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Foraging by mice in spatially and temporally variable agricultural fields: Implications for volunteer corn, invertebrate and weed pest control

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**Foraging by mice in spatially and temporally variable agricultural fields: Implications
for volunteer corn, invertebrate and weed pest control**

by

Tatyana Flick

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

Major: Ecology and Evolutionary Biology

Program of Study Committee:
Brent Danielson, Major Professor
Matt Liebman
Karen Abbott

Iowa State University

Ames, Iowa

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For my parents with love

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iv
ABSTRACT	v
CHAPTER 1 GENERAL INTRODUCTION.....	1
Background	1
Objectives	4
Thesis Organization	5
References	6
CHAPTER 2 RESOURCE DISTRIBUTION INFLUENCES OVERWINTER FORAGING BY MICE IN AGRICULTURAL FIELDS: IMPLICATIONS FOR VOLUNTEER CORN CONTROL	8
Summary	8
Introduction	10
Methods	14
Results	18
Discussion	19
Acknowledgements.....	28
References	28
CHAPTER 3 TEMPORAL VARIATION IN INVERTEBRATE AND SEED CONSUMPTION: UNDERSTANDING THE DIETS OF MICE IN A NOVEL AGRICULTURAL HABITAT	35
Abstract	35
Introduction	36
Methods	39
Results	42
Discussion	44
Acknowledgements.....	48
References	48
CHAPTER 4 GENERAL CONCLUSIONS.....	57
Conclusions	57
Future Directions	62
References	64

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ABSTRACT

The prairie deer mouse (*Peromyscus maniculatus bairdii*) is a common year-round resident of Midwestern agricultural fields, and provides several ecosystem services. Previous studies and preliminary findings have shown that the mouse consumes large quantities of weed seeds and waste grain during the fall and winter. However, it is unknown how the spatial and temporal variation in resource types and their distribution affects foraging by deer mice in these crop fields. The following two studies were designed to 1) experimentally test how resource distribution (patchiness) within a field affects foraging by deer mice and 2) examine the temporal variation in diet composition of deer mice living in conventional corn fields. The results of these two studies add to our understanding of how weed populations and volunteer corn are regulated by deer mice in corn fields, which has important weed management implications. Ultimately, increased knowledge of the temporal variation in the deer mouse's diet and understanding how mice respond to variations in resource patchiness contribute to our basic ecological understanding of foraging in variable environments as well as emphasizing the value of these mice in the future of Midwestern agriculture.

CHAPTER 1. GENERAL INTRODUCTION

Background

Agricultural land-use now dominates more than 50% of ice-free land globally (Ellis *et al.* 2010). In the past century, developments in machinery, genetics and chemicals have allowed for the intensification of agricultural practices and significant increases in productivity (McLaughlin & Mineau 1995). Undoubtedly, these changes have allowed for immeasurable advances and benefits for humans globally. Within these landscapes, however, there are often environmental concerns about habitat loss, decreases in biodiversity and loss of ecological function as well as related management concerns such as pest control (including pesticide resistance issues) and overall crop productivity. As a result, many worry that these highly productive, intensively managed and often oversimplified systems are unsustainable (e.g., Benton *et al.* 2003; Tschardtke *et al.* 2012; Service 2013). The importance and vast extent of these systems demands ongoing research into ways in which we can mitigate the negative effects while still providing overall benefits and products.

In the drive to find solutions that could reduce the negative impacts of agricultural land-use, the natural checks and balances that are already in place are often overlooked. Could incorporating more ecologically based ideas into the management of these systems allow for reduced chemical inputs and overall negative impacts? The answer in many cases is yes (Liebman & Gallandt 1997). For example, recent work suggests that wildlife may have an important role in pest control within these systems (e.g., Westerman *et al.* 2005). Identifying and understand the role that key organisms play in agricultural settings may open

new avenues in managing agricultural systems, directly benefiting management and also indirectly addressing other associated environmental concerns.

This thesis will focus on studying one such organism, which has the potential to provide important benefits to agricultural production through increased pest control in a highly intensified cropping system. In the Midwestern United States, the conversion of land from native prairie to intensive row-crop agriculture has resulted in an increasingly homogeneous landscape and a heavy reliance on pesticide applications (Rhemtulla *et al.* 2007; Meehan *et al.* 2011). Focusing on more ecologically based pest management in this system will have direct and indirect positive effects on management and additional environmental concerns surrounding this major land-use (i.e., increased pest control and reduced chemical inputs).

The prairie deer mouse (*Peromyscus maniculatus bairdii*) is a common small mammal found throughout most of North America and is one of the few year-round residents of Midwestern agricultural fields. Studies have shown that this mouse potentially provides several ecosystem services by preying on pest species found within conventional crop fields (Clark & Young 1986; Harrison *et al.* 2003; Westerman *et al.* 2008; Heggenstaller *et al.* 2006). Unlike several other small mammals, the deer mouse is active year round and therefore has the potential to influence several prey populations, especially during the winter when few other organisms are active. Additionally, mice are not deterred by herbicide resistance in weeds and crop volunteers (weeds resulting from fallen waste grain) nor can these weeds develop resistance to mouse predation, showing that these mice have key management advantages over chemical pest control methods. Understanding the factors that influence individual mice as well as whole populations living within these fields will not only

increase our understanding of how this specific species can benefit agriculture but also act as an example of how wildlife can be effectively incorporated into more ecologically minded agricultural practices, which would have global environmental and management implications.

Foraging by prairie deer mice has the potential to influence several pest populations (e.g., weeds, volunteer corn, invertebrates) living within crop fields and, therefore, understanding what factors influence their foraging and overall ecology in these novel environments will be important in the future of conventional agriculture. Specifically, this work will look to understand how the spatial distribution and temporal variability in resources influences how efficiently mice can forage, what specific resources contribute to their diet at various points throughout the year, how these factors influence the overall mouse populations as well as the pest control implications of these findings.

Although agricultural systems are often characterized by overall structural simplification, heterogeneity may still persist at various scales (Benton *et al.* 2003; Vasseur *et al.* 2013). For example, within a particular crop field, we may find spatial complexity arising from patterns in topography, variation in soil composition, and weed patchiness to name a few (Cousens *et al.* 2006; Blanco-Moreno *et al.* 2008). If we focus specifically on weeds (a pest that may be controlled by deer mice), we see that although weed patches are often temporally and spatially stable, the number, composition, size, and distribution of these patches may vary from one field to another. Management and farming practices, such as tillage and the use of pesticides, can affect this spatial heterogeneity of weed patches (i.e., size, shape and number of patches) within a field during a given year which may have ecological consequences. This spatial variation in weed ‘patchiness’ may affect the behavior,

abundance and distribution of deer mice (and other organisms) within these fields as well as the potential productivity of the crop field in general (Blanco-Moreno *et al.* 2008).

