sorex* is noted for having exceptionally high metabolic rate, but low capacity for energy reserves, making them particularly vulnerable to starvation (Crowcroft 1954; Vogel 1976).

### **Management Implications**

A clearer understanding of habitat selection criteria of small mammal communities, specifically soricids, across disturbed landscapes reveals conservation and management strategies useful to land managers. Soricids have the potential to serve as bio-indicators of habitat quality as their ecophysiology requires specific microhabitat conditions to sustain daily activities. Evaluating what drives local soricid population dynamics is complex; however data presented here suggests that the availability of adequate microhabitat both directly and indirectly impact the presence of soricids. Maintaining a

mosaic of adequate forest floor microhabitat within and across a larger landscape may help mitigate larger scale disturbances, such as deer over-browsing, and can be easily incorporated into existing management efforts, such as promoting increased herbaceous cover, and incorporating fallen or felled logs and limbs across the landscape.

## LITERATURE CITED

- Brannon, M. P. (2000) Niche relationships of two syntopic species of shrews, *Sorex fumeus* and *S. cinereus*, in the southern Appalachian Mountains. *Journal of Mammalogy* 81, 1053–1061.
- Bellow, A. S, Pagels, J. F., and Mitchell, J. G. (2001) Macrohabitat and microhabitat affinities of small mammals in fragmented landscape on the upper coastal plain of Virginia. *American Midland Naturalist* 146, 345-360.
- Carey, A. B., Johnson, M. L. (1995) Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* 5, 336–352.
- Churchfield, S. (1990) *The natural history of shrews*. Comstock Publishing Associates, Ithaca, N.Y.
- Churchfield, S. (1981) Water and fat contents of British shrews and their role in the seasonal changes in body weight. *Journal of Zoology* 194, 165-173.
- Crowcroft, P. (1954) *An ecological study of British Shrews*. Dissertation. University of Oxford.
- Getz, L. L. (1961) Factors influencing the local distribution of shrews. *American Midland Naturalist* 65, 67-88.
- Getz, L. L., Hofmann, J. E., McGuire, B. and Madan, K. (2004) Population dynamics of the northern short-tailed shrew, *Blarina brevicauda*: insight from a 25 year study. *Canadian Journal of Zoology* (82), 1679-1686.
- Jabin, M., D. Mohr, H. Kappes, and W. Topp. (2004) Influence of deadwood on density of soil macro-arthropods in a managed oak beech forest. *Forest Ecology and Management* 194, 61-69.
- Kirkland, G. L., Jr., and R. J. Griffin. (1974) Microdistribution of small mammals at the coniferous-deciduous forest ecotone in northern New York. *Journal of Mammalogy* 55, 417–427.
- Laerm, J., Ford, W. M., McCay, T. S., Menzel, M. A., Lepardo, L. T., and Boone, J. L. (1999) Soricid communities in the southern Appalachians. Pages 177-193 in R. O. Eckerlin, Ed. *Proceedings of the Appalachian biogeography symposium*. Virginia Museum of Natural History Special Publication No. 7.
- Maser, C., Anderson, R. G., Cromack Jr., K., Williams, J. T., Martin, R. E. (1979) Dead and downed woody material. In: Thomas, J.W.(Ed.), *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington*. USDA Forest Service Agricultural Handbook No. 553, pp. 78-95.

