THE INFLUENCE OF SMALL MAMMALS ON SUCCESSION AND RESTORATION OF POST-AGRICULTURAL WETLANDS

By

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A Dissertation submitted to the Graduate School-New Brunswick
Rutgers, the State University of New Jersey in partial fulfillment of the requirements for the degree of Doctor of Philosophy Graduate Program in Ecology and Evolution written under the direction of Dr. Rebecca C. Jordan and approved by _____________________________

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New Brunswick, New Jersey

January, 2014
Advancements in modern industry and technology are creating an abundance of post-agricultural lands that are in need of skilled restoration efforts to manage the confluence of factors involved with whole-ecosystem functioning. The influence of small mammals in succession and restoration has been undervalued in traditional restoration studies. This study uses post-agricultural cranberry farms to help answer questions surrounding the role of small mammals in their succession and restoration. The first chapter investigates those species inhabiting post-agricultural wetlands and how they compare to more natural species assemblages in reference locations. Meadow voles (*Microtus pennsylvanicus*) were the most abundant species present and had a strong correlation to post-agricultural sites with wet habitat characteristics; the second-most abundant species present, white-footed mice (*Peromyscus leucopus*), had a strong correlation to sites with dry characteristics. Post-agricultural wetlands were more similar to each other than to any more natural reference locations. The second chapter investigates the diet of the meadow vole through microhistological fecal analysis and
discusses the impact diet has on vegetative characteristics of post-agricultural wetlands. Meadow voles were found to ingest significant amounts of vegetation (grasses, sedges, rushes, leaves of shrubs, mosses), as well as minimal quantities tree leaves, shrub stems, flowers, fungus, seeds, and insects. Meadow vole herbivory on specific vegetation is evidence that high numbers of this species can alter characteristics of post-agricultural wetlands. The third chapter investigates the potential for small mammals to influence post-agricultural wetlands by dispersing seeds through defecation. Greenhouse trials had low rates of seedling establishment from meadow voles, but evidence suggests that this species has the ability to participate in endozoochory. The fourth chapter additionally investigates small mammal diet by proposing genetic methodology for exploring insectivory using unique regions of 18S rRNA and gel electrophoresis to distinguish insect orders by size. The ability to process this level of diet composition data without more expensive techniques such as sequencing would allow for expanded investigations at multiple levels. Overall, this research highlights the significant difference in small mammal species assembly within post-agricultural wetlands and the impact that these species can have when they occur in abundance within post-agricultural wetlands.
ACKNOWLEDGEMENTS

A dissertation is an adventurous journey with many curves, bumps, and forks in the road. The destination is often clouded in fog, but eventually the sun breaks through the clouds and the finish line is bright and shining. No journey can be accomplished alone and this one was no exception. There are many people that stayed the course with me and provided navigation through the fog; without them I would still be lost. I would first like to thank my advisor, Dr. Rebecca Jordan, for her guidance and support during my eight-year endeavor. Her ability to foster scientific curiosity is contagious, and her capacity to encourage me to pursue my goals is unmatched. Dr. Walter Bien has been a mentor to me since my first steps into collegiate life, guiding me through my undergraduate research and Master’s degree, and through to this dissertation. Without him, I would have never discovered the wonders of the NJ Pine Barrens and fallen in love with this magical place. The additional members of my committee, Dr. Peter Morin, Dr. Karl Kjer, and Dr. Rick Ostfeld have provided their expertise to strengthen my research skills and broaden my academic horizons. Their challenging natures always demand the best of me and I am a better person because of them.

I would not have succeeded in my graduate career without the help, support, and camaraderie of the Jordan lab – Wes Brooks, Steven Gray, David Mellor, and Ryan Burrows – the Bien lab at Drexel University – Ron Smith, Dane Ward, Marilyn Sobel, and Kate Reinholt – and my fellow E&E grad students, namely Elena Tartaglia, Ai Wen, Holly Vuong, Julian Avery, and many more. The field work involved with this research would never have be accomplished without the countless gnat-filled, muddy, early morning hours put in by so many undergraduate volunteers, most notably Ryan Rebozo,
Heather Kopsco, and Christina Leshko. Family and friends were not spared the joys involved with hands-on research either; thanks to Marguerite Shenko, Marci Thompson, Diane Parker, R. Hack, and Hannah Schoch for agreeing to help without knowing what they were getting in to. In addition, my brown thumb would have done me in during my experimental greenhouse studies if not for the diligent care of Nicki Graf and her staff at the Rutgers Floriculture Greenhouse. I must also acknowledge the General Biology program – Dr. Diana Martin, Estie Leibovich Ruskin, Nicole Shea, and so many others – for giving me the experiences necessary to realize my desire to be an educator.

Traveling the road of a dissertation is not a purely professional undertaking. It demands time and energy from every aspect of life. I would like to thank my husband, Albert Shenko, for all that he has done to encourage and support me in my endeavors, including rainy field days, data disasters, and extra weekend parenting shifts. Although my son Benjamin is unaware of it, he has been one of my strongest sources of support. I see the world differently through his eyes and I want to succeed for him. My mother, Halina Buchanan, and parents-in-law, Al and Marge Shenko, have also been instrumental in promoting my success. My pursuit of “furry woodland creatures” has been arduous, but worth every bug bite.
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INTRODUCTION TO THE DISSERTATION

Restoration and conservation of wetland areas is a pressing concern and with the spread of urbanization, reclamation of abandoned wetlands is becoming more important as natural areas disappear. The key to restoration success is an understanding of the working components and interactions in these ecological systems. Important components of these wetland ecosystems are small mammals whose ability to influence plant community assembly has been undervalued in restoration (Howe et al. 2006). Most notably, the influence of small mammal species on vegetation patterns, seed dispersal mechanisms, and the availability of these mammals as prey have not been assessed as drivers of ecosystem condition.

This dissertation focuses on small mammals within post-agricultural cranberry bogs located within Pine Barrens habitat in southern New Jersey (NJ). Cranberry agriculture has been a staple of the area since the first bogs were planted as early as 1835 (Applegate et al. 1998). The modifications to natural wetlands necessary to create agricultural bogs include logging and clear-cutting larger vegetation, draining existing water, damming natural waterways, and filling peaty soils with additional sand and gravel (Eck 1990). These modifications change the natural balance of the system and generally been associated with decline in wildlife populations and general ecosystem health (Green et al. 2005; Tilman et al. 2001).

Particularly unique to the NJ Pine Barrens, is the potential for rare species refugia within highly modified habitats (Fairbrothers 1998; Wen 2013). This potential is greater when considering that proliferation of post-agricultural land has increased recently, as land used for modern cranberry agriculture now only accounts for only one-third of the
land used at the height of production in the state (Zampella et al. 2006). Currently, this post-agricultural land is undergoing natural succession and, in some cases, active restoration to attempt to increase the ecological value of the land. Given the potential of small mammals, through consumption and dispersal, to affect early succession species such as grasses, forbs, and mosses, it is prudent to understand the plausible impact of small mammal feeding patterns.

The NJ Pine Barrens is home to several small mammal species. Historically, upland pine forests and old-fields within the NJ Pine Barrens have supported four native species of small mammal, the most abundant of which is the white-footed mouse (*Peromyscus leucopus*). Other upland inhabitants include the short-tail shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*), and pine vole (*Microtus pinetorum*). Wetland habitats have supported seven native species in relatively similar density, including the masked shrew, short-tail shrew, white-footed mouse, meadow vole (*Microtus pennsylvanicus*), southern bog lemming (*Synaptomys cooperi*), red-back vole (*Myodes gapperi*), and meadow jumping mouse (*Zapus hudsonius*). Limited historical sampling with cranberry bogs include three species, the masked shrew, white-footed mouse, and red-back vole (Connor 1953). Recent population sampling shows a similar species diversity among these habitats (Shenko (née Buchanan) 2006; Shenko et al. 2012). Throughout the northeast United States, old-field habitats favor meadow voles over the white-footed mouse, and white-footed mice dominate areas with a shrub understory and forest edges (Getz 1961; Manson et al. 1999; Ostfeld et al. 1999).

To understand the potential for small mammal impacts on post-agricultural sites within the NJ Pine Barrens, I set out to determine species presence in modified former
cranberry bogs as compared to a non-modified reference site. Additionally, I quantified available versus consumed food sources, and tested the potential for seed dispersal. Finally, I discuss the potential for molecular techniques as an aid for small mammal diet study. Below I outline my four chapters and describe some of the conclusions I have drawn.

The first chapter of this dissertation discusses those small mammal species that inhabit post-agricultural cranberry bogs and compares those species with those occurring in less-impacted reference sites within the Pine Barrens. Small mammals are widely understood to serve an integral role in food web dynamics by providing nutrient and energy transfer within ecosystems (Wike et al. 2000). These species can also alter vegetation patterns through seed and seedling predation (LoGiudice & Ostfeld 2002; Manson et al. 2001; Manson & Stiles 1998; Ostfeld & Canham 1993; Ostfeld et al. 1997, 1999; Schnurr et al. 2004). Identifying the underlying small mammal species assemblage within post-agricultural bogs and how those compare to natural communities in the area is critical to understanding the impacts of alterations at this level of ecosystem functioning.

The second chapter of this dissertation focuses specifically on the diet of the most abundant small mammal within the study site, the meadow vole (*Microtus pennsylvanicus*), and how the diet of this organism can effect succession and restoration within the system. Generally, small mammals can ingest a wide variety of food sources that include insects, vegetation, seeds, fungus, and fruits. Their foraging activities can have significant influence on vegetative habitat characteristics (Howe & Lane 2004; Howe et al. 2006; Manson et al. 2001; Ostfeld & Canham 1993; Ostfeld et al. 1997,
Meadow voles are known to feed primarily on green vegetation (Getz 1961), but have also been known to ingest seedlings and secondarily maintaining old-field grassland habitat (Manson et al. 2001; Ostfeld & Canham 1993; Ostfeld et al. 1997, 1999). By employing microhistological techniques to fecal samples from meadow voles, this research can link the specific foraging habits of the meadow vole within post-agricultural bogs to the direction of overall succession and restoration.

The third chapter of this dissertation expands on the role of small mammals in succession and restoration of post-agricultural cranberry bogs by examining the possibility of these species as endozoochorus seed dispersers. Seed dispersal through ingestion and subsequent defecation is widely known in variety of taxa (Stiles 2000), but evidence for this in small mammals is limited to rats in Hawaii (Shiels & Drake 2011) and New Zealand (Williams et al. 2000). Endozoochory is an important method of seed dispersal that can aid germination rates (Hickey et al. 1999; Ramos et al. 2006; Robles et al. 2005; Schaumann & Heinken 2002), and the possibility of this type of impact on succession and restoration of wetland systems is an important component to understanding ecosystem functioning.