In addition to the characteristic spatial simplification, agricultural landscapes also have modified temporal regimes. Unlike natural ecosystems, crop-management regimes often influence the temporal availability of several resources, such as invertebrates and seeds, which are important to deer mice and other organisms. For example, the application of insecticides reduces invertebrate availability, crop harvest increases the availability of both weed seeds and waste grain on the surface of the soil, and tilling reduces the availability of these same seeds by burying them underground. Thus, the deer mice living within these fields experience spatially and temporally variable foraging environments.

By focusing on key species that live in conventional crop fields (e.g., deer mice) and studying their ecology, I hope to gain a better understanding of how wildlife can provide ecosystem function benefits, such as pest control, which could induce a change in conventional agricultural practices and potentially reduce the negative impacts of intensification without reducing productivity.

Objectives

Two studies were conducted in conventional corn fields around Ames, Iowa, USA. The first study was a large-scale experimental manipulation that addressed the general questions (1) how does patch configuration within a crop field affect foraging by deer mice? and (2) do mice play a role in controlling volunteer corn? The objectives of this study were to test the predictions that (1) individual deer mice would increase foraging (functional response) in fields with many small patches, (2) more mice (numerical response) would

forage in fields with many small patches and (3) foraging by mice on corn waste grain would significantly reduce corn-seed densities over winter. In order to test these predictions as well as separate the effects of seed density and patch configuration, I set up replicated treatments with varying levels of ‘patchiness’ while controlling for seed density and total patch area.

The second study focused on the temporal variation in diet composition (specifically the inclusion of invertebrates in the diet) of deer mice living in conventional corn fields. In order to gain insight into the year-round diet of deer mice, this study compared the proportions of invertebrates consumed by mice (using stomach content analysis) to the availability of invertebrates in the environment throughout the crop growing season. A better understanding of their year-round diet as well as dietary switches will be important for understanding how mice regulate pest populations within corn fields.

Ultimately, these two studies provide us with insights into some of the factors that influence mouse foraging and their population dynamics which highlights their potential value to the future of agriculture throughout midcontinental North America.

Thesis Organization

This thesis is composed of four chapters; a general introduction, a manuscript based on the first study prepared for publication in the *Journal of Applied Ecology*, a second manuscript based on the second study prepared for submission to the *Journal of Mammalogy*, and a general conclusion. The manuscripts will be submitted for publication under the authorship of Tatyana Flick, who conducted and summarized the research, as well as Brent Danielson, who supervised the research projects and edited the manuscripts. The protocols

used in this thesis were approved by the Iowa State University Animal Care and Use Committee (Study 1: ID # 9-12-7434-M; Study 2: ID # 5-12-7369-W).

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CHAPTER 2. RESOURCE DISTRIBUTION INFLUENCES OVERWINTER FORAGING
BY MICE IN AGRICULTURAL FIELDS: IMPLICATIONS FOR VOLUNTEER CORN
CONTROL

A manuscript to be submitted to the *Journal of Applied Ecology*

Tatyana J. Flick and Brent J. Danielson

Summary

1. Row-crop agriculture is the predominant land-use throughout most of the Midwest, USA. In fields within this region, prairie deer mice *Peromyscus maniculatus* may be important predators of both weed seeds and waste grain. With the growing reliance on glyphosate resistant crop varieties understanding factors that influence both individual foraging and populations in general will be important for future control of GR volunteer corn as well as other pests. We address how resource patchiness influences overwinter foraging and mouse populations in cornfields.
2. We experimentally manipulated the configuration of corn waste-grain patches within four conventional cornfields in central Iowa, while controlling for total patch area and within-patch seed density. We measured whether the patchiness of this resource influences individual foraging (using giving-up density buckets) and population response as well as total overwinter seed removal.
3. We tested the predictions that (1) individual deer mice will increase foraging in fields with many small patches (functional response) and (2) more mice will forage in fields with many small patches (numerical response).

4. Resource patchiness influenced individual deer mouse foraging with greater foraging occurring in large corn patches within less patchy fields. Additionally, mice living in more patchy fields experienced greater benefits from food resources whether or not they actually lived on a corn patch.
5. Deer mice generally did not respond numerically to resource patchiness or food addition. It is unclear what factors regulate mouse population densities in cornfields in the Midwest, USA.
6. Deer mice removed on average between 59-66% (94.4 - 105.6 kg/ha) of the corn seeds from the soil surface.
7. *Synthesis and applications.* With the occurrence of glyphosate resistant crop volunteers, pest control in conventional crop fields is an ongoing challenge. Deer mice are one of the few organisms that are able to reduce weed seed and waste grain densities during the winter potentially providing a valuable ecosystem service. Our work shows that these mice are able to remove large amounts of waste grain from the soil surface over winter and that resource distribution can influence how efficiently they can do this. This suggests that management aimed at minimizing volunteer corn and maximizing overall seed predation should focus on increasing deer mouse populations within their fields as well as their foraging efficacy by reducing concentrated grain spills.

Keywords

Glyphosate resistant, overwinter foraging, patch configuration, patchiness, pest control, row-crop, seed predation, volunteer corn, waste grain.

Introduction

In the Corn Belt region, cropland now accounts for 55.3% (91 million acres) of the total land-cover, which is the highest percentage of cropland observed throughout the USA (Nickerson *et al.* 2011). Over time this conversion of land from native prairie to intensive row-crop agriculture has resulted in an increasingly homogeneous landscape (Rhemtulla, Mladenoff & Clayton 2007). Within this landscape however, heterogeneity at a smaller scale may still be present. For example, within a particular crop field, we may find spatial complexity arising from patterns in topography, variation in soil composition and weed patchiness (Cousens *et al.* 2006; Blanco-Moreno *et al.* 2008). The number, composition, size and distribution of weed patches within a field may vary from one field to another; however these patches often appear to be temporally and spatially stable within a particular field (Clay *et al.* 1999). Management and farming practices, such as tillage and the use of pesticides, can affect this spatial complexity of weed patches (i.e., size, shape and number of patches) within a field during a given year, which may have ecological consequences. Specifically, this spatial variation in weed “patchiness” (that is the spatial pattern of the patches) may affect the behavior, abundance and distribution of wildlife found within these fields as well as the potential productivity of the crop field in general (Blanco-Moreno *et al.* 2008).