- McCay, T. S., Laerm, J., Menzel, M. A., and Ford, W. M. (1998) Methods used to survey shrews (Insectivora: Soricidae) and the importance of forest-floor structure. *Brimleyana* 25, 110-119.
- McCay, T. S. and Storm, G. L., (1997) Masked shrew (*Sorex cinereus*) abundance, diet and prey selection in an irrigated forest. *American Midland Naturalist* 38: 268–275.
- Merritt, J. (1986) Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*) in an Appalachian montane forest, USA. *Journal of Mammalogy* 67, 450-464.
- Miller, D. H. and Getz, L. L. (1977) Factors influencing the local distribution and species diversity of forest small mammals in New England. *Canadian Journal of Zoology* 55, 806–814.
- Mitchell, J. C., Rinehard, S. C., Pagels, J. F., Buhlman, K. A., and Pague, C. A. (1997) Factors influencing amphibian and small mammal assemblages in central Appalachians forests. *Forestry and Ecological Management* 96, 65-76.
- Morris, D. W. (1984) Patterns and scale of habitat use in two temperate-zone, small mammal faunas. *Canadian Journal of Zoology* 62, 1540-1547.
- Pagels, J. F., Uthus, K. L., and Duval, H. E. (1994) The masked shrew, *Sorex cinereus*, in a relictual habitat of the southern Appalachian Mountains. Pages 103-110 in J. F. Merritt, G. L. Kirkland, and R. K. Rose, eds. *Advances in the biology of shrews*. Carnegie Museum Natural History Special Publication 18.
- Parmley, D. and Harley, D. (1995) The relative seasonal abundance of shrews in two central Georgia deciduous woodlots. *Georgia Journal of Science* 53, 83-8.
- Pasanen, S and Hyvarinen, H. (1970) Seasonal variation in the activity of phosphorylase in the interscapular brown fat of small mammals active in winter. *Aquilo Series Zoologica* 10, 37-42.
- Tauber, M. J., Tauber, C.A., Nyrop, J. P., and Villani, M.G. (1998) Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and test mechanisms. *Environmental Entomology* 27, 523-530.
- Tacutu, R., Craig, T., Budovsky, A., Wuttke, D., Lehmann, G., Taranukha, D., Costa, J., Fraifeld, V. E., de Magalhaes, J. P. (2013) "Human Ageing Genomic Resources: Integrated databases and tools for the biology and genetics of ageing." *Nucleic Acids Research* 41(1), 1027–1033
- Vogel, P. (1976) Energy consumption of European and African shrews. *Acta Theriologica* 21,195-206.

Wrigley, R. E., Dubois, J. E., and Copland, H. W. R. (1979) Habitat abundance and distribution of six species of shrews in Manitoba, Canada. *Journal of Mammalogy* 60, 505-520.

Yahner, R. H. (1982) Microhabitat use by small mammals in farmstead shelterbelts. *Journal of Mammalogy* 64, 440-445.

## CHAPTER VII

### CONCLUDING REMARKS AND MANAGEMENT RECOMMENDATIONS

#### **Summary**

Deer are keystone species. This implies that the selective foraging behavior of deer, together with other activities, may contribute to a cascade of effects upon multiple taxonomic levels within forest ecosystems.

I have clearly shown that differential foraging at various spatial scales reduces the structural complexity of the forest floor and have laid out mechanisms by which these changes may indirectly affect litter-dwelling arthropods and small mammals. These changes, threaten the future trajectory of forest succession, and when coupled with biological invasions and global climate change may lead to alterations in associated communities and ecosystem properties (Horsley and Marquis 1983; Stromyer and Warren 1997; Augustine et al. 1998b; Cote et al. 2004; Wardle and Bardgett 2004; Harrison and Bardgett 2008, Martin et al. 2010).

The expected response of decreased overall arthropod abundance in areas heavily impacted by deer was not evident. However, community composition differed as a result of browsing intensity. Several major litter-dwelling arthropod taxa varied substantially with deer impact (such as Carabidae and Araneae) indicating that deer may have