The fourth chapter of this dissertation departs from further elucidating components to succession and restoration in post-agricultural cranberry bogs and suggests a method of further investigating small mammal diet through molecular scatology. Molecular scatology is a growing genetic methodology for exploring diet components in a wide assortment of taxa (Bradley et al. 2007; Clare et al. 2009; Corse et al. 2010; Deagle et al. 2010; Hofreiter et al. 2010; Hoss et al. 1992; Rolfe 2011; Zeale et al. 2011), including many cryptic species in which more invasive diet methodologies
would be impossible (Jarman et al. 2002; Piggott & Taylor 2003; Waits & Paetkau 2005). The microhistological techniques utilized in the second chapter have limitations based on digestibility of forage and available reference materials (Clare et al. 2009; Holechek & Vavra 1981; Holechek et al. 1982; Keys Jr. & Van Soest 1970; Soininen et al. 2009). The genetic techniques described in the fourth chapter would complement microhistological diet studies to produce a broader view of the insects included in many small mammal diets. The information produced from broader diet studies of small mammals would be an important contribution to overall knowledge of the relationships between small mammals and the succession and restoration of post-agricultural lands.
LITERATURE CITED


CHAPTER 1: SMALL MAMMAL SPECIES ASSEMBLY WITHIN POST-AGRICULTURAL WETLANDS

ABSTRACT

Reclamation and restoration of abandoned post-agricultural land requires an understanding of the working components within components of these modified ecosystems. One important group is small mammals that serve as prey for vertebrate carnivores, predators of insects and seeds, and manipulators of vegetative communities. To examine the relationship between small mammals and ecological restoration, this study is focused on assessing the relationship between small mammal assemblages and post-agricultural cranberry farms undergoing ecological restoration. As part of an ongoing restoration effort, this study seeks to evaluate (1) baseline small mammal species presence and abundance within post-agricultural land undergoing restoration, (2) compare small mammal communities between post-agricultural lands with varying hydrologic habitats, and (3) compare and assess small mammal communities in post-agricultural lands with those in reference natural habitats. Results show that meadow voles (Microtus pennsylvanicus) are the most abundant small mammal in both wet and dry sites with a strong correlation to wet sites; white-footed mice (Peromyscus leucopus) have a strong correlation to dry sites. Overall similarity to reference habitats was low.

INTRODUCTION

Restoration of native habitats is a multifaceted endeavor involving biotic and abiotic components of the ecosystem. Understanding the complexity of biotic interactions is critical to successful long-term restoration efforts (Ehrenfeld & Toth 1997; Palmer et al. 1997). Small mammals have multiple roles within naturally-functioning habitats that
transfer primary production to higher-order predators. They are responsible for nutrient and energy transfer within the ecosystem (Wike et al. 2000). These higher-order predators in New Jersey include many threatened and endangered species including the timber rattlesnake (*Crotalus horridus*), northern pine snake (*Pituophis melanoleucus*), bald eagle (*Haliaeetus leucocephalus*), American kestrel (*Falco sparverius*), barred owl (*Strix varia*), and bobcat (*Lynx rufus*). Whole-ecosystem restoration is necessary in order to provide a functional habitat for these common and protected species.

Small mammals are not only a link between trophic levels, but also can be drivers of succession and ecosystem health through manipulation of the plant community. Grassland soil health and biodiversity has been linked to digging and burrowing activities of small mammals (Martin 2003). Granivorous small mammals can disrupt natural fruit-bearing tree seed dispersal cycles by utilizing frugivore latrines as food sources (LoGiudice & Ostfeld 2002). Small mammal seed predators can influence tree recruitment patterns (Schnurr et al. 2004), and seed predation by white-footed mice (*Peromyscus leucopus*) can effect microhabitat conditions and alter tree invasion into old-fields, thereby changing overall plant community structure (Manson & Stiles 1998). Meadow voles (*Microtus pennsylvanicus*) are keystone herbivores in old-field succession, where seedling predation by meadow voles has a stronger effect on old-field succession than seed predation by white-footed mice. Meadow voles maintain a grassland system and prevent tree invasion in old-fields (Manson et al. 2001; Ostfeld & Canham 1993; Ostfeld et al. 1997, 1999).

Small mammals can have significant impacts on ecosystems, yet they are often not the target group during restoration studies. Modifications that increase habitat
heterogeneity are generally expected to increase diversity within mammal taxa associated with that ecosystem. Forest modifications that promote old-growth forest regeneration support increased complexity within vegetative communities and increased diversity in small mammal assemblage, but forest conversions do promote colonization of common generalist species (Carey & Wilson 2001; Masters et al. 1998). Restoration of wet prairie habitat has shown that meadow voles can drastically alter plant community composition and structure within four years (Howe & Lane 2004). Over time, the plant community is dominated by those species that are unpalatable to meadow voles, an effect similar to that of herbivory by ungulates (Howe et al. 2006; Ostfeld & Canham 1993). Restoration efforts have also been shown to cause immediate declines in small mammal species with partial recovery within 3-5 years or to have no effect on small mammals at all (Stone 2007; Wike et al. 2000). Little data has been published on the response of small mammals to modified habitats within the study region. White-footed mice are known to be early colonizers to recent wildfire areas of pine barrens habitats and abundant in anthropogenically-disturbed habitats (Shenko et al. 2012; White 1961).

The study area occurs within the New Jersey Pinelands, the largest contiguous area of pine barrens habitat found in the world. The area is protected by the Pinelands National Reserve Act of New Jersey, and is comprised of a mosaic of land-use areas that include agricultural lands, suburban developments, military installations, and forested areas. The study site, Franklin Parker Preserve, is a 3,400 acre preserve located in Woodland Township, Burlington County, New Jersey, that includes pine forests and post-agricultural cranberry farms. Cranberries were actively farmed on the property from 1940s to the 1990s; the New Jersey Conservation Foundation purchased and preserved
the land in 2003 (Wen 2010). Wetland restoration activities began in 2005 as part of an initial restoration effort between the NJ Conservation Foundation and United States Department of Agriculture. Mound-and-basin complexes were created to increase habitat heterogeneity throughout the property starting in October 2008.

There are 18 small mammal species known to occur in the region, although there is little more than abundance data and general information for most species (Applegate 1974; Connor 1953; McCormick 1970; Rhoads 1903; Shenko (née Buchanan) 2006; Stone 1908; Wolgast 1998). The native cricetid rodents include the white-footed mouse, meadow vole, pine vole (*Microtus pinetorum*), red-backed vole (*Myodes gapperi*), southern bog lemming (*Synaptomys cooperi*), meadow jumping mouse (*Zapus hudsonius*), and marsh rice rat (*Oryzomys palustris*). Non-native murid rodents known to occur are the Norway rat (*Rattus norvegicus*), house rat (*Rattus rattus*), and house mouse (*Mus musculus*). Sciurids include the eastern chipmunk (*Tamias striatus*), red squirrel (*Tamiasciurus hudsonicus*), and grey squirrel (*Sciurus carolinensis*). Insect specialists known to occur are soricid shrews, including the short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*), and least shrew (*Cryptotis parva*), and talpid moles, including the common mole (*Scalopus aquaticus*) and star-nosed mole (*Condylura cristata*).

The primary research focus of this chapter is to establish baseline data about small mammal diversity within post-agricultural lands currently undergoing both restoration and natural succession. Site classification and small mammal trapping commenced with the initiation of site-wide restoration activities in October 2008 and continued until September 2010. This research is particularly timely since the modification of these
particular habitats has not been assessed to determine whether natural communities will return post-abandonment or whether more interventions are required. Determining species richness and abundance of small mammals is important for ecosystem conservation efforts.

**METHODS**

*Research Hypotheses:*

1. Does vegetative community composition correlate to small mammal community assembly?
   
   **Hₐ₁-₁:** Small mammals typically found in wetlands will occur in post-agricultural bogs that have a wetland vegetative community.

   **Hₐ₁-₂:** Small mammals typically found in uplands will occur in post-agricultural bogs that have a vegetative community typically associated with dry habitats.

2. Do soil turnover restoration activities impact small mammal community assembly within the post-agricultural bogs?

   **Hₐ₂-₁:** Post-agricultural bogs that have undergone restoration have a similar suite of small mammal species when compared to post-agricultural bogs that have not been turned over.

3. Do small mammals occurring in post-agricultural bogs exhibit common population fluctuations associated with season?

   **Hₐ₃-₁:** Small mammals in post-agricultural bogs will show increases in population size in summer months and decreases in winter months.
4. Do post-agricultural cranberry farms resemble similar reference natural habitats with regard to small mammal species?

\( H_{A4-1} \): Post-agricultural farms with wetland characteristics and natural wetland habitats have a similar suite of small mammal species.

\( H_{A4-2} \): Post-agricultural farms with upland characteristics and natural upland habitats have a similar suite of small mammal species.

**Site Characteristics**

Sites for this study were randomly chosen based on gross vegetative structure outlined in Figure 1 and feasibility of live-trapping given periodic flooding episodes. Restored sites represented those with mound-and-basin complexes. These restrictions limited study sites to one non-restored dry site, one non-restored wet site, three restored dry sites, and three restored wet sites.

Vegetation sampling was conducted by placing three 20m transects within each 150m trapping transect. Each 20m transect was sampled using vegetation cover estimation with Daubenmire cover class methodology for vegetation and ground cover estimation (Elzinga et al. 2001). Vegetation and ground cover were analyzed in 1m x 1m quadrats and vegetation identified to species when possible.

The percentage data obtained from Daubenmire cover class methodology was arcsine transformed for use in statistical analysis. Site characteristics were analyzed using principal components analysis (PCA) to group sites and reduce variables for further analysis in IBM SPSS Statistics Version 20. Sites with plants characteristic of upland Pine Barrens habitat were classified as dry post-agricultural sites and sites with plants
characteristic of wetland Pine Barrens habitat were classified as wet post-agricultural sites (McCormick 1998).