Consequently, the primary objectives of this study were to determine how the patchiness of food resources affects the overwinter foraging of *Peromyscus maniculatus bairdii* Wagner (prairie deer mice) in crop-dominated landscapes as well as to determine the role that they play in controlling volunteer corn (an economically important weed) in intensively managed crop fields (Marquardt *et al.* 2012).

Although many studies in agricultural landscapes emphasize the negative impacts that this land-use may have on various species and biodiversity in general, these ecosystems provide us with opportunities to study the species remaining in these systems as well as how they may provide ecosystem services that could be important in both crop production and ecosystem function. One such species is the prairie deer mouse, which is one of the most common year-round residents of Midwestern crop fields. Previous studies have shown that the deer mouse can consume large quantities of weed seeds and waste grain, especially during the fall and winter months (Harrison, Regnier & Schmoll 2003; Westerman *et al.* 2005; Heggenstaller *et al.* 2006), which may have significant impacts on weed and volunteer corn (weeds that result from waste grain) densities, providing an important ecosystem service and potentially increase farm profitability. Several studies have looked at how deer mice are one of the dominant predators of weed seeds in this system and have strongly emphasized their importance in controlling weed populations (e.g., Westerman *et al.* 2005). Although this continues to be an important topic, we have found that deer mice prefer consuming corn a great deal more than soybeans *Glycine max* or other weed seeds that may be available, such as foxtail *Setaria faberi* Herrm and velvetleaf *Abutilon theophrasti* Medik (unpublished data). This suggests that understanding how overwinter foraging influences waste-grain densities may be of significant importance to gaining a better picture of the role these mice play in conventional crop fields.

An average of 180 to 298 kilos of corn per hectare is lost in the field every year during harvest (Foster, Gray & Kaminski 2010), resulting in undesirable volunteer corn in the following spring. With the growing reliance on glyphosate resistant (GR) corn varieties, controlling this volunteer corn is becoming a serious concern to crop producers (Stewart

2011). The presence of volunteer corn (especially GR corn) in soybean and cornfields negatively impacts production by increasing losses in current crop yield due to competition and increased costs associated with removal (both chemical and mechanical) (Beckett & Stoller 1988; Gressel 2005; Cerdeira & Duke 2006). The possibility that rodents may be an effective method for reducing volunteer corn has been previously mentioned by Getz & Brighty (1986) and Stewart (2011), but this hypothesis has not been explicitly tested. Similar to weed patches, corn waste grain is often distributed in patches throughout the cornfield suggesting that the spatial distribution of these patches may also affect the behavior, abundance and distribution of deer mice found within these fields.

Studies on foraging by deer mice and other small mammals in agricultural fields have generally focused on the effects of seed density on seed predation (Davidson & Morris 2001; Westerman *et al.* 2008; Bricker, Pearson & Maron 2010). Patches within fields or entire crop fields with higher seed densities often have higher levels of seed predation rates (seeds seed⁻¹ week⁻¹) by small mammals (Westerman *et al.* 2008). In contrast, while the effects of seed density on seed predation by small mammals are relatively well studied, there are few studies that have looked at the effects of patch configuration (also referred to herein as patchiness, which concerns the spatial pattern of the patches independent of composition or amount) on foraging in agricultural fields. Studies have shown that other small mammals, such as wood mice *Apodemus sylvaticus* Linnaeus in Europe, are able to distinguish between different patches at the spatial scale of crop fields (Angelstam, Hansson & Pehrsson 1987; Tew, Todd & Macdonald 2000). Perhaps the prairie deer mice in the Midwest can also distinguish and respond to variations in weed and/or waste grain patchiness.

Mouse populations found in fields that have many small patches (greater patchiness) compared to fields that have few large patches (lower patchiness) should have differential foraging in response to this spatial arrangement of resources. Mice may respond to these patches both at an individual level (functional response) and/or at a population level (numerical response) (Holling 1959). Since crop fields with many small patches will, on average, have smaller distances between patches, we hypothesize that mice within these fields will have a greater functional response possibly due to decreased foraging costs for travel between a patch and any other point in the field. Therefore, we would expect to see a greater amount of seeds per mouse removed from fields with many small patches when compared to fields with a few large patches. Studies have also shown that deer mice will have a greater functional response (be able to remove more seeds per individual) at lower population densities (Davidson & Morris 2001). Following this, we hypothesize that the resource distribution in fields with many small patches may result in more even distributions of mice across these fields (i.e., lower overall density because mice are not concentrated around a few large resource patches) potentially allowing for a greater functional response. Finally, we hypothesize that the lower average local density around each resource patch may also allow for a greater numerical response in fields with many small patches when compared to fields with few large patches since these mice will be less likely to be limited by other density-dependent factors (ex. space, burrow availability, intraspecific interactions, etc).

Our objectives for this study were to address both the ecological question of how resource distribution (patchiness) within a crop field affects foraging by deer mice as well as the applied question concerning the role that these mice play in controlling volunteer corn. To address these questions, we tested the predictions that (1) individual deer mice would

increase foraging in fields with many small patches (functional response) and (2) more mice would forage in fields with many small patches (numerical response). Additionally, we predict that overwinter foraging by mice will significantly reduce the amount of corn waste grain remaining on the soil surface in the spring. To explicitly test how patch configuration alone influences foraging by these deer mice, we experimentally set up fields with varying levels of “patchiness” while controlling for within-patch seed density and total patch area.

Methods

Experimental Set-up

Our study was conducted from November 2012 to April 2013 in four cornfields (*Zea mays*) owned by Iowa State University near Ames, Iowa, USA (Bennett Farm, Woodruff Farm, Main Kelley Farm and East Kelley Farm). Bennett Farm was dropped from the study due to extensive flooding at various points throughout the study as well as the presence of wintering geese towards the end of the study. All four fields were harvested and cultivated immediately prior to establishing our experimental treatment plots. Additionally, the corn biomass was removed from all fields except for the Main Kelley Farm where it was tilled into the soil.

Within the four replicate fields, three treatment plots measuring 100 x 100 m (1 hectare) were delineated. Plots were located > 10 m from the nearest edge of the field and at least 50 m from each other. Each of these plots contained a 4 x 4 grid of evenly spaced (25 m apart) wooden burrows designed to monitor the mouse population within the boundaries of the plot. Previous work had shown that prairie deer mice living in cornfields preferentially occupied these burrows when they were provided, using them for both nesting and caching

throughout the fall and winter (personal observation, Figure 1). Burrows were buried in the soil in pairs (mice often use one burrow for nesting and the other for caching seeds) so that the entrances of the two burrows were pointing away from each other and the lids of the burrows were flush with the soil surface for easy access. Since the majority of natural biomass had been removed from the crop fields, cotton bedding was placed in each burrow to provide material for nesting.