important effects upon species interactions and ecological functions mediated by those taxa of invertebrates. Of the taxa examined here, carabid beetles responded most to the indirect effects of browsing by deer at both small (exclosure study) and large (comparative study) spatial scales. Carabid beetles are a relatively abundant ecologically diverse group of taxa filling multiple niches on the forest floor and, as such, have been considered by some to be important ecological indicators of overall ecosystem health and functioning (Niemela 2001; Rainio and Niemela 2003; see also Work et al. 2008). The finding of more carabid beetles, in more structurally diverse habitats suggests the browsing activities of deer indirectly impact this ecologically important group of arthropods. Another notable community level shift in response to browsing is the shift towards more non-native arthropods in areas heavily impacted by deer. As suggested by the invasional meltdown hypothesis (Simberloff and Von Holle 1999), selective browsing and the associated changes in habitat may facilitate and support invasion of other non-native and invasive taxa. This effect, only observed across broad spatial scales, implies that local, intact pockets of habitat can still persist within otherwise degraded habitats, and therefore may serve as refugia to native species. This has important ecological implications as invasion by non-native species are among the most important global-scale problems facing natural ecosystems today (Vitousek 1990; Vitousek et al. 1996; Mack 2000; Walker and Steffen 1997).

This research also suggests an indirect relationship between the effects of browsing by deer and small mammal community composition. Again, as for invertebrates, the effect was upon species composition, rather than overall abundance. As expected, insectivorous small mammals, which are noted for sensitivity to changes within the forest floor

microhabitat, responded negatively to the indirect effects of browsing. This shift in community composition is important because the activities of these species increase the functional diversity of ecosystems; they serve as a vital prey base for many species including raptors, reptiles and other mammals, and play a key role in forest floor food webs. By regulating the abundance and species composition of other litter-dwelling arthropods, insectivorous small mammals may indirectly affect the detrital food web, altering nutrient cycling regimes; or further facilitate the invasion of non-native invasive species.

The comparative nature of this study makes it difficult to infer cause and effect relationships between the browsing activities of deer and the taxonomic diversity of ecologically important groups present on the forest floor. As a result, caution is necessary in the interpretation of this study. Confounding factors such as site history, location, and productivity may influence how measured response variables respond to browsing pressures. Differential past and present browsing pressure as well as local variability in foraging behavior among sites may also contribute to variability in response variables. Combined with local species richness and diversity the above-mentioned factors define the capacity of a site to respond to over-browsing and may determine the trajectory a site may take in response over-browsing. One such example of how variability among sites may alter the impact of deer on forest ecosystem dynamics is the presence of non-native earthworms. Most previously glaciated regions across North America lacked earthworms prior to European settlement, and earthworms of both European and Asian origin are now rapidly invading these forests (Bohlen et al. 2004). This recent and widespread invasion of non-native earthworms across the northern forests

of North America has raised concern from ecologists regarding the preservation biodiversity. Earthworms are ecosystem engineers; their feeding and burrowing activities incorporate leaf litter biomass into the soil, altering soil chemistry, mixing soil layers altering nutrient cycling and retention, and changing plant communities on earthworm invaded sites (Bohlen et al. 2004; Hale 2005). Recent research suggests that earthworm activity has led to a loss of native plant species diversity and an increase in leaf litter decomposition, ultimately altering soil structure and nutrient availability leading to drier, xeric soils (Hale et al. 2004; Hale et al. 2008; Holdsworth et al. 2007). Additionally, these activities disrupt seedling establishment and contribute to widespread recruitment failure (Hale et al. 2004; Hale et al. 2008; Holdsworth et al. 2007).

Invasion by earthworms has been documented at each field site in this study and mean earthworm density did not differ in areas of high and low impact (S. Laux, unpublished data; Table 7.1). Their presence is assumed to have contributed to the overall quality and quantity of the forest floor microhabitat habitat, specifically, leaf litter cover and seedling density at these sites. Because both earthworms and deer are important ecosystem engineers, it is important to recognize the potential synergistic interaction between earthworm invasions and the browsing activities by deer. Earthworm invasion in conjunction with over-browsing by deer may facilitate invasions of other exotic species such as European slugs and exotic plants such as buckthorn and garlic mustard (Bohlen et al. 2004). Because deer preferentially feed on plant species most impacted by earthworms, the impact of deer on understory plants is proportionately greater in areas invaded by earthworms (Bohlen et al. 2004). This implies management of deer at

densities appropriate for areas without earthworms may not be sufficient enough to prevent habitat damage in areas invaded by earthworms.