*Live-Trapping Methods at Franklin Parker Preserve*

This study focused on small mammals from the orders Rodentia and Soricomorpha weighing less than or equal to 100 g and able to fit within a Fitch live trap of dimensions 33 cm x 5.5 cm x 5 cm. Trapping was conducted in eight sites within four initial habitat treatments: dry post-agricultural cranberry bogs with and without restoration activities and wet post-agricultural cranberry bogs with and without restoration activities (Figure 1). Post-agriculture sites are of equal abandonment age and approximately equal distances from adjacent pine forest to limit differences in edge effect (Figure 2). Each site was trapped for 3 nights, bi-monthly over two years (2008-2010). At each site, Fitch live traps were located along opposing sides of a 150m transect, 5m apart and 10m from the next set. This created a 5m x 150m grid design (0.075ha) with 30 traps per site. Animals were marked using individually-numbered ear tags (National Band & Tag Co. #1005-1).

Because of limited study site size and low recapture rate, catch-per-unit-effort (CPUE) was computed as an index of relative abundance. CPUE was defined as the number of individuals initially captured per site per trap night. Sprung traps were not included in the trap night calculations. Trapping sessions were divided into 5 seasons as follows for seasonal analysis: Fall (late September to early October), Winter (December), Spring (March), Early Summer (late May to early June), and Late Summer (July to early August). Small mammal abundance indices were compared to the first three PCA factor
scores for site characteristics using pairwise Pearson’s correlations. Abundances of small mammals between restored and non-restored sites was tested using multivariate analysis of variance. All statistics were performed in IBM SPSS Statistics Version 20 at the 0.05 level of significance.

Small mammal species composition was compared to the reference location using the Morisita-Horn similarity index. The index utilizes both presence and abundance of mammal species to compare habitats to each other. The similarity index is defined by: 

\[ I_M = \frac{2\sum x_i y_i}{(l_1 + l_2)N_1 N_2} \]

where \( I_M \) represents the Morisita-Horn similarity index, \( x, y \) represent the number of individuals of species \( i \), \( l \) represents Simpson’s dominance index, and \( N \) presents the total number of individuals.

*Live-Trapping Methods at Reference Location (Warren Grove Gunnery Range)*

Eight sites were selected from previous research in the area that represent characteristic habitats within the pine barrens similar to those a Franklin Parker Preserve but with only minimal historic anthropogenic influence. Each site was trapped bi-weekly from May to August 2004. At each site, Fitch live traps were located along opposing sides of a 100m transect, 5m apart and 10m from the next set. This created a 5m x 100m grid design (0.05ha) with 20 traps per site. Animals were marked using individually-coded passive integrated transponder (PIT) tags (Shenko et al. 2012).

Data for the eight sites were pooled into broad categories representing wetland and upland sites and transferred into CPUE format for comparison to abundances at Franklin Parker Preserve. Reference wetland sites included areas of bog savanna,
hardwood swamp, and Atlantic white cedar bog. Reference forest sites included pine-oak upland and pygmy pine plains, and dry grassland areas (McCormick 1998).

**RESULTS**

1. Does vegetative community correlate to small mammal community assembly?

   Principal Component 1 (PC1) accounted for 26.5% of the variation in the data (Figure 3). PC1 showed a positive association with *Andropogon virginicus*, *Cyperus* spp., *Hypericum gentianoides*, *Juncus biflorus*, *Juncus tenuis*, *Lechea racemulosa*, *Lyonia lingustrina*, *Panicum virgatum*, *Pinus rigida*, *Polytrichum* spp., *Vaccinium corymbosum*, *Vaccinium macrocarpon*, and *Xyris torta*, as well as a positive association with lichens, downed woody debris, and sand present at the surface. PC1 showed a negative association with *Carex striata*, *Eleocharis olivacea*, *Hypericum perforatum*, *Juncus canadensis*, *Juncus pelocarpus*, *Muhlenbergia uniflora*, *Proserpinaca pectinata*, *Rhexia virginica*, *Rubus hispidus*, *Rumex acetosella*, *Scirpus cyperanus*, and *Triadenum virginicum*, as well as a negative association with organic soil at the surface.

   Principal component 2 (PC2) accounted for 24.7% of the variation in the data and showed a positive association with *Acer rubrum*, *Andropogon glomeratus*, *Andropogon virginicus*, *Chamaedaphne calyculata*, *Cyperus* spp., *Eleocharis olivacea*, *Eleocharis tenuis*, *Euthamia tenuifolia*, *Panicum rigidulum*, *Scirpus americanus*, *Sphagnum* spp., and *Viola lanceolata*, as well as dead organic matter and water present at the surface. PC2 showed a negative association with *Glyceria obtusa*, *Hypericum perforatum*, *Kalmia angustifolia*, *Lacnanthes caroliniana*, *Leersia oryzoides*, *Sagittaria engelmanniana*, *Schizachryium scoparium*, *Smilax* spp., *Sparganium americanum*, and *Utricularia* spp., as well as lichen and sand present at the surface. Together, PC1 and PC2 accounted for
51.1% of the variability in the data (Figure 3); the addition of PC3 in further analyses accounted for 69.8%.

Based on this analysis of the data, sites C, H, G, and F were broadly characterized as wet sites (Figure 3) because of a predominance of obligate wetland plant species, organic soil, and water at the surface. Sites A, B, D, and E were characterized as dry sites (Figure 3) because of their association with some old-field plant species and sand present at the surface.

The sites at Franklin Parker Preserve were dominated by meadow voles. Dry sites had relatively equal abundance of meadow voles and white-footed mice, where wet sites had an abundance of meadow voles only (Figure 4 – top panel). Pairwise Pearson’s correlations ($\rho$) showed a significant negative correlation ($\rho=-0.79$, $p<0.05$, $n=8$) between total meadow vole CPUE and PCA factor 1, and a significant positive correlation ($\rho=0.85$, $p<0.01$, $n=8$) between total white-footed mouse CPUE and PCA factor 1. This corresponds to a correlation between meadow voles with wet habitats and white-footed mice with dry habitats.

2. Do soil turnover restoration activities impact small mammal community assembly within the post-agricultural bogs?

Multivariate analysis of variance showed no significant difference in mammal CPUE between restored sites (dry: A, E, D; wet: F, G, H) and the non-restored sites (dry: B; wet: C) for any species (meadow voles: F=3.31, $p>0.05$, df=3; white-footed mice: F=2.01, $p>0.05$, df=3; meadow jumping mice: F=0.07, $p>0.05$, df=3; short-tailed shrews:
3. Do small mammals occurring in post-agricultural bogs exhibit common population fluctuations associated with season?

Multivariate analysis of variance showed a significant difference in meadow vole CPUE between wet and dry sites and between seasons (F=35.32, p<0.001, df=1; F=4.36, p<0.001, df=9). Meadow voles had a higher mean CPUE in wet sites than in dry sites across all seasons, with an increase in mean meadow vole CPUE occurring through the summer and fall (Figure 5). White-footed mice CPUE was significantly different between wet and dry sites (F=23.40, p<0.001,df=1), but no significant difference between seasons. White-footed mice had a higher mean CPUE in dry sites than in wet sites across all seasons, and a trending decrease in mean CPUE in the summer (Figure 6).

4. Do post-agricultural cranberry farms resemble similar reference natural habitats with regard to small mammal species?

The reference location (Warren Grove Gunnery Range) had the greatest number of species in wetland areas. The wetlands had an abundance of meadow jumping mice, southern bog lemmings, southern red-backed voles, and white-footed mice. Reference dry sites were dominated almost entirely by white-footed mice (*Peromyscus leucopus*) (Figure 4 – bottom panel).

Regarding community assembly similarities (Table 1), dry sites were 89.8% similar to wet sites at Franklin Parker Preserve. Comparison to habitats in the reference
location yielded very low similarity. Dry sites a Franklin Parker Preserve were 34.4% and 20.6% similar to reference dry sites and reference wet sites, respectively. Wet sites at Franklin Parker Preserve were not similar to any reference locations with a 7.6% similarity to reference wetland locations and less than 1% similarity to reference dry sites.

**DISCUSSION**

Site classification criteria at Franklin Parker Preserve suggest that at the time of the study, post-agricultural cranberry bogs could be roughly classified into two broad habitat types. Some bogs undergoing restoration and natural succession had vegetative features that resembled hydric, wetland habitats in the region and other post-agricultural bogs had vegetative features more similar to xeric, upland habitats within the pine barrens. This distinct habitat difference is correlated to differences in small mammal species assembly. Small mammal species within the scope of this study typically found in upland habitats in the region include pine voles, eastern chipmunks, and least shrews, while those typically found in wetlands include meadow voles, red-backed voles, southern bog lemmings, meadow jumping mice, and marsh rice rats. Species known to occur in both upland and wetland habitats in the region include white-footed mice, short-tailed shrews, and masked shrews (Connor 1953; Rhoads 1903; Shenko (née Buchanan) 2006; Stone 1908; Wolgast 1998). Franklin Parker Preserve had low species richness as compared to other pine barrens habitats. Five species were found on the study sites: meadow voles, white-footed mice, meadow jumping mice, short-tailed shrews, and masked shrews. Only meadow voles and white-footed mice were found in abundance.
There was a strong correlation between wet vegetative features and meadow voles, and dry vegetative characters had a strong correlation with white-footed mice, but wet and dry sites were similar to each other regarding small mammal richness and abundance. Seasonally, meadow voles in wet sites showed a natural cycle of population fluctuation that remained more constant in dry sites. On the contrary, white-footed mice in dry sites showed natural population cycle fluctuations that remained more constant in wet sites. This may be due to environmental conditions more favorable for reproduction in the respective species.

Post-agricultural bogs at Franklin Parker Preserve that had undergone mound-and-basin topographic changes did not show differences in vegetative community or small mammal species assembly. This may change as restoration and natural succession increase with time. Within anthropogenically-modified habitats, the presence of woody debris and a complex understory are important for a diverse small mammal community. While overall species richness and diversity may not be affected by a homogeneous microhabitat, small mammal community structure and abundance declines (Glennon & Porter 2007). Small mammal species composition differs in response to fragmented land, and agricultural fragmentation particularly can have unknown effects on the ecosystem as a whole (Nupp & Swihart 2000).

In addition to altering small mammal community structure, habitat fragmentation can alter population structure within species. Meadow voles exhibit skewed sex ratios within fragmented habitat, where females persist in these patches and males persist in non-fragmented habitats with greatly increased home range size (Collins & Barrett 1997). Small mammal populations exposed to habitat fragmentation can experience reduced
genetic variability and altered genetic structure (Gaines et al. 1997). Small mammals have the ability to disperse over long distances and thus have the potential to minimize population effects from fragmentation (Ostfeld & Manson 1996).