Corn waste grain was added to two of the three treatment plots in each field to experimentally manipulate patch configuration while controlling for total patch area and within-patch seed density (Figure 2) (McGarigal & Cushman 2002). Total patch area in both of these experimental treatments was equal to 0.5 hectares. Treatment 1 (high patchiness) consisted of eight 25 x 25 m patches (from here on referred to as the “many small” (MS) patch treatment). Treatment 2 (low patchiness) consisted of two large 50 x 50 m patches (from here on referred to as the “few large” (FL) patch treatment). In addition to the two experimental treatment plots, a third treatment plot was set up as a control (no waste grain added), which allowed us to control for the effect of the artificial burrows without the additional food. Each experimental corn patch was centered on a burrow pair to simplify the interpretation of the results (i.e., a burrow was either in a corn patch or not, Figure 2). The experimental patches were seeded with whole kernel corn during December 2012 using a hand operated seed spreader. To ensure constant within-patch corn density, we applied 20 kg of corn per 25 x 25 m grid cell (320 kg/ha), which is within the range of observed densities of corn waste-grain within crop fields (Foster, Gray & Kaminski 2010).

Burrow Sampling

Burrow occupancy was monitored every two weeks from December 2012 to March 2013. Burrow sampling was terminated in mid-March 2013 due to flooding of the burrows caused by extensive rain fall. Sampling occurred during the day when mice were nesting in the burrows. Mice were weighed, sexed, ear-tagged and returned to their burrows. Additionally, notes were taken on the reproductive status of all mice and any litters found in the burrows were monitored (young mice were ear-tagged once they were large enough). Although we observed waste grain caches in most of the burrows (Figure 1) we were unable to quantify the amount of usable corn cached because the corn was usually mixed with other materials, of varying quality, and often frozen in the burrow.

Foraging Sampling

Foraging by mice in all three treatments was monitored using giving-up density (GUD) buckets. As mice forage in the buckets, they experience diminishing returns and will cease to forage when the benefit from foraging in the bucket is less than the surrounding habitat (Charnov 1976; Brown 1988). GUD buckets were used to measure the relative functional response of mice within each 25 x 25 m grid cell by allowing for comparisons of foraging in corn patch cells vs non-patch cells as well as the overall relative foraging between treatments (Brown 1988). GUDs were expected to be higher in corn patch cells than in non-patch cells (due to the difference in resource availability). If, however, mice respond differently to the resource distributions in the two experimental treatments, we expect the GUDs of MS corn patches to differ from those in the FL treatment and similarly GUDs in the MS non-corn patches to differ from the GUDs in the non-corn patches of the FL treatment. The buckets contained 15.5 g of whole-kernel corn uniformly mixed into 2 L of fine, light-colored sand. GUD buckets were placed approximately 1 m away from each burrow pair and

left out for 3 days (2 nights of foraging) before being collected. GUDs were measured twice during the experiment (February 18th 2013 and March 9th 2013). Corn remaining in the bucket at the end of the period was removed using a wire sieve and was then dried in a Fisher Scientific Isotemp oven at 120 degrees for 1 hour. Dried corn samples were then weighed to determine the giving-up density for each of the 25 x 25 m grid cells.

Surface Seed Density Sampling

Surface densities of seeds were sampled in April 2013 at the end of the study. Twelve 1 x 1 m quadrat samples were taken to measure the surface seed density along a diagonal transect in each individual 25 x 25 m cell for all the replicates. We opted to sample along diagonal transects in case there was differential removal of waste grain closer to the center of the plot near the mouse burrows when compared to the edge of the plot.

Analysis

To test our predictions, we used several response variables to get a clearer understanding of how resource patchiness affects the foraging by deer mice. More specifically, we tested for significant differences between the three treatments with respect to the mass of corn remaining in the GUD buckets within each grid cell (functional response), the number of first captures (numerical response), the total number of captures including all first captures and subsequent re-captures on each experimental plot (also a numerical response) and the average number of corn seeds remaining on the surface in the two corn treatments (MS and FL). We ran four ANOVAs using proc glm in SAS (version 9.3) to assess whether there was a difference in each response variable between the three treatments (C, MS, FL). In each model, we included treatment as the main effect and field as a block effect (fixed effect). When running the ANOVAs for both numerical responses, we summed

the number of mice observed within each treatment in a given field over all sample times. In contrast, we used the raw GUD measurements for each grid cell within each treatment because in addition to testing whether there was a difference in the functional response between treatments, we were also interested in the within-treatment differences that may occur as a result of the foraging measurement being either in a patch (1) or in a non-patch (0). Mouse presence within a grid cell was also included as a factor in the model. Following our initial tests, post-hoc analyses using Tukey's HSD were done to test all pair-wise comparisons to determine where the significant differences occurred.

Results

A total of 254 individual mice were observed and tagged during the course of the study. Including recaptures, we observed mice 532 times. In addition to the deer mice observed in the burrows, we also observed and tagged five prairie voles *Microtus ochrogaster* Wagner. However, their small sample size precluded them from this study. In addition to observing adult mice, we recorded 23 litters born in the burrows. On average there were more litters born in MS treatments (total 11) than the control (total 9) and the FL treatment (total 3) however these differences were not statistically significant ($F=1.00$, $p=0.44$).

There was a significant difference in the average giving-up density between the experimental treatments at the patch level ($F= 3.34$, $p=0.0114$). There was also a significant difference in the average GUD depending on sample date ($F=15.00$, $p=0.0002$) and whether or not mice were present in the burrow within the sampled grid cell ($F=5.68$, $p=0.0182$). Post-hoc comparisons show that at the $p=0.05$ level there was a significant difference in the

average GUDs in corn patches within the FL treatment compared to GUDs within the control treatment. Although not significantly different, average GUDs in the non-corn patches as well as the corn patches of the MS treatment were higher than the average GUDs in the control as well as the non-corn patches in the FL treatment (Table 1).

There was no significant difference in the average number of first captures or the average total number of mice between the three treatments plots ($F=0.2328$, $p=0.8023$; $F=0.5117$, 0.6340 respectively). On average, the control treatment had more mice than both the experimental treatments, although this was not significant due to the high variation between fields (specifically Main Kelley) (Table 2). The Main Kelley field consistently had more mice throughout the study when compared to the East Kelley Field and Woodruff field (Table 3), however there was no significant field effect (first captures: $F=1.47$, $p=0.33$; total mice: $F=2.96$, $p=0.16$).