<b>Table 7.1 Mean earthworm density.</b> Mean density (+/- SE) by site and deer impact. Earthworms were collected using hot mustard extraction in 2008. Taxa collected by genus include: Lumbricus, Aporetodea, Octocasion, Amyntus, Allolobophora and Dendrobaena. Differences between areas of high and low deer impact were non-significant ( $t = -0.17$ , $p = 0.44$ )	
	<b>Mean Earthworm Density (#/m<sup>2</sup>)</b>
<b>High Impact</b>	
RR	40.0 (9.7)
OP	20.4 (11.0)
RV	128.9 (23.4)
NC	19.6 (5.6)
<b>Overall Mean</b>	<b>52.0 (26.0)</b>
<b>Low Impact</b>	
BW	18.7 (7.3)
H1	33.5 (8.6)
H2	122.4 (28.5)
<b>Overall Mean</b>	<b>56.1 (33.0)</b>

## **Management Recommendations**

In recent decades, resource managers have shifted away from species-specific management to a more ecosystem based approach when it comes to deer management (Overbay 1992; Grumbine 1994; deCalesta and Stout 1997; Thomas 1994; Putman et al. 2011). Ecosystem based management can broadly be defined as the integration of scientific knowledge of ecological relationships within a complex sociopolitical framework toward the goal of protecting native ecosystem integrity over the long-term (Grumbine 1994). Understanding the underlying mechanisms behind which deer indirectly affect ecologically important taxa, is essential for the future management both deer and forest ecosystems.

Moving past species-specific management goals, i.e. managing deer numbers to benefit hunters or the timber industry, and towards a more integrated goal of managing ecosystems by mitigating the response of organisms to the impacts of deer will provide a more comprehensive and effective means to protect our resources. Obtaining reliable estimates of deer densities or abundance from which ‘threshold’ density are determined are difficult and may provide misleading information. Even though deer are large highly visible animals they are also highly mobile and their ability to adapt to human dominated landscapes allow them to change behaviors in different areas depending on both the biotic and abiotic surroundings of their habitat. For example, if a few deer spend much of their time browsing in one localized area they may cause more habitat damage than many deer browsing intermittently across a landscape. Additionally, because deer may preferentially browse on local landscaping or agricultural crops (Seagle 1999) it can be assumed that areas estimated to support high deer densities but surrounded by suburban

landscapes or agricultural fields may experience less of a negative impact on ecological resources than areas surrounded by natural habitat. This makes it hard to apply universal conditions or assumptions about deer browsing activities and their impact on local ecological resources. Therefore, densities estimates alone are unlikely to be good predictors of the impact of deer on their environment and recent studies suggest estimates of deer density poorly correlate with the impacts sustained within an ecosystem (Augustine et al. 1998b; Illius 2004; Putman et al. 2011). Furthermore, many researchers have proposed abandoning the use of ‘threshold’ densities below which ecological assessments and management decisions are be made (deCalesta and Stout 1997; Morellet et al. 2007; Tierney et al. 2009; Putman et al. 2011). More appropriately, the goal of management should be to assess impacts to forest ecosystems sustained as a result of over-browsing and gage success in terms of ecological function (Morellet et al. 2007; Putman et al. 2011). I propose integrating the response by a suite of ecologically important taxa, indirectly associated with the browsing activities of deer, as a tool to help guide management discussions. Rather than abandoning the use of ‘threshold’ densities, I suggest managers continue to monitor deer numbers, not as a goal to management, but as a means to learn more about the relationship between browse intensity and local ecosystem response. This approach, however, will not be successful without adequate behavioral information on local deer herds and surrounding habitat and land-use patterns.

As with any management regime, clear and concise objectives need to be outlined to ensure effective and successful management of forest ecosystems. I propose the following guidelines when integrating the use of ecological response variables to deer management.