Habitat alteration and fragmentation can have considerable impacts on small mammal populations. Small mammal diversity and community structure can be used as an indicator of both short-term and long-term anthropogenic disturbance (Leis et al. 2008), and small mammals can be good bioindicators of habitat quality (Pearce & Venier 2005). Small mammal species succession into disturbed areas depends greatly on the vegetative community (Monamy & Fox 2010; Richardson 2010; Schweiger et al. 2000). Microhabitat heterogeneity is important in maintaining small mammal community diversity and integral for specialist species to persist in a habitat, and vegetative cover is necessary to maintain small mammal communities (Bellows et al. 2001; Monamy & Fox 2000; Price et al. 2010; Sauvajot et al. 1998). Complex microhabitats with vertical structure aid in predator avoidance, reduce competition, and promote woodland species like the white-footed mouse, and small mammals will be more abundant in high quality habitats (Kaufman et al. 1993; Lemaitre et al. 2010; Morris & MacEachern 2010).

When comparing the species assembly at Franklin Parker Preserve to that of the reference locations, similarity between locations was low. While southern bog lemmings, meadow jumping mice, red-backed voles, and white-footed mice were the predominant species in reference wetlands, wet sites at Franklin Parker Preserve were dominated by meadow voles; meadow jumping mice and white-footed mice were present at low levels. Abundances of meadow jumping mice and white-footed mice were comparable to those of reference wetland locations, but the proportionately higher amount of meadow voles
made similarity between these sites low (7.6%). Boonstra & Hoyle (1986) report that meadow voles strongly outcompete meadow jumping mice when occurring in the same habitat and keep meadow jumping mice at perennially low population size. While the mechanisms of competition is unclear, interference competition based on vegetative cropping by meadow voles negatively impacts potential seedfall for meadow jumping mice (Boonstra & Hoyle 1986). While Franklin Parker Preserve and the reference location had similar amounts of meadow jumping mice, the large amount of meadow voles may be impacting colonization of meadow jumping mice into wetland sites. Linzey (1984) reports that meadow voles and southern bog lemmings strongly compete when occurring sympatrically. These species were shown to share similar diet preferences but the meadow vole is the superior competitor, excluding southern bog lemmings from the area (Linzey 1984). At Franklin Parker Preserve, the high meadow vole CPUE could drive the absence southern bog lemmings, while at the reference locations, low meadow vole CPUE could allow for existence of southern bog lemming populations. Dry sites at Franklin Parker Preserve were more similar to reference dry sites (34.4%) than reference wet sites (20.6%), due to the presence of white-footed mice. White-footed mice dominate uplands within pine barrens habitats and can occur in lesser abundances in wetland habitats. Manson et al. (1999) report that white-footed mice prefer areas with more structural complexity than meadow voles, with meadow voles dominating dry old-field habitats. High vole density is inversely correlated with probability of capturing white-footed mice (Manson et al. 1999). The differences between species assembly within Franklin Parker Preserve and reference sites could be due to dispersal patterns altered by the historic agricultural uses of the area, as well as the fragmented nature of these bogs.
within the overall preserve. Competitive exclusion by high numbers of meadow voles may also be a driver of differences exhibited in study sites.

Habitat conditions at Franklin Parker Preserve reflect historical land conversion for cranberry agriculture, natural succession post-agriculture, and significant habitat modification to create mound-and-basin complexes as part of overall restoration efforts. The long-term effects of these significant land-use changes have significant impacts on the biotic and abiotic components of the ecosystem, of which small mammals play important roles. The dissimilarity of species assembly between sites at Franklin Parker Preserve and reference locations within the NJ Pinelands reflect the early state of restoration captured by this research.

**MANAGEMENT IMPLICATIONS**

Restoration, as an ongoing process, needs periodic monitoring to evaluate overall progress and return of pre-disturbance ecosystem function. Small mammals contribute to ecosystem function by providing a prey-base for higher-order predators, predating upon insects and seeds, dispersing seeds, and manipulating vegetation. This research has shown that post-agricultural habitats exhibit an altered small mammal community assembly when compared to similar natural reference locations immediately following restoration activities. Further land management protocols and restoration activities should encompass small mammal community assembly. Periodic monitoring of the small mammal community at Franklin Parker Preserve is recommended to evaluate restoration progress. Vegetation at Franklin Parker Preserve was analyzed only to characterize site differences and not to compare vegetative characteristics with other areas of the Pine
Barrens. While outside the scope of this research, in-depth analysis into vegetative habitat characteristics as compared to other wetlands within the New Jersey Pine Barrens would help to elucidate small mammal species differences present at the preserve, as well as expound overall restoration success for the area.
LITERATURE CITED


Stone, W. 1908. The mammals of New Jersey. Academy of Natural Sciences.


Figure 1. Site design for live trapping at Franklin Parker Preserve, Burlington County, NJ.
Figure 2. Site locations for live trapping at Franklin Parker Preserve, Burlington County, NJ. Sites A,D, E, F, G, and H received turnover modification. Sites B and C were not modified.
Figure 3. Principal components analysis of vegetation and ground cover components for eight live-trapping sites at Franklin Parker Preserve, Burlington County, NJ. The solid line denotes dry sites and the dashed line represents wet sites.
Figure 4. Top panel: Graph of individual mammal species catch-per-unit-effort (CPUE) at Franklin Parker Preserve, Burlington County, NJ. The dry sites are within the solid bracket and the wet sites are within the dashed bracket. Bottom panel: Graph of individual mammal species CPUE at the reference location of Warren Grove Gunnery Range, Burlington County, NJ. Note scale differences.
Figure 5. Graph of seasonal mean catch-per-unit-effort (CPUE) for meadow voles at Franklin Parker Preserve, Burlington County, NJ. The dry sites are represented with the solid line and the wet sites are represented with the dashed line. Error bars represent standard deviation. Seasonal designations are as follows: Fall (late September to early October), Winter (December), Spring (March), Early Summer (late May to early June), and Late Summer (July to early August).
Figure 6. Graph of seasonal mean catch-per-unit-effort (CPUE) for white-footed mice at Franklin Parker Preserve, Burlington County, NJ. The dry sites are represented with the solid line and the wet sites are represented with the dashed line. Error bars represent standard deviation. Seasonal designations are as follows: Fall (late September to early October), Winter (December), Spring (March), Early Summer (late May to early June), and Late Summer (July to early August).
Table 1. Morisita-Horn similarity index comparing mammal species at trapping sites in both Franklin Parker Preserve and the reference location of Warren Grove Gunnery Range, Burlington County, NJ.

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<thead>
<tr>
<th></th>
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<th>Wet</th>
</tr>
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<tbody>
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<td></td>
</tr>
<tr>
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<td>0.007</td>
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<tr>
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CHAPTER 2: MEADOW VOLE DIET COMPOSITION IN POST-AGRICULTURAL WETLANDS UNDERGOING SUCCESSION

ABSTRACT

Small mammal diet can influence native habitat restoration efforts. To assess the influence of small mammal diet can have on plant succession and restoration within post-agricultural cranberry bogs, this study investigates the diet composition of the most abundant small mammal within the system, the meadow vole. Microhistological analysis of fecal samples reveals that meadow voles feed on a wide variety of food sources, but major forage components include grasses, sedges, rushes, mosses, and leaves of shrubs. Diet composition remains constant throughout post-agricultural sites with seasonal shift related to plant availability, and diet components vary in quantity between wet and dry sites. These data highlight the role that meadow voles play in the assembly of plant communities undergoing succession in post-agricultural wetlands.

INTRODUCTION

Small mammal foraging habits play an important function within whole-ecosystem restoration because of the linkages between herbivory and vegetative community structure (Ehrenfeld & Toth 1997; Palmer et al. 1997). The influence of diet can complicate native habitat restoration efforts, and a complete understanding of forage components is necessary for successful restoration. Many small mammals are herbivores and seed predators (Crawley 2000). Herbivory by small mammals has been shown to significantly alter standing vegetation and modify vegetative community succession in old-field habitats (Howe & Lane 2004; Howe et al. 2006; Manson et al. 2001; Ostfeld &
Canham 1993; Ostfeld et al. 1997, 1999; Pusenius et al. 2000). Seed predation can have significant effects on propagule success within a habitat (Howe & Brown 2000; LoGiudice & Ostfeld 2002; Ostfeld et al. 1997; Schnurr et al. 2004). While many small mammals can have negative impacts on vegetative establishment, some interactions facilitate propagation. Soil disturbances cause by small mammal burrowing and digging can improve soil health and seed dispersal (Martin 2003). Frugivorous small mammals are known to facilitate germination of seeds through scarification and digestion (Elmouttie & Mather 2012), and ingestion of seeds has been reported to lead to successful endozoochorous dispersal (Shiels & Drake 2011; Williams et al. 2000). Caching behavior is widespread within small mammal taxa and can also facilitate vegetative dispersal (Vander Wall 1990).

Microhistological analysis of stomach or fecal samples has been the traditional means of diet assessment for many organisms. The technique requires fragments of prey species to be identifiable in stomach or fecal samples and is greatly dependent upon digestibility of prey species and skill in identification (Holechek & Vavra 1981; Holechek et al. 1982; Keys Jr. & Van Soest 1970). The technique has been used to assess the diets of many small mammals, including the southern bog lemming and meadow jumping mouse (Shenko (née Buchanan) 2006), the Allegheny woodrat (Castleberry et al. 2002), northern flying squirrel and Townsend’s chipmunk (Colgan III et al. 1997), and tundra and grey red-backed voles (Soininen et al. 2009). The diets of small mammals known to occur within wetlands of the pine barrens generally include seeds, berries, insects, and herbaceous vegetation (Hamilton 1941; Shenko (née Buchanan) 2006), with
some species like the meadow vole (*Microtus pennsylvanicus*) feeding most commonly on grass-like vegetation (Getz 1961).

While habitat characteristics can influence small mammal community structure, the species present at a specific site play an integral role in plant community assembly during habitat succession. Because meadow voles are the dominant small mammal at Franklin Parker Preserve, diet composition was examined in sites differing in hydrologic habitat features. This information provides insight into the role of meadow voles as active participants in the plant community assembly of post-agricultural wetlands.

**METHODS**

*Research Hypotheses:*

1. What are the major diet components of meadow voles within post-agricultural cranberry bogs?

   \( H_{A1} \): Meadow voles within post-agricultural bogs have similar diets to those reported in life history literature.