There was a marginally significant difference ($\alpha = 0.1$) in the average corn density remaining on the soil surface in experimental patches between the MS treatments and the FL treatments ($F=2.858$, $p=0.098$). Post-hoc analyses indicate that there was significantly less corn remaining on the surface in treatments with a few large patches (mean= 36.4 ± 4.5 kernels/m²) compared to treatments with many small patches (mean= 44.0 ± 4.5 kernels/m²).

Discussion

Functional Response

We found a significant difference in the functional response of deer mice to some of the experimental treatments at the patch scale. Giving-up densities (a measure of relative foraging) were significantly lower in the control than in the corn patches within the FL

treatment. As expected, the lower GUDs in the control versus the FL treatment indicate a lower-quality environment within the control patches. In the control, mice foraged longer and, therefore, removed more corn in contrast to the FL treatment where the benefits of foraging decreased over time as the density of corn in the bucket approached the density in the surrounding patch. Notably, there was no significant difference in foraging between the FL non-corn patches and the control, which suggests that mice foraging in the non-corn patches within the FL treatment also experienced a lower-quality environment even though there was supplementation of resources at a larger scale (ie. the treatment scale). This follows our predictions that some mice living on the FL treatment (namely those in the non-corn patches that are not adjacent to a corn patch) did not benefit from the corn addition due to the patch configuration. Although mice in the non-corn patches could potentially travel from their burrows to a supplemented patch (<37.5m), our results suggest that they may have limited access to these patches (for example interference by conspecifics residing in the area between their burrow and the patch). This suggests that the level of resource patchiness (while controlling for total area and seed density) did influence the foraging of mice within these fields on an individual basis.

In contrast, we did not find a significant difference in the functional responses of mice living in the MS treatment (on neither corn nor non-corn patches) and those living on a control plot. Although GUDs in the corn patches as well as non-corn patches within the MS treatment were higher (12.4g) than the control (10.0g) there was a large amount of variation in the data (Table 1). If the differences in measured functional response were naturally small (note the difference between the MS and FL corn-patch GUDS was 1.3g, which was about 4 corn kernels) we would require a larger sample size to detect these differences. If the

direction of this trend was indicative of the true differences, then mice in the MS treatment might have experienced a higher-quality environment than those living on control treatments. Given more data, this would suggest that our predictions that mice living on MS treatments might have greater functional responses (on both patches and non-corn patches) due to the configuration of the patches, which allowed for greater access to the resources from anywhere in the plot, would be supported.

An interesting trend in the GUD results that may provide some direction for future studies is the difference in foraging on a corn patch vs a non-corn patch in the two experimental treatments (MS & FL). Mice foraging on the MS treatment had the same GUD on both corn patches and non-corn patches, whereas there was a greater difference in foraging on corn patches and non-patches in the FL treatment, with average GUDs on the non-patches similar to that observed on the control treatment. The difference in treatment effects of mice living on non-corn patches could be due to differential access to the supplemented resources. Mice living on non-corn patches within the MS treatments were never more than 12.5 m away from a corn patch, therefore they could easily travel between their burrow and the patch multiple times during the night. Mice living on the FL treatment, on the other hand, may have experienced further travel distances to the nearest patch depending on which non-patch grid cell they lived in (between 12.5 m to 37.5 m to the nearest patch). Theory would suggest that although these mice would have to travel farther to exploit patches, they would maximize the energy obtained from each trip by increasing their load size (Houston & McNamara 1985). Our results however do not seem to support this idea further supporting the alternative idea that these mice experienced limited access to the supplemented resources possibly as a result of longer travel distances, increased negative

interactions with conspecifics and/or increased risk while foraging in comparison to mice in the MS treatment. Finally, although Davidson & Morris (2001) have shown that mice show a greater functional response at lower densities, our numerical results suggest that there was no difference in the number of mice living on our various treatment plots. This further supports the idea that the observed trends in functional response were more likely tied to the reduced costs/benefits of foraging in environments with patchy resource distributions.

Westerman *et al.* (2009) showed that weed seed predation by vertebrates (primarily deer mice) in cornfields is unrelated to the number of rodent captures. In their study, treatment plots measured 50 x 50 m and were divided into four 25 x 25 m quadrants (high seed density, medium density, low density and control), thus their seed patches were comparable in size to ours (25 x 25 m and 50 x 50 m). Their results suggest that although seed predation was related to within-patch seed density, mice may have been moving between quadrants resulting in captures in all four quadrants. Similarly in our MS plot, mice observed in non-patches can easily travel this distance and forage in the corn patch at this scale, supporting our arguments in the previous paragraph.

Numerical Response

The deer mouse populations did not respond consistently to resource patchiness or resource availability in general. Given that there was no significant difference in the numerical response between our three treatments (including the control), our results suggest that the addition of food itself does not necessarily result in a greater numerical response by deer mice living in these cornfields. Although this result is not what we expected (or the norm with food supplementation studies), it is consistent with several other studies on small mammals showing that populations do not always respond numerically to food addition

especially on time scales of less than a year (Havera & Nixon 1980; Gilbert & Krebs 1981; Young & Stout 1986; Pusenius & Schmidt 2002; Diaz & Alonso 2003; Prevedello *et al.* 2013). Work by Westerman *et al.* (2008) on weed seed predation in crop fields within Iowa, USA has shown that both invertebrates and vertebrate seed predators are often unable to respond numerically to differences in within-patch seed density especially immediately after seed addition.