1) Set clearly defined management goals and objectives. Is the goal to control deer numbers or deer impacts? The answer may impact your approach to monitoring and managing deer. Further, unclear or vague goals and objectives can lead to inappropriate response variables being measured at inappropriate spatial and temporal scales with poor precision or reliability.

2) Clearly define and interpret the impact. Identifying the consequences of the perceived impact will help managers determine what level of impact is acceptable from both an ecological and human perspective.

3) Identify the scale at which to gauge the impact. Is the goal to maintain or restore local reservoirs of native species diversity within the context of a larger fragmented landscape—such as Cleveland Metroparks, or is the goal to abandon small-scale restoration and focus more on large-scale impacts.

4) Identify clear and obtainable methods by which to gauge success. These methods may vary depending at what temporal scale management is based. Will success be determined over the short-term, i.e. shifts in annual small mammal population dynamics or over the long-term, i.e. monitoring seedling recruitment and the trajectory of forest succession or monitoring trends in arthropods diversity as it pertains to important ecosystem services such as pollination or trophic interactions within detrital food webs?

Monitoring shifts in species composition of select forest floor species, dependent on the structural complexity of the forest floor and indirectly associated with the browsing activities of deer, as a means to guide management decisions will take time and continued research. Over the short-term, I suggest that resource managers continue to improve the structural complexity of the forest microhabitat by retaining downed wood near trails and

park structures and enforcing no mow zones near forest edges to further promote the development of a forest understory and herbaceous layer. The continued monitoring and management of biological invasions is also critical to successfully manage the impacts of deer. Over the long-term, I recommend initiating behavioral studies of deer foraging behavior and habitat use patterns across a wide spectrum of habitats available within and surrounding Cleveland Metroparks. Designing a study with the objective to learn more about how deer utilize habitat across space and time, will provide managers with the missing link of ‘how’ deer impact habitat and if these impacts can be predicted by deer numbers alone or if data on local spatial and temporal deer behavior are more predictive when trying to manage for the affects of deer. No matter the goal of management—decrease human impact, reduce plant damage, maintenance of healthy herds, or the preservation of biological diversity and ecological integrity—confounding factors such as earthworms, plant species composition, ratios of native vs. non-native species, differential habitat use and human impact in surrounding areas need to be considered to effectively manage ecosystems to minimize the negative effects of deer.



## LITERATURE CITED

- Alverson, W. S., Waller, D. M., and Solheim, S. I. (1988) Forest too deer: edge effects in northern Wisconsin. *Conservation Biology* 2, 348-358.
- Ammer, C. (1996) Impacts of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *Forest Ecology and Management* 88, 43-53.
- Augustine, D. J., and Frelich, L. E. (1998) Effects of white-tailed deer on populations of an understory forb in fragmented forests. *Conservation Biology* 12, 995-1004.
- Augustine, D. J. and McNaughton, S. J. (1998a) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62, 1165-1183.
- Augustine, D. J., Frelich, L. E., and Jordon, P. A. (1998b) Evidence for two alternative stable states in an ungulate grazing system. *Journal of Applied Ecology* 8, 1260-1269.
- Baines, D., Sage, R. B., and Baines, M. M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology* 31, 776-783.
- Bargett, R. D. and Wardle, D. A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84(9), 2258-2268.
- Bergstrom, R. and Edenuis, L. (2003) From twigs to landscapes—methods for studying the ecological effects of forest ungulates. *Journal for Nature Conservation* 10, 203-211.
- Bohlen, P. J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P. M., and Parkinson, D. (2004) Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment* 2(8), 427-435.
- Bultman, T. L. and Uetz, G. W. (1982) Abundance and community structure of forest floor spider communities following litter manipulation. *Oecologia* 55, 34-41.
- Côté, S. D., Rooney, T. P., Tremblay, J., Dussault, C., and Waller, D. M. (2004) Ecological impact of deer overabundance. *Annual Review of Ecology and Systematics* 35, 113-147.
- deCalesta, D. S. and Stout, S. L. (1997) Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildlife Society Bulletin* 25(2), 252-258.
- Flowerdew, J. R. and Ellwood, S. A. (2001) Impacts of woodland deer on small mammal ecology. *Forestry* 74, 277-287.