2. Does meadow vole diet vary in post-agricultural cranberry bogs with differing vegetative communities?

   \( H_{A2} \): Meadow vole diet composition correlates to vegetative community availability.

3. Does meadow vole diet vary in post-agricultural cranberry bogs within season?

   \( H_{A3} \): Meadow voles’ diet composition changes throughout the year.
Site Characteristics:

This study was a part of a live-trapping study investigating the ecological roles of small mammals within post-agricultural cranberry bogs undergoing natural succession and restoration at Franklin Parker Preserve, Burlington County, New Jersey. The location was historically managed for commercial cranberry farming from about 1940-1990 and purchased by the New Jersey Conservation in 2003 (Wen 2010). Restoration efforts began in 2005 and complex soil turnover modification commenced at the time of this study in October 2008.

Sites within Franklin Parker Preserve were selected based on whether they were dominated by obligate hydrophytes (wet) or facultative plants (dry), periodic flooding events, and presence/absence of mound-and-basin complexes created as part of soil turnover restoration modifications. These criteria allowed for only one non-restored dry site, one non-restored wet site, three restored dry sites, and three restored wet sites. Vegetation was monitored throughout the growing season using three 20m transects within each 150m trapping transect. Daubenmire cover class methodology was used inside 1m x 1m quadrats to determine species present and relative vegetative cover (Elzinga et al. 2001).

Microhistological Methods:

Fecal pellets were collected from live-trapped animals via a clear vinyl strip placed below the mesh portion of the Fitch live trap of dimensions 33 cm x 5.5 cm x 5 cm. These samples were stored in a 90% ethanol solution and kept below 0°C. The samples were pooled into composite samples representing each site per season from fall
of 2008 to late summer of 2010 with the following designations: Fall (late September to early October), Winter (December), Spring (March), Early Summer (late May to early June), and Late Summer (July to early August). The samples were sent to the Washington State University Wildlife Habitat Nutrition Laboratory (WHNL) in Pullman, WA for analysis.

At the WHNL, fecal material was broken down by agitation in a household blender, washed over a 75μm mesh screen, and stored in 95% ethyl alcohol for one week. The fecal material was then bleached, stained with lactophenol blue, and mounted to microscope slides using a glycerin mounting gel. The epidermal fragments recovered from the fecal material were then be compared to the plant reference material for identification (Davitt & Nelson 1980).

Diet composition was determined by a identifying epidermal fragments present in fecal samples under microscopy. Each composite fecal sample sent to the WHNL was divided into four slides with 25 random views per slide, for a total of 100 views per fecal sample. Slides were viewed at 100x magnification and increased to 200x-450x when necessary for identification. Positively identified fragments were measured for area covered at 100x with a 10x10 square eyepiece grid. This coverage area was then translated into percent diet composition by dividing it by total coverage area of all species. Diet composition was reported as specific as possible, at least to forage class, if not genus or species. Visible fungal spores and animal remains were analyzed with the same methodology.
Data analysis:

Vegetative characteristics of sites were analyzed using principal components analysis (PCA) to group sites and reduce variables for comparison to diet data. Diet compositions were reported as percentage data and arcsine transformed. Multivariate analysis of variance was used to test variation in major diet components occurring over 5% between sites and seasons. PCA was used to reduce individual diet variables and visualize diet overlap between study sites and seasons. The first three diet composition factor scores were then compared to the first three PCA factor scores for site characteristics using pairwise correlations to elucidate site-based diet trends. All statistics were performed in IBM SPSS Statistics Version 20.

RESULTS

In order to elucidate site-based differences in diet data, vegetative community characters were taken into account. Vegetative characteristics follow those presented in Chapter 1 of this dissertation. Principal Component 1 (PC1) represented 26.5% of the variation in the vegetative data. *Andropogon virginicus, Cyperanus spp.*, *Hypericum gentianoides*, *Juncus biflorus, Juncus tenius, Lechea racemulosa, Lyonia lingustrina, Panicum virgatum, Pinus rigida, Polytricum spp., Vaccinium corymbosum, Vaccinium macrocarpon, Xyris torta*, lichens, downed woody debris, and sand present at the surface were positively associated with PC1. *Carex striata, Eleocharis olivacea, Hypericum perforatum, Juncus canadensis, Juncus pelocarpus, Muhlenbergia uniflora, Proserpinaca pectinata, Rhexia virginica, Rubus hispidus, Rumex acetosella, Scirpus*
cyperanus, *Triadenum virginicum*, and organic soil at the surface were negatively associated with PC1.

Principal component 2 (PC2) represented 24.7% of the variation in the vegetative data. *Acer rubrum, Andropogon glomeratus, Andropogon virginicus, Chamaedaphne calyculata, Cyperus spp., Eleocharis olivacea, Eleocharis tenius, Euthamia teniufolia, Panicum rigidulum, Scirpus americanus, Sphagnum spp., Viola lanceolata*, dead organic matter, and water present at the surface were positively associated with PC2. *Glyceria obtusa, Hypericum perforatum, Kalmia angustifolia, Lacnanthes caroliniana, Leersia oryzoides, Sagittaria engelmanniana, Schizachryium scoparium, Smilax spp., Sparganium americanum, Utricularia spp.*, lichens, and sand present at the surface were negatively associated with PC2. PC1 and PC2 represented 51.1% of the variation in vegetative characters (Chapter 1, Figure 3); PC3 represented an additional 18.7% of the variation in the vegetative data, so that PC1, PC2, and PC3 together represented 69.8% of the variation. Sites were divided based on PC data into two groups that reflect major vegetative communities. Sites A, B, D, and E were grouped as sites with dry vegetative components and sites C, F, G, and H were grouped as sites with wet components. Figure 1 shows percent cover of vegetative species available as food sources in both wet and dry sites.

Major diet components of meadow voles (Table 1) include sedges of the genera *Carex* and *Dulichium*, rushes of the genus *Juncus*, and grasses of the genera *Panicum* and *Amphicarpum*, as well as mosses from the genera *Sphagnum* and *Polytrichum* and the herbaceous plants, *Lacnanthes caroliniana* and *Xyris torta*. Leaves of shrubs from
*Kalmia angustifolia* and the genus *Gaylussacia* were also ingested in quantities greater than 5% of the diet composition.

In regard to meadow vole diet components, multivariate analysis of variance showed no significant difference (F=0.83, p>0.05, df=49) between individual sites; however, multivariate analysis of variance did show a significant difference (F=210.86, p<0.05, df=6) in diet composition between wet and dry sites. Between-subjects tests showed significantly more (F=9.98, p<0.01, df=1) *Lacnanthes caroliniana* consumed in wet sites and significantly more (F=18.31, p<0.01, df=1) *Polytrichum* mosses consumed in dry sites. Multivariate analysis of diet composition between components accounted for over 5% of diet composition showed a significant difference (F=2.89, p<0.01, df=44) among seasons. Between-subjects tests showed a significant difference in seasonal consumption of *Xyris torta* (F=7.11, p<0.01, df=4), *Gaylussacia* leaves (F=4.56, p<0.01, df=4), *Kalmia angustifolia* leaves (F=7.46, p<0.01, df=4), *Amphicarpum purshii* (F=21.54, p<0.01, df=4), *Panicum* spp. (F=4.99, p<0.01, df=4), and *Dulichium arundinaceum* (F=14.80, p<0.01, df=4).

Within dry sites, diet components that accounted for over 5% of diet composition include *Carex* spp. in the fall and *Kalmia angustifolia* leaves in the winter. *Gaylussacia* leaves, *Kalmia angustifolia* leaves, *Carex* spp., *Juncus* spp., and *Polytrichum* mosses were the major diet components in spring, and *Lacnanthes caroliniana*, *Xyris torta*, *Carex* spp., *Dulichium arundinaceum*, *Juncus* spp., and *Polytrichum* moss were the major diet components in early summer. In late summer, *Amphicarpum purshii*, *Panicum* spp., and *Carex* spp. were the major diet components (Figure 2 – left column).
Within wet sites, diet components that accounted for over 5% of diet composition include *Carex* spp. and *Juncus* spp. in the fall, and *Gaylussacia* leaves, *Kalmia angustifolia* leaves, *Carex* spp., and *Sphagnum* mosses were the major diet components in the winter. *Carex* spp. were the only major diet component in the spring. *Lacnanthes caroliniana, Xyris torta, Carex* spp., and *Dulichium arundinaceum* were the major diet components in early summer, and *Lacnanthes caroliniana, Amphicarpum purshii, Panicum* spp., and *Carex* spp. were the major diet components in late summer (Figure 2 – right column).

Seasonal diet composition data was pooled for comparison to vegetative characteristics of each site. PCA showed that PC1 accounted for 35.9% of the variation in the data, PC 2 accounted for 19.4% of the variation in the data, PC 3 accounted for 16.7% of the data. Together, these three components explained 72.1% of the variation in the data. PC 1 was negatively correlated with presence of *Carex* spp., *Dulichium arundinaceum*, and *Lacnanthes caroliniana*, and positively correlated with *Gaylussacia* leaves and *Polytrichum* mosses. PC 2 was negatively correlated with *Sphagnum* mosses, and positively correlated with *Juncus* spp., *Dulichium arundinaceum*, and *Panicum* spp. PC3 was negatively correlated with *Carex* spp., and positively correlated with *Juncus* spp. and *Sphagnum* mosses (Figure 3). Pairwise correlation showed a significant positive correlation ($\rho=0.76$, $p<0.05$, $n=8$) between PC1 for vegetative data and PC1 for diet data. This represents a positive association of dry vegetative characteristics with consumption of available food sources.
DISCUSSION

Meadow voles at Franklin Parker Preserve ate a wide variety of food sources including herbaceous vegetation, leaves and stems of shrubs, tree leaves, mosses, flowers, seeds, fungi, and insects; however, most food sources occurred only in minor quantities. Sedges and flowering plants can potentially be underrepresented in the diet and grasses can be overrepresented as a result of differential digestion rates in meadow voles (Neal et al. 1973). Food sources that occurred in quantities over 5% of diet composition in any single season were comprised of herbaceous vegetation, shrub leaves, and mosses. These food sources are consistent with published life history data on meadow voles (Reich 1981; Riewe 1973; Zimmerman 1965). Major food sources had a statistically significant difference in quantity between sites and seasons, but where diets were comprised of the same components. The only difference in components was representation of mosses. In dry sites, *Polytrichum* mosses accounted for over 5% of the diet composition, but in wet sites, *Sphagnum* mosses accounted for over 5% of the diet composition. This correlates to abundance of these mosses at wet and dry sites (Figure 1).