The absence of a numerical response suggests that factors other than food determine the overall size of the populations of deer mice living within these cornfields within the time scale of one year. Such factors could include burrow availability, social behavior, predators, etc. Pusenius & Schmidt (2002) found that another small mammal, the meadow vole *Microtus pennsylvanicus* Ord, did not show a significant response to food addition in risky (mowed) habitats suggesting that predation risk is the limiting factor in these habitats. Similarly, Yunger (2002) showed that white footed mice *Peromyscus leucopus* Rafinesque experienced greater predation pressure and lower survivorship, which resulted in a population decline, on treatments with food supplementation. Alternatively, a large collection of studies show changes in home-range size and territoriality (especially in females) when additional food is provided, suggesting that our non-result may be related to some of these factors (Taitt 1981; Collins & Barrett 1997; also see Boutin 1990). Studies on the home ranges of deer mice show a great amount of variability in the size of home ranges depending on habitat type (anywhere from 108.5m² in greasewood habitat to 5868m² in sage-steppe) (Feldhamer 1979; Wolff 1985; Williams *et al.* 1994; Wood, Cao & Dearing 2010). The only study that we are aware of that has measured home-range sizes for *P. maniculatus* in a similar habitat to our study (soybean monocultures) shows average home-range sizes of

710±411 m² for females and 776±33 m² for males (Williams *et al.* 1994). In our experiments, the locations of burrows that the mice occupied were pre-determined by our experimental design, which may have constrained the mice to maintain approximately equal home-range areas on our plots (1 grid cell = 625 m²). Although it is possible that additional mice could have built burrows between our equally spaced artificial burrows (resulting in overall smaller home ranges on the plot), preliminary studies in similar fields the year before indicated that trapping the entire experimental grid with Sherman traps resulted in very few (if any) untagged individuals, indicating the artificial burrows in these fields were able to “capture” all the mice in the area (mice occupying burrows were tagged prior to trapping). We did however observe some mice that seemed to occupy two neighboring burrows which would suggest that both burrows were within their (larger) home range but there did not seem to be any identifiable trends in these patterns between our three treatments. These observations suggest that the mice on our experimental plots maintained home ranges more or less the size of one to two grid cells (625 – 1250 m²) and that these home ranges probably did not differ with respect to our three treatments (consistent with findings by Wolff 1985). Given this, we expected that the deer mice living in these cornfields would be burrow limited, which would explain why they responded to the burrows in our experimental treatment plots as well as the control plots, regardless of food availability/distribution. This however did not seem to be the case since there were several burrows that remained unoccupied throughout the study. These results indicate that we do not yet know what regulates these populations. Thus, we emphasize the importance of the work that remains to be done in this regard. Better understanding what factors regulate deer mouse populations in cornfields across the Midwest will aid in our understanding of how these mice benefit pest control within these fields.

Previous studies have shown that deer mouse densities are higher in agricultural fields than in native prairies (their historical habitat) (Kaufman, Kaufman & Clark 2000; White *et al.* 2012). The average number of mice on our treatments on any given sample date was 11 mice/hectare (but ranged from 2 to 26) which is comparable to the average densities observed by Wolff (1984) measured from April to November in mixed deciduous forest. Additionally, we observed male-female pairs in a large number of boxes throughout the course of the study, which suggests that these mice were able to maintain higher densities (as well as maintain greater likelihood of reproductive activity) on our experimental plots by overlapping male and female home ranges. Again, studies that have observed higher densities in one habitat type over another often suggest food availability or quality as the main cause of higher population numbers. Although this may be true in general (ie., when comparing cornfields to prairie habitats for example), our study shows that there are other factors within these crop fields that must be playing a role in fine tuning population densities within each individual field.

In addition to the lack of response in the overall number of individual mice, we did not see any significant difference in the total number of mice (1st captures plus additional recaptures) between the three different treatments. This suggests that resource patchiness (or food addition in general) did not result in higher turnover in less favorable environments or higher site fidelity in more favorable environments. Several studies have shown that there should be higher immigration to more favorable patches, especially when these patches contain additional food (Taitt 1981; Galindo-Leal & Krebs 1998; Banks & Dickman 2000; Yunger 2002). Not only did we fail to see higher immigration to our experimental treatment plots compared to the control plots but we only had 4 mice (out of 254) move from one

treatment plot to another. These observations suggest that 1. our experimental plots did not necessarily draw in mice from the surrounding area and that 2. the mice most likely did not sample all three plot types within a field before selecting a burrow or area to forage as was observed in Peles, Williams & Barrett (1997). These points indicate that the mice observed on each of our plots were most likely already living in the near (<50m) vicinity before we established our experiment, suggesting that there is heterogeneity in mouse population densities within seemingly homogenous fields as well as between fields in the same geographic area. This also supports the conclusion made by Davis *et al.* (2013) that weed-seed predation within crop a field is very site specific.

One caveat to these conclusions is that we do not know whether this lack of numerical response to resource patchiness would hold true over a longer temporal scale. The fact that we observed more overwinter reproduction on the MS treatment may indicate that over time fields with many small evenly distributed patches may have higher mouse populations when compared to fields with few larger patches. Several studies have shown that small mammals often breed more and earlier in the season when provided with additional food, especially in temperate climates; our study supports this (Taitt 1981; Bomford 1987; Boutin 1989; Galindo-Leal & Krebs 1998; Banks & Dickman 2000; Diaz & Alonso 2003). What is noteworthy is that our study adds to this by suggesting that food distribution itself may also further influence winter breeding with potentially more breeding and therefore higher population growth in fields with more patchy resource distributions.

Waste Grain Removal

Overwinter foraging by deer mice living in our study fields resulted in a substantial reduction of the total amount of waste grain remaining on the surface of the soil in the spring.

On average, between 59-66% of the corn applied to each patch (20 kg per patch) was removed during the course of the study. This suggests that not only is there support for effective weed control by deer mice in cornfields (Harrison, Regnier & Schmoll 2003; Westerman *et al.* 2005; Heggenstaller *et al.* 2006; Westerman *et al.* 2008; Williams *et al.* 2009; Davis & Raghu 2010) but that the overwinter foraging by these mice may be a very important factor in lowering the waste-grain densities in fields before spring germination, potentially controlling volunteer corn. A few agronomists have suggested that rodents may play a role in reducing volunteer corn, especially in no-till fields (Getz & Brighty 1986; Stewart 2011). Until now, no studies have explicitly determined if this is actually occurring. Additionally, Davis *et al.* (2008) observed that there were a greater number of volunteer corn plants in tilled fields than in untilled fields. Tillage may allow seeds to escape the overwinter predation by mice supporting Davis *et al.*'s (2008) observation. This result could have huge ecological applications in controlling future volunteer corn problems, especially given the nearly ubiquitous use of glyphosate resistant (GR) corn. Biological control of various pest species has been well studied in many different cropping systems but what makes this system interesting and unique is that the pest in this case (GR volunteer corn) is similar to the targeted crop as well as resistant to the main control strategies. Although new chemicals are being designed to combat GR corn, they are not always effective, especially when trying to control volunteer corn within a cornfield (Deen *et al.* 2006; Steckel, Thompson & Hayes 2009; Green & Owen 2011; Green 2007). Deer mice, on the other hand, are very cost effective (essentially free) and as we have shown are capable of removing these pesticide resistant weeds. Understanding what factors influence the abundance of mice within crop fields as well as their foraging will greatly benefit our knowledge of how these little mice can

further benefit farmers via increased pest control. This study focused on one of these factors and looked at how patchiness in resources (just the spatial pattern alone) can influence both the number of mice as well as their foraging. From our results, we can conclude that the spatial distribution of resources does matter and that fields with many small patches of waste grain as well as larger (single) patches will have greater foraging by mice on an individual level. We also show that the spatial distribution of waste grain does not necessarily influence the overall number of mice within a field within any given year, however higher reproduction on treatment plots with more patchy resources may suggest greater population growth and subsequently even higher waste grain removal over a longer time scale. Future research should focus on determining what limits the deer mouse populations within conventional cropping systems.