- Gill, R. M. A. (1992) A review of damage by mammals in north temperate forests. 1. Deer. *Forestry* 65, 145-169.
- Gill, R. M. A. and Beardall, V. (2001) The impact of deer woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74(3), 209-218.
- Grumbine, R. (1994) What is ecosystem management? *Conservation Biology* 8(1), 27-38.
- Hairston, N. G., Jr. and Hairston, N. G., Sr. (1993) Cause-effect relationships in energy flow, trophic structure and interspecies interactions. *American Naturalist* 142, 379-411.
- Hale, C. M., Frelich, L.E., and Reich, P.B. (2005) Exotic European earthworm invasion dynamics in northern hardwood forests of Minnesota, USA. *Ecological Applications* 15(3), 848-860.
- Hale, C.M. (2004) Ecological consequences of exotic invaders: interactions involving European earthworms and native plant communities in hardwood forests. Ph.D dissertation. University of Minnesota, Department of Forest Resources, St Paul, MN.
- Hale, C.M. 2008. Perspective: Evidence for human-mediated dispersal of exotic earthworms: support or exploring strategies to limit further spread. *Molecular Ecology* 17:1165-1169.
- Harrison, K.A. and Bardgett, R.D. 2008. Impacts of grazing and browsing by large herbivores on soils and soil biological properties. In I.J. Gordon, & H.H.T. Prins (Eds.), *The ecology of browsing and grazing*. pp. 201-206. Springer.
- Hazenbrock, E., Bruinderink, G. W. T. A., and vanBiezen, J. B. (1995) Changes in the occurrence of small mammals following the exclusion of red deer, roe deer and wild boar. *Lutra* 38, 50-58.
- Hester, A. J., Edenius, L., Buttenschön, R. M., and Kuiters, A. T. (2000) Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73, 381-391.
- Hobbs, N. T. (1996) Modification of ecosystem by ungulates. *Journal of Wildlife Management* 60, 695-713.
- Holdsworth, A. R., Frelich, L. E. and Reich, P. B. (2007) Regional extent of an ecosystem engineer: earthworm invasion in northern hardwood forests. *Ecological Applications* 17,1666-1677.
- Horsley, S. B. and Marquis, D. A. (1983). Interference by weeds and deer with Allegheny hardwood reproduction. *Canadian Journal of Forest Resources* 13, 61-69.

- Illius, A. W. (2004) Linking functional responses and foraging to population dynamics. In *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. K. Danell, R. Berstrom, P. Duncan, and J. Pastore, Eds. 71-96. Cambridge University Press, UK.
- Langellotto, G. A., and Denno, R. E. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139, 1-10.
- Leopold A. (1943) Deer irruptions. *Wisconsin Conservation Bulletin* 8, 3–11.
- Leopold, A. (1949) *A sand county almanac*. Oxford University Press, New York.
- Lessard, J. P., Reynolds, W. N., Bunn, W. A., Genung, M. A., Gregger, M. A., Felker-Quinn, E., Barrios-Garcia, M.N., Stevenson, M. L., Brown, C. B., Patrick, M., Rock, J.H., Jenkins, M. A., Bailey, J. K., and Schweitzer, J. A. 2012. Equivalence in the strength of deer herbivory on and above and below ground communities. *Basic and Applied Ecology*. 13: 59-66.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and Bazzaz, F. A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3), 689-710.
- Martin, J. L., Stockton, S. A., Allombert, S., and Gaston, A. J. (2010) Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: Lessons from a deer introduction. *Biological Invasions*. 12, 353-371.
- McCabe, T. R. and McCabe, R. E. (1997) *Recounting whitetails past. The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C.
- McInnes, P. F., Naiman, R. J., Pastor, J., and Cohen, Y. (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73, 2059- 2075.
- McShea, W. J., and Rappole, J. H. (1992) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology* 14 (4), 1161-1170.
- McShea, W. J., Underwood, H. B., and Rappole, J. H. (1997) *The science of overabundance: deer ecology and population management*. Smithsonian Institution Press, Washington, D.C., USA.
- Milchunas, D. G. and W. K. Lauenroth. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63, 327, 366.