Meadow voles are known to shift their diet with seasons (Lindroth & Batzli 1984; Linzey 1984). During the fall, consumption of *Sphagnum* mosses and grasses of the genus *Panicum* were greatest in dry sites, but consumption of *Sphagnum* mosses was lower in wet sites. Wet sites had more consumption of *Panicum* and rushes of the genus *Juncus*. Fall was the only season with significant consumption of *Sphagnum* mosses in dry sites. This may be an indicator of the use of *Sphagnum* mosses as a source of hydration in the drier sites in fall or of accidental ingestion. Meadow voles at Franklin Parker Preserve consumed either *Polytrichum* or *Sphagnum* mosses during all seasons in
both wet and dry sites, contrary to findings by Linzey (1984) that show a seasonal switch to mosses in winter.

Meadow voles in wet sites ate substantial quantities of *Lacnanthes caroliniana* during all seasons but spring. This is likely due to availability of plant during its growing season and its abundance in wet sites. Consumption of this flowering plant by meadow voles may aid plant diversity at Franklin Parker Preserve, where this species forms large carpets in some post-agricultural bogs with preferred microhabitat characters.

Interestingly, meadow voles consumed *Gaylussacia* leaves in significant quantities in both wet and dry sites, but while these shrubs are known to occur at Franklin Parker Preserve, they did not occur in sufficient quantities to be detected during the vegetation surveys. This is most likely due to the random design of the vegetation survey, but it may also be evidence of meadow voles actively seeking out these evergreen shrubs as a food source, particularly in winter and spring when other food sources may be less abundant. Meadow voles at Franklin Parker Preserve did increase their consumption of *Kalmia angustifolia*, another evergreen shrub, during these same seasons. Dry sites in spring provided a more varied diet, including not only these evergreen shrubs, but also sedges of the genus *Carex*, rushes of the genus *Juncus*, and *Polytrichum* mosses. Consumption of major food sources in wet sites during spring was minimal, as meadow voles heavily increased their consumption of *Carex* at this time. Consumption of *Carex* was relatively steady across seasons and sites otherwise.

Early summer and late summer were the only seasons when there was any significant consumption of *Amphicarpum purshii* at both wet and dry sites. This grass has subterranean propagules that become available during this season (Cheplick & Quinn
Meadow voles may be utilizing this seasonally abundant food source during the short window in which it is available. Grasses from the genus *Panicum* were consumed in smaller quantities during the year, but had significant increases in consumption during late summer corresponding with maturation of these plants (Rhoads & Block 2007). *Panicum* is known to be a major food source for meadow voles in a wide variety of habitats (Zimmerman 1965).

Nutritionally, meadow voles are known to choose food sources that are low in digestive inhibitors and high in protein, particularly when populations are in high density. As density increases, voles show no tendency to switch to lower quality food sources to compensate for additional food competition. Foods high in protein aid in digestion of toxic secondary metabolites associated with herbivory in voles (Bergeron & Joudoin 1989; Bergeron & Jodoin 1987; Bucyanayandi & Bergeron 1990). Meadow voles selectively choose habitats with better food quality and move to habitats of better quality when vole density increases (Morris & MacEachern 2010; Oatway & Morris 2007). Consumption of large seeds by meadow voles has been shown to change overall vegetative structure of prairies (Howe & Brown 2000), and selective herbivory of mature prairie vegetation alters plant community composition eliminating otherwise common plants within the system and creating plant communities composed of non-preferred food choices (Howe & Lane 2004; Howe et al. 2006). Meadow vole predation on tree seedlings affects both colonization and survival, greatly impacting and delaying old field succession in areas of high vole density (Manson 2000; Manson et al. 2001; Ostfeld & Canham 1993; Ostfeld et al. 1997; Pusenius et al. 2000; Pusenius & Schmidt 2002).

Although meadow voles at Franklin Parker Preserve did not predate on seeds or seedlings
in high quantities, their known impacts on old field and prairie succession suggest that preferential feeding on major food sources at Franklin Parker Preserve could influence succession and restoration efforts within the preserve.

**MANAGEMENT IMPLICATIONS**

Meadow voles at Franklin Parker Preserve preferentially feed on grasses, sedges, rushes, mosses, some flowering plants, and evergreen leaves. Diet composition varies between wet and dry sites and with seasons. Available literature on the influence of meadow voles in successional grasslands indicates that they have a significant potential to alter succession and restoration efforts. Restoration efforts at Franklin Parker Preserve should monitor populations of small mammals, particularly large populations of meadow voles that may influence the colonization and survival of plant species. Further experimental and exclusionary studies are recommended in order to elucidate whether meadow vole diet is influencing plant community composition or whether plant availability is influencing meadow vole diet.
**LITERATURE CITED**


**Table 1. Diet composition of meadow voles at Franklin Parker Preserve, Burlington County, NJ.** Diet is presented as mean percentage composition categorized by season and grouped by wet or dry vegetative characters of study sites. Components above 5% are bolded.

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<th>Dry Sites (n=4)</th>
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<th>Spring</th>
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<th>Late Summer</th>
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Figure 1. Mean percent cover of vegetative characters for wet and dry post-agricultural cranberry bogs at Franklin Parker Preserve, Burlington County, NJ. Multiple species occurring within a genus were pooled for comparison to diet composition data.
Figure 2. Mean diet composition of major diet components (>5%) for meadow voles at Franklin Parker Preserve, Burlington County, NJ. Left column represents dry sites, right column represents wet sites. Panels differentiate seasons.
Figure 3. Principal components analysis of diet composition data for meadow voles occurring at Franklin Parker Preserve, Burlington County, NJ. Top panel shows wet sites, bottom panel shows dry sites. Markers denote seasons.
CHAPTER 3: EXPLORING SMALL MAMMAL ENDOZOOCHORY IN RESTORATION OF POST-AGRICULTURAL WETLANDS

ABSTRACT

Seed dispersal through ingestion and defecation is a common occurrence for many frugivorous mammals, yet the phenomenon is understudied for small species generally thought to only be seed predators. This research investigates whether rodents ingesting small seeds through grazing herbivory can disperse seeds capable of germination and seedling establishment via defecation. Fecal samples collected as part of a small mammal live-trapping study were planted in standard germination medium and kept in a greenhouse under environmental conditions mimicking the natural habitat. While overall germination and seedling establishment was low, a small number of individual plants were able to successfully establish. This shows that small mammals can play a role in endozoochorous seed dispersal and potentially influence local plant distribution patterns.

INTRODUCTION

Seed dispersal is a critical aspect of whole-ecosystem restoration because understanding the fate of propagules within an ecosystem is essential to meeting restoration targets (Bakker et al. 1996; Palmer et al. 1997; Young et al. 2005). Animals are known to disperse seeds passively through adhesion and accidental ingestion or actively through frugivory and caching behavior (Stiles 2000). In particular, endozoochory, as the latter sentence is termed, is a well-documented mechanism of seed dispersal in mammals. Passive dispersal via accidental ingestion has been reported in large herbivores that take in seeds while grazing on adjacent foliage. Active dispersal
through frugivory, however, differs in that the animal actively chooses to eat fruit containing seeds (Stiles 2000). Regardless of the method of ingestion, viability of the seed after initial mastication and subsequent physical and chemical breakdowns during digestion is critical to seed survivability. The variety of animals documented to disperse seeds spans many taxa including earthworms, beetles, tortoises, fish, and frogs, but the majority of dispersal has been documented among birds, ants, and mammals. Mammals are second to birds in vertebrate seed dispersal in terms of their ability to disperse seeds trans-continentally on migration routes (Chambers & MacMahon 1994; Stiles 2000).

The ability of seeds to survive endozoochory and produce seedlings has been shown across many groups of mammals including, primates, bats, elephants, and some omnivorous carnivores (Stiles 2000). Beyond survival, the physical and chemical digestion processes of some mammals have been shown to promote germination rates. Goats have been shown to increase germination rates in Mediterranean silver broom legumes (Robles et al. 2005), sheep promote germination of rock roses in Spain (Ramos et al. 2006), and martens improve germination of berries in Alaska and Central Europe (Hickey et al. 1999; Schaumann & Heinken 2002). Rodents are widely known as seed predators (Crawley 2000), and many small mammals are known to disperse seeds through caching activities (Vander Wall 1990). Research documenting the ability of small mammals to disperse seeds via ingestion, however, has been very limited.

What evidence that does exist regarding endozoochorous small mammal seed dispersal, has been scant and has only focused on rats. Rats are known to disperse the small seeds of Hawaiian and New Zealand shrubs after consuming the fruit (Shiels & Drake 2011; Williams et al. 2000). The primary focus of this paper is to explore the
possibility of endozoochory in the small mammals inhabiting post-agricultural cranberry bogs, and the possible interaction between dispersal and overall vegetative restoration.

**METHODS**

*Research Questions*

(1) Do small mammals disperse viable seeds through ingestion?

- $H_{A1a}$: Seeds dispersed by small mammals are viable and will germinate.
- $H_{A1b}$: Plant species with small seeds are dispersed via small mammal fecal matter.

(2) Do different small mammal species disperse different plant species?

- $H_{A2}$: Meadow voles will disperse different plants than white-footed mice.

*Seed Dispersal Methods*

Fecal samples were obtained as part of a live-trapping study of small mammals at the Franklin Parker Preserve, Burlington County, New Jersey. The preserve is a former cranberry farm which has been undergoing succession for over 20 years and currently commencing a wetland restoration plan. Study sites were randomly placed in post-agricultural bogs with both wet and dry habitat characters. Trapping sessions were divided into 5 seasons as follows for seasonal analysis: Fall (late September to early October), Winter (December), Spring (March), Early Summer (late May to early June), and Late Summer (July to early August). Fecal samples were collected from plastic sheets placed underneath the mesh portion of a Fitch live trap and any vegetation existing
on the surface of the pellets was removed. The samples were allowed to air dry for at least one week before seed dispersal analysis.

In order to prepare the dried samples for the germination study, the samples were soaked for twenty-four hours in distilled water. The samples were then planted in standard seed germination medium (Farfard® 4M mix: 40% peat, pine bark, vermiculite, dolomitic limestone) and allowed to germinate under ambient light and temperature regimes at the Rutgers Floriculture Greenhouse, Middlesex County, New Jersey. Full sun was chosen to mimic the open, full sun nature of the post-agricultural cranberry bogs. Samples were watered daily for twelve weeks. Plants that germinated were grown until the point of plant identification. Established seedlings were removed from the greenhouse and placed outdoors to continue to grow. Plant species abundance was recorded for comparison with small mammal disperser and habitat type.