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Table 1. Mean giving-up densities (GUD) at the within treatment patch level (corn patch, non-corn patch) measured in grams of corn remaining in the bucket after 2 nights of foraging by *P. maniculatus*. Treatments included the control (C) without added corn, many small patches treatment (MS) with eight 25 x 25 m corn patches, and the few large patch treatment (FL) with two 50 x 50 m corn patches.

Treatment	Patch	Average GUD (g)	Std Dev
C	non-corn patch	10.0	5.6
FL	non-corn patch	11.5	5.3
FL	corn patch	13.7	3.9
MS	non-corn patch	12.4	4.7
MS	corn patch	12.4	5.3

Table 2. Mean number of mice captured on the three experimental treatment plots from East Kelley field, Main Kelley field and Woodruff field. Means of “first capture” include individual mice that were tagged for the first time and “total mice” includes all new mice as well as recaptured mice. Treatments included the control (C) without added corn, many small patches treatment (MS) with eight 25 x 25 m corn patches, and the few large patch treatment (FL) with two 50 x 50 m corn patches.

Treatment	Variable	Mean	St Dev	Min	Max
C	First Capture	23.3	11.72	10	32
FL	First Capture	19.3	3.06	16	22
MS	First Capture	22.0	6.24	15	27
C	Total Mice	51.0	32.42	22	86
FL	Total Mice	37.7	2.89	36	41
MS	Total Mice	47.0	17.35	32	66

Table 3. Mean number of mice captured on each field over the entire study. Means of “first capture” include individual mice that were tagged for the first time and “total mice” includes all new mice as well as recaptured mice.

Field	Variable	Mean	St Dev	Min	Max
East Kelley	First Capture	15.7	6.03	10	22
Main Kelley	First Capture	24.0	8.00	16	32
Woodruff	First Capture	25.0	4.36	20	28
East Kelley	Total Mice	30.0	7.21	22	36
Main Kelley	Total Mice	62.7	25.17	36	86
Woodruff	Total Mice	43.0	2.00	41	45



Figure 1. Example of a pair of wooden mouse burrows used by a prairie deer mouse *Peromyscus maniculatus* for both caching corn waste grain (left burrow) and nesting (right burrow) in one of the experimental plots during the winter. Burrows were buried in the soil after the fields were harvested and tilled. This image shows burrows with their lids removed.

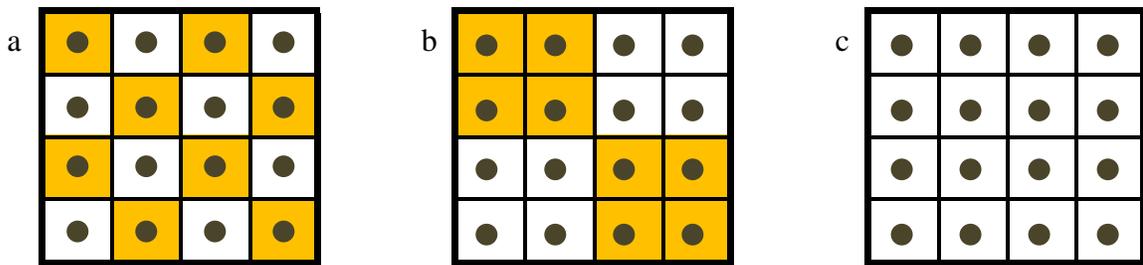


Figure 2. 100 x 100 m Experimental treatment plots (a) MS treatment (many small patches - high patchiness) (b) FL treatment (few large patches - low patchiness) (c) control. Yellow areas indicate the patches where corn has been added to the soil surface (equal density, 20 kg per 25 x 25 m grid cell) and the brown circles indicate the placement of the wooden burrow boxes. Grid cells within each treatment plot, measuring 25 x 25 m, are considered a corn patch (yellow) or non-corn patch (white).

CHAPTER 3. TEMPORAL VARIATION IN INVERTEBRATE AND SEED
CONSUMPTION: UNDERSTANDING THE DIETS OF MICE IN A NOVEL
AGRICULTURAL HABITAT

A manuscript to be submitted to the *Journal of Mammalogy*

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Abstract

The prairie deer mouse (*Peromyscus maniculatus bairdii*) is a common year-round resident of Midwestern agricultural fields, and provides several ecosystem services by consuming large quantities of weed seeds and waste-grain during the fall and winter. However, these seeds are not available throughout the year suggesting that the deer mice must forage on other resources (e.g., invertebrates found in crop fields) at different times throughout the year. The following study asked how the proportion of invertebrates in deer mouse diets changes over time and how this compares to the temporal change in availability. We analyzed stomach contents to determine how the proportion of invertebrates in the mouse's diet changed during the crop growing season (June to November) and used pitfall traps to sample invertebrate abundance. Our results show that mice had a higher probability of consuming invertebrates early in the season. We also found a significant interaction between season and invertebrate availability, such that deer mice had a high probability of consuming invertebrates regardless of availability in the spring and when availability was high in the fall. Additionally, we found that females consumed a higher proportion of invertebrates than males, especially when availability is high. Our study shows that the

specific timing of the consumption of invertebrates and other pest prey (such as weed seeds and waste-grain) is ideal in that predation pressure on invertebrates is high in the spring when certain invertebrates prey on crop seedlings but then low in the fall when other invertebrates beneficially contribute to weed seed predation. Thus, understanding the contribution of invertebrates to the deer mouse's diet and how the use of this resource changes through the year gives us a better understanding of how these mice manage to thrive and contribute to pest control within intensively managed crop fields.

Keywords

Diet composition, temporal variation, invertebrates, weed seeds, agriculture, ecological pest control, prairie deer mice.