- Morellet, N., Gaillard, J. M., Hewison, A. J. M., Ballon, P., Bascardin, Y., Duncan, P., Klein, F., and Maillard, D. (2007) Indicators of ecological changes: new tools for managing populations of large herbivores. *Journal of Applied Ecology* 44, 634-643.
- Morin, P. J., (1999) *Community Ecology*. Blackwell Science Inc., Malden.
- Niemelä, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *European Journal of Entomology* 98(2), 127-132.
- Pastor, J., Dewey, B., Naiman, R. J., McInnes, P., Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74, 467-480.
- Polis, G. A. and Strong, D. R. (1996) Food web complexity and community dynamics. *American Naturalist* 147, 813-846.
- Putman, R., Watson, P., and Langbein, J. (2011) Assessing deer densities and impacts at the appropriate level of management: a review of methodologies for use beyond the site scale. *Mammal Review* 41(3), 197-219.
- Rainio, J. and Niemela, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity Conservation* 12, 487-506.
- Rambo, J. L. and Faeth, S. H. 1999. Effects of vertebrate grazing on plant and insect community structure. *Conservation Biology* 11, 1047-1054.
- Rooney, T. P. and Waller, D. M. (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181, 165-176.
- Seagle, S. W. (1999) Can ungulates foraging in multiple-use landscapes alter forest nitrogen budgets? *Oikos* 103(1), 230-234.
- Simberloff, D. and VonHolle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1, 21-32.
- Stromayer, K. A. K. and Warren, R. J. (1997) Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25, 227-234.
- Suominen, O. (1999) Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. *Ecography* 22, 651-658.
- Thomas, J. W. (1994) Trends in forest management in the United States. *The Forestry Chronicle* 70(5), 546-548.
- Tierney, G. L., Faber-Landendoen, D., and Mitchell, B. R. (2009) Monitoring and evaluating the ecological integrity of forest ecosystems. *Frontiers in Ecology and the Environment* 7, 308-316.

- Tilghman, N. G. (1989) Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53, 524-532.
- Underwood, H. B and Coffey, M. A. (1999) Evaluation of distance sampling for deer density estimation at Cuyahoga Valley National Recreation Area (CUVA): part II. National Park Service, Brecksville, Ohio, USA.
- Vitousek, P. M. (1990) Biological invasions and ecosystems process—towards an integration of population biology and ecosystem studies. *Oikos* 56, 7-13.
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., and Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist* 84, 468-478.
- Wagner, J. D., Toft, S., and Wise, D. H. (2003) Spatial Stratification in litter depth by forest-floor spiders. *The Journal of Arachnology* 31, 28-39.
- Walker, B. H. and Steffen, W. (1997) An overview of the implications of global changes for natural and managed terrestrial ecosystems. *Conservation Ecology* 2(2): 2 [online: {<http://www.consecol.org/vol1/iss2/art2>}].
- Waller, D. M., and Alverson, W. S. (1997) The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25, 217-226.
- Wardle, D. A. and Bardgett, R. D. (2004) Human-induced changes in large herbivorous mammal density: The consequences for decomposers. *Frontiers in Ecology and the Environment*. 2, 145-153.
- Work, T. T., Koivula, M., Klimaszewski, J., Langor, D., Spence, J., Sweeney, J., and Hébert, C. (2008) Evaluation of carabid beetles as indicators of forest change in Canada. *Canadian Journal of Entomology* 140, 393-414.