RESULTS

There were 262 total fecal samples used from small mammals at Franklin Parker Preserve. Most samples (255) were from meadow voles (*Microtus pennsylvanicus*) and seven from white-footed mice (*Peromyscus leucopus*). Eight samples successfully established seedlings that survived to identification (Table 1). Those plants were: orangegrass, Canada St. Johnswort, slender spikerush, two occurrences of fireweed, two occurrences of panic grass, and a poverty rush. All plants were dispersed by meadow voles. Six of the eight plants were sampled from wet habitats and one of the panic grasses and the path rush were sampled from dry habitats, but established samples spanned across the year.
DISCUSSION

Seed size and seed output are important factors in the ability of animals to disperse seeds (Bruun & Poschlod 2006; Pakeman et al. 2002). All plants that germinated in this study are prolific seeders and produce small seeds that are 0.5 to 0.9 mm in length (Rhoads & Block 2007; Society 2013; USDA 2013). The primary dispersal mechanism for fireweed is wind (Darbyshire et al. 2012), while the others are most likely primarily dispersed either passively or actively by animals other than small mammals. Different species of St. John’s-worts are known to be dispersed by wind and animal movement (Crompton et al. 1988), and path rush is documented as an adhesion disperser (Fleming 1974). Panic grasses and spikerushes have been documented to be dispersed by ingestion and adhesion by waterfowl (DeVlaming & Vernon 1968; Vivian-Smith & Stiles 1994).

Seed predation by small mammals, including those of the genera *Microtus* and *Peromyscus*, has been well documented (Borchert & Jain 1978; Crawley 2000; Howe & Brown 2000; Manson & Stiles 1998; Ostfeld et al. 1997). Evidence from this germination study is consistent with findings about white-footed mice as exclusive seed predators; however, this does raise the possibility that meadow voles disperse seeds. While the germination rate of plants from the feces of meadow voles was low (3%), the sheer ability of seeds to survive digestion and germinate is noteworthy.

In addition to seed dispersal, small mammals have the ability to engineer habitat conditions to promote a favorable environment (LoGiudice & Ostfeld 2002; Manson et al. 2001; Ostfeld & Canham 1993; Ostfeld et al. 1997, 1999). Meadow voles have been shown to have significant effects on vegetation in fields undergoing succession. Granivory
and herbivory by meadow voles can directly influence vegetative community composition (Howe & Brown 2000; Howe & Lane 2004; Howe et al. 2006). Seedling predation by meadow voles can prevent forest regeneration and maintain old-field habitat conditions, denoting meadow voles as keystone herbivores in old-field systems (Manson et al. 2001; Ostfeld & Canham 1993; Ostfeld et al. 1997, 1999). Rats (Rattus rattus, R. norvegicus, R. exulans) are documented to have the ability to change vegetative structure on invaded islands through seed manipulation. They are both seed predators and dispersers, with the ability to disperse small seeds of after ingesting the surrounding fruit (Shiels & Drake 2011; Williams et al. 2000). Meadow voles have been documented to have variable home range sizes dependant on sex, age, and habitat quality, with those in fragmented habitats having greater home range size (Bowers et al. 1996; Collins & Barrett 1997; Jones 1990). They also have the potential to move long distances (>1 km) during dispersal events (Ostfeld & Manson 1996). The consequences of such movement patterns can have significant implications for the role of meadow voles in vegetation dispersal associated with habitat restoration and succession.

In addition, the additive effects of food web dynamics could also have impacts on seed dispersal. Avian predators have been reported as effective secondary seed dispersers when ingesting frugivorous lizards (Nogales et al. 2002). Might it be possible for predatory birds feeding on the abundant populations of meadow voles at Franklin Parker Preserve to disperse seeds?

While this study suggests the probability that meadow voles can contribute to the dispersal capabilities of some plants, further research in this area is warranted. There may be a disparity between seeds passed through digestion and those that successfully
germinate, as could have been the case in this study. Therefore, deconstructing fecal samples to analyze seeds that have passed and tailoring germination conditions may optimize success and would give a better picture of the survivability of seeds post digestion.

This study demonstrates that seeds ingested by meadow voles can successfully establish seedlings under greenhouse conditions; in situ germination studies within post-agricultural wetlands is warranted to elucidate differences in seedling establishment under natural conditions. Additionally, those species dispersed by meadow voles are primarily dispersed by other means. The small impact of local dispersal could be affected by meadow vole activity and warrants further study. The ability of meadow voles to further influence vegetative communities through seed dispersal increases the importance of understanding these animals in succession and restoration efforts.
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Table 1. Germination data from fecal samples obtained at Franklin Parker Preserve, Burlington County, NJ and processed at Rutgers Floriculture Greenhouse, Middlesex County, NJ.

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<th>Germinated plant</th>
<th>Disperser</th>
<th>Study Site</th>
<th>Season</th>
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<tr>
<td>Orangegrass (<em>Hypericum gentianoides</em>)</td>
<td>Meadow vole (914)</td>
<td>G (wet)</td>
<td>Winter 2009</td>
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<tr>
<td>Canadian St. John’s-wort (<em>Hypericum canadense</em>)</td>
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<td>Meadow vole (722)</td>
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<td>Fall 2009</td>
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<tr>
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<td>Meadow vole (597)</td>
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<tr>
<td>Panic grass (<em>Panicum sp.</em>)</td>
<td>Meadow vole (931)</td>
<td>G (wet)</td>
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<tr>
<td>Panic grass (<em>Panicum sp.</em>)</td>
<td>Meadow vole (717)</td>
<td>E (dry)</td>
<td>Late summer 2009</td>
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<tr>
<td>Path rush (<em>Juncus tenuis</em>)</td>
<td>Meadow vole (687)</td>
<td>E (dry)</td>
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CHAPTER 4: A METHOD OF MOLECULAR SCATOLOGY FOR USE IN SMALL-SCALE DIET STUDIES OF INSECTIVOROUS ANIMALS

ABSTRACT

Diet studies are in integral component of understanding the relationships between organisms and how they interact with their environment. Traditionally, these studies have been done either through direct observation or through microhistological analysis of feces or stomach contents. Molecular analysis of feces and stomach contents has grown with the advent of modern genetic technologies, allowing researchers to analyze remnant genetic material occurring in very small quantities. These techniques, however, have generally been restricted to research programs with significant technological and monetary resources. This research explores a methodology of molecular scatology using the basic molecular tools of polymerase chain reaction and gel electrophoresis to distinguish prey-specific primers by size alone. The ability to distinguish possible prey species in this way broadens the scope of molecular diet analysis to include those research programs with fewer resources and allow the inclusion of these methodologies into standard laboratory classrooms.

INTRODUCTION

Determining trophic relations has long been critical to the study of ecology. Understanding food relationships requires not only an understanding of what is available but also what is actually ingested. Though many small mammal species may eat a wide variety of food, understanding what is being eaten within a populations is critical when considering local survival and distribution. Diet analyses, therefore, are an integral
component to understanding how groups of small mammals interact with their environment.

Traditional diet analyses, such as stomach content or fecal techniques via microscopy can produce identification errors and incomplete data. In addition, there may be biases with over or underrepresentation of certain food items. (Clare et al. 2009; Holechek et al. 1982; Soininen et al. 2009). Further, traditional microhistological techniques require prey remains to be identifiable in feces or stomach content samples, often making highly digested fragments impossible to identify. Using molecular techniques does not require identifiable prey pieces. Molecular scatology uses remnant genetic material of food sources expelled in fecal matter to assess an organism’s diet and can complement or even supersede the data produced through traditional techniques and are much more specific than stable isotope and fatty acid detection (Deagle et al. 2005; Rolfe 2011).

Molecular scatology has been used to assess the diets of a wide variety of organisms, including wild primates (Bradley et al. 2007; Hofreiter et al. 2010), bats (Clare et al. 2009; Rolfe 2011; Zeale et al. 2011), freshwater fish (Corse et al. 2010), penguins (Deagle et al. 2010), and brown bears (Hoss et al. 1992). Molecular scatology has been a useful tool for determining trophic interactions of invasive species and between co-occurring species of concern (Blanchet 2012; Farrell et al. 2000; Purcell et al. 2004). It also allows for non-invasive methods of diet determination for species that are rare, cryptic, or with conservation concerns (Jarman et al. 2002; Piggott & Taylor 2003; Waits & Paetkau 2005). Such techniques have enabled researchers to make important
management decisions regarding wildlife populations when that data would have be otherwise unattainable.

Soininen et al. (2009) compares microhistological techniques with that of molecular scatology on the diet of two vole species. Their results show that the two techniques are complementary to each other, but the molecular technique gives higher taxonomic resolution than microhistology (Soininen et al. 2009). Further, the use of prey-specific primers can reliably allow molecular techniques to detect small amounts genetic material that remain in highly digested samples (Deagle et al. 2005; Jarman et al. 2004; Symondson 2002; Valentini et al. 2009). This research explores molecular scatology techniques to provide information specific to using available protocols for small mammals, particularly for food sources within insect orders.

Most available protocols require sequencing of remnant genetic material after performing a polymerase chain reaction (PCR), which can be prohibitively expensive and sometimes impractical (Corse et al. 2010; Sheppard & Harwood 2005). This research investigates molecular techniques that in combination with microhistology, can use an alternative post-PCR tool like gel electrophoresis to identify remnant genetic material of food items. Such information can provide a critical research tool for future work in this area.

Research Question

This research will isolate primers that are unique to specific insect orders. While the ability to amplify targeted regions of genetic material through primer design is well-established, key primers in these insect orders have not been developed. This work is
critical, however, because by using targeted primers that are unique to specific insect orders, remnant genetic material in fecal samples can be amplified to differentiate prey sources present in the sample. Primers can be designed so that target fragments from different orders will differ in length, and these length differences can be detected on an agarose gel without the expense of sequencing.

**METHODS**

The procedure for genetic extraction is important to remove potential inhibitors and isolate available genetic material for amplification, but there are many methods reported to have performed well in recovering genetic material from fecal samples. These methods include extraction from the commercially available QIAamp® DNA stool mini kit (QIAGEN - Hilden, Germany) (Machiels et al. 2000) and DNeasy® *mericon* food kit (QIAGEN - Hilden, Germany) (Zarzoso-Lacoste et al. 2013), and non-commercial cetyltrimethylammonium bromide (CTAB) methods like those described in Zhang et al. (2006). The method of genetic extraction depends on the amounts of animal or plant matter likely to be part of the organism’s diet and should be chosen based on that information.