Introduction

Agricultural systems in the Midwest USA are intensively managed. Nonetheless, conventional management tools are unable to fully control pest populations. Recent work suggests that wildlife may have an important role in pest control within these modified systems (e.g., Westerman *et al.* 2005). One such species is the prairie deer mouse (*Peromyscus maniculatus bairdii*), which is a year-round resident of Midwestern agricultural fields and may provide several ecosystem services by preying on pest species found in crop fields. Previous studies have shown that these mice consume large quantities of weed seeds and waste grain, especially during the fall and winter (Harrison *et al.* 2003; Westerman *et al.* 2005; Heggenstaller *et al.* 2006; Williams *et al.* 2009; personal observation). Thus, foraging by deer mice during the winter may have a significant impact on weed and volunteer corn

densities. However, weed seeds and waste grain availability changes throughout the year, suggesting that the deer mice must forage on other resources (ex. invertebrates found in crop fields) at different times throughout the year (Clark & Young 1986). Thus, although we understand the basis of their winter diet and the applied importance of this (in terms of weed and volunteer corn pest control), we know relatively little about their diet and role in these agricultural ecosystems for the remainder of the year. Understanding the timing of changes in the diet of these mice may have important effects on weed-seed mortality and thus weed population dynamics. Weed seeds are only available for a short time period before moving into the soil and therefore could potentially escape predation if mice are focused on eating other prey items at this time (Heggenstaller & Liebman 2005). Additionally, a better understanding of their complete year round diet will not only improve our understanding of the ecology of the prairie deer mouse and how it has capitalized on these novel environments but will also provide insight into what regulates their populations, which would have important pest control implications.

Like many other generalist species, we expect that deer mice switch between various food resources based on multiple factors including resource availability, quality, and preference for different prey species. With seasonally abundant resources, more profitable prey will always be consumed and less profitable prey types will be consumed only when the most profitable prey are sufficiently less abundant (Pulliam 1974). As a result, diet breadth should expand or contract depending on the quality and availability of resources (i.e., a forager will include more food types when the most profitable prey type is rare or hard to access) (Hughes 1993). In temperate agricultural systems, potential prey species such as invertebrates, weed seeds, and waste grain tend to vary seasonally, with protein rich

invertebrates becoming abundant during the summer months and various high-energy seeds becoming abundant in the fall. Nutritional constraints, such as high protein requirements for reproduction/lactation, could lead to partial preference for items (such as invertebrates) that are an important source of the required nutrient (Pulliam 1975).

Crop management regimes cause sudden and extreme changes in the temporal availability of various resources. For example, application of insecticides reduces invertebrate availability, and crop harvest increases the availability of both weed seeds and waste grain on the surface of the soil after which tilling reduces the availability of these same seeds by burying them underground (Heggenstaller & Liebman 2005; Westerman *et al.* 2006; Devine & Furlong 2007). Thus, deer mice living within these fields often experience dramatic changes to their foraging environment. As a result of these unique circumstances, we do not know if or when these mice will switch between various resources, such as the switch between invertebrates and seeds. If mice focus primarily on one food type, other food types may be escaping predation. In agricultural fields, if mice continue to primarily eat invertebrates during the time when weed seeds are abundant, these seeds will have time to move into the soil, thus becoming protected from future predation. Therefore, knowing when the mice ‘switch’ to these resources and what factors influence that switch will be important for understanding how (or even if) invertebrate pests, weed populations, and volunteer corn are regulated by deer mice in corn fields. Ultimately, an increased knowledge of the mouse’s diet and overall value in these agricultural fields will be increasingly important in the sustainability of Midwestern agriculture.

The goal of this study was to investigate the temporal variation in diet composition of deer mice and, in particular, to understand the role of invertebrates as an important

component of their diet during the crop growing season (i.e., between planting and harvesting). To do this, we ask how the proportion of invertebrates in deer mouse diet changes over time and how does this compare to the temporal change in availability? Understanding the contribution of invertebrates to the deer mouse's diet and how the use of this resource changes through the year will give us a better understanding of how these mice manage to thrive and contribute to pest control within these intensively managed crop fields.

Methods

Study Site & Set-up

Our study was conducted from June 2012 to November 2012 in five conventional corn fields (*Zea mays*) owned by Iowa State University located near Ames, Iowa, USA. Although sampling even earlier in the spring would have been preferred, access to these fields was limited during spring tillage and planting. The fields used for the study included Woodruff Farm, Main Dairy, East Dairy, Main Kelley Farm, and East Kelley Farms. The fields are primarily surrounded by other conventionally managed corn and soybean fields. All five fields were tilled and planted with seed corn before the beginning of the study.

In each field, two permanent transects were established at least 20 m from the edge of the field to avoid catching non-target species associated with the field edge. Transects were 20 m apart and ran parallel to each other as well as the direction of the corn rows. Four trapping stations were marked using pin flags every 20 m along the length of each transect. Whenever possible, we avoided establishing transects in low areas of the field to avoid potential flooding during the course of the study. We carried out invertebrate and small mammal trapping every two weeks (during the same week) for the duration of the study.

Sampling every two weeks was expected to provide the temporal resolution required to note when changes in the diets of deer mice occur while also minimizing the number of mice required.

Invertebrate Trapping

Pitfall traps were permanently set up at each one of the four trapping stations along both transects within all of our study fields. Pitfall traps consisted of two nested 1 L plastic drinking cups burried in the ground so that the rim of the top cup was flush with the soil surface. Disposable plates were held in place 1 cm above the top of each pitfall cup using bamboo skewers. Pitfalls were set open five days prior to the collection of mice so that we could obtain a relative sample of the invertebrates present and available for consumption that week. The cups were filled approximately 2 cm deep with 50:50 water propylene glycol solution (Hanley & Barnard 1999; Brooks *et al.* 2003; O'Rourke *et al.* 2006). After five days the contents of the pitfall traps were collected into whirlpaks and refrigerated at 4°C until identification. Invertebrates were identified to order, counted, and then allowed to air dry for two weeks before being weighed.

Small Mammal Trapping

Small mammals were sampled every two weeks at the end of pitfall sampling. Museum Special and Victor snap traps were set at each trap station during the afternoon (one trap per station; total of 4 Museum Specials and 4 Victor traps per field). Traps were baited with rolled oats. Due to the expected variations in mouse samples obtained from different fields and the temporal nature of the study, we aimed to collect about 20 mice per trapping session (i.e., an average of 3-4 mice per field). Snap traps were checked at sunrise the following morning. Mice caught in the traps were bagged and stored on ice for transport to

the lab. Once in the lab, the mice were weighed and sexed before having their stomachs removed. Stomachs