Zarzoso-Lacoste et al. (2013) report that the DNeasy® *mericon* food kit is the best extraction protocol for omnivorous animals. The DNeasy® *mericon* food kit uses both CTAB and the enzyme Proteinase K (PK) to digest plant and animal tissue, increasing its ability to extract genetic material from a wide variety of food sources. The included QIAamp silica spin columns remove a significant amount of PCR inhibitors (Zarzoso-Lacoste et al. 2013).
Zhang et al. (2006) report that CTAB methods produce more recoverable genetic material than commercially available kits when samples are taken from animals ingesting large amounts of vegetation. Vegetation has been known to produce a large amount of PCR inhibitors. In this method, genetic extraction takes place by washing fecal matter in ethanol, centrifuging, and washing again in TNE buffer. The samples are then mixed with TNE buffer and PK, incubated and centrifuged again. The supernatant is suspended in potato starch and centrifuged. The new supernatant is mixed with sodium chloride and CTAB solution, incubated, and extracted twice with a phenol:chloroform:isoamyl alcohol solution. The supernatant is then added to binding buffer, placed in a spin column, and centrifuged. Filters are then washed with 75% ethanol so that the RNase can then be added to DNA for PCR (Zhang et al. 2006).

Here, it is recommended that PCR be employed to amplify remnant genetic material from food sources within fecal matter. Primers used for this analysis are designed to specifically highlight homologous portions of genomic material that contain enough variation to ascertain taxonomic differences. An alignment of a hypervariable portion of the nuclear rRNA gene (18S) was selected for possible insect food sources (Kjer 2004). The alignment used to create recommended primers is found in Table 1 and recommended primers are listed in Table 2. Genetic sequences used to design primers were obtained from the GenBank database, although known insect samples should be collected from field sites in order to establish a species specific database of the length of the amplified fragments. Incubation time and temperature follow standard laboratory procedure tailored to results being produced during testing. Post amplification, PCR products could be processed through gel electrophoresis with known standards. Distance
traveled as compared to standards will quantify the presence/absence of taxonomic groups within fecal samples.

**DISCUSSION**

This study targeted the 700-1400 base pair region of the 18S rRNA gene because of the amount of diversity between taxa in this region (Kjer 2004). The primers recommended in Table 2 provide unique forward or reserve primers for 14 of 22 insect orders commonly found in North America. Those orders without primers provided in Table 2 did not possess sufficient diversity in the targeted region to construct a unique forward or reverse primer, but it is possible that those primers exist in areas outside of the targeted region. Additional research should investigate that possibility.

The primers provided in Table 2 amplify regions of the 18S rRNA gene that are 300-500 base pairs in length. Size of amplifiable material available from remnant fecal material should be tested for size in order to assess the applicability of these primers for this method (Deagle et al. 2006). The mean fragment size of amplifiable genetic material that remains non-degraded after digestion has been found to be 100-200 base pairs (Clare et al. 2009; Deagle et al. 2006; Valentini et al. 2009).

Primers were tested with the basic local alignment search tool (BLAST) for the possibility of amplifying non-target genetic material. After manually removing GenBank accession errors from the search results, seven of the orders with primers provided did not have any likely cross-matches. Collembola, Protura, Archaeognatha, Emphemeroptera, Dermaptera, and Pthiraptera did have minimal cross-matches with other orders. These cross-matches may be due to less apparent GenBank errors or due to
the large and diverse natures of these orders. Regional genetic diversity within groups can be a compound factor. It is recommended that these primers be tested against reference samples taken from insects occurring in the specific study area in order to rule out possible cross-matches.

**METHODOLOGICAL IMPLICATIONS**

This method of molecular scatology using prey-specific primers and gel electrophoresis is designed to be carried out with basic laboratory equipment and skill level. It is most widely applicable in situations where only a few prey sources are being investigated or where broad diet range is in question. It can also be a valuable teaching tool in introductory level undergraduate courses. If more resources are available, sequencing of genetic material after amplification provides much greater resolution when species specific identification is required.
LITERATURE CITED


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**Table 1. 18S rRNA alignment after Kjer (2004).**
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### References

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- [Dipterida](https://example.com/dipterida)
- [Hymenoptera](https://example.com/hymenoptera)
- [Euschmidtia cruciformis](https://example.com/euschmidtia-cruciformis)
- [GRZ97569 Grylloblatta rothi](https://example.com/grz97569-grylloblatta-rothi)
- [AF220569 Microhodotermes viator](https://example.com/af220569-microhodotermes-viator)
- [AF201421 Distocupes sp](https://example.com/af201421-distocupes-sp)
- [AY121139 Chelisoches morio](https://example.com/ay121139-chelisoches-morio)
- [AY037170 Parajapyx emeryanus](https://example.com/ay037170-parajapyx-emeryanus)
- [AY037168 Parajapyx emeryanus](https://example.com/ay037168-parajapyx-emeryanus)
- [X77785 Polistes dominulus](https://example.com/x77785-polistes-dominulus)

### Notes

- All sequences have been amplified using universal primers.
- All data is available in GenBank under the specified accessions.
- Further details and references are available in the cited literature sources.
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**Note:** The accessions numbers and descriptions are placeholders and should be replaced with actual scientific names and accession numbers.
Table 2. Recommended prey-specific insect primers for 18S rRNA molecular scatology.

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**no unique primers found**

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**no unique primers found**
CONCLUSION TO THE DISSERTATION

The anthropogenic modification of natural lands for agriculture is a staple component of human history. The advent of modern agricultural techniques has allowed higher crop production on smaller tracts of land, facilitating a proliferation of post-agricultural areas that have the opportunity to return to more natural conditions. Ecological succession alone is often not enough to return specialized habitats like wetlands to naturally functioning ecosystems without the intervention of active habitat restoration efforts. This dissertation investigated conditions within post-agricultural wetlands of the New Jersey Pine Barrens at the start of active restoration efforts, but after a decade of natural succession. Specifically, this dissertation focuses on small mammal communities because of their integral role in linking primary productivity with higher-order components of the ecosystem and their ability to influence vegetation patterns within the habitat.

The site selected to investigate the influence of small mammals in post-agricultural wetlands was the Franklin Parker Preserve, Burlington County, New Jersey. The preserve was originally natural wetland habitat that was converted to cranberry farming in the mid-20th century. It was actively farmed until the end of the century and then became the property of the New Jersey Conservation Foundation with hopes of returning the area to a naturally-functioning wetland system once again. In order to assess those small mammals utilizing these post-agricultural wetlands, I conducted live-trapping surveys within selected areas of Franklin Parker Preserve over the course of two years (2008-2010). These surveys showed that the most abundant small mammal on the property is the meadow vole (*Microtus pennsylvanicus*). Meadow voles occurred in sites
with both wet and dry vegetative characteristics, but were more abundant in wet sites. Dry sites also had significant amounts of white-footed mice (*Peromyscus leucopus*). The diversity of small mammals at Franklin Parker Preserve was compared to previous studies I conducted in natural wetlands with little anthropogenic disturbance at Warren Grove Gunnery Range, Burlington County, New Jersey. Similarity between locations was extremely low, indicating that the suite of small mammal species within the post-agricultural wetlands of Franklin Parker Preserve does not represent that of natural wetlands within the New Jersey Pine Barrens. The abundance of meadow voles within these post-agricultural wetlands coupled with the absence of other species known to occur in natural wetlands is likely to impact ecosystem functioning. Because of this disparity, trophic linkages may not support natural ecosystem functioning and have detrimental influence on restoration efforts.

To further explore the influence of meadow voles in post-agricultural wetlands, I investigated the diet of meadow voles within this habitat. Fecal microhistological analysis revealed that meadow voles had a strongly herbivorous diet that focused on grasses, sedges, rushes, mosses, and some forbs and leaves of shrubs. Consumption of individual species varied between wet and dry sites and among seasons, but was not correlated to availability of those plants in the habitat. Due to constraints of the dissertation, I could not further elucidate whether selective feeding by meadow voles was altering plant composition within the habitat. Overall, the specific diet of the highly abundant meadow vole has the potential to significantly impact vegetation patterns within post-agricultural wetlands, but experimental removal studies would be needed to answer the question further.
In addition to microhistological analysis of meadow vole diet, I investigated the possibility of endozoochorous seed dispersal in this species. Utilizing standard greenhouse methodology for seed germination, I was able to grow eight plants of six different species from fecal samples of meadow voles. These species are all early colonizers that thrive on disturbance and commonly disperse seeds in other ways. Dispersal through endozoochory is a minor facet; however, this is a significant finding in that current scientific literature focuses on endozoochory in larger, more frugivorous species. The ability of meadow voles to have local dispersal impacts on some species increases their influence on vegetation patterns.

The results of this dissertation show that the suite of small species utilizing post-agricultural wetlands at Franklin Parker Preserve is not similar to that of natural wetlands in the region. The most abundant species, the meadow vole, has a specific diet composition and possesses the ability to disperse some seeds on a very local level. This study was conducted at the very beginning of a restoration project after a significant period of natural succession, and thus provides an initial snapshot at the start of a long-term restoration process. This information has significant implications for the course and priorities of restoration efforts on the property.

Current management of vegetation and hydrological regimes need to account for the disparity in small mammals. The increase in habitat heterogeneity created with the mound-and-basin topographic modification may be sufficient enough to encourage recruitment of typical wetland species after a longer period of time; however, increasing connectivity with other wetland habitats in the area increases immigration potential. Creating additional corridors to allow for species flow would benefit the restoration
efforts at Franklin Parker Preserve. Long-term monitoring efforts need to include
assessment of both flora and fauna, including monitoring of small species that are critical
trophic links within the ecosystem. In-depth vegetative habitat analysis of Franklin Parker
Preserve is necessary to gain a clearer picture of basic differences between areas within
the preserve and other wetlands in the area. Additional experimental studies should also
be conducted to assess specific habitat changes that can increase recruitment of more
species. Experimental studies should also include assessing impacts of meadow voles on
patterns of specific plant species. The goals of ecological restoration involve recreation of
natural whole-ecosystem function and without adequate information at all levels of the
ecosystem, such goals would be difficult to attain.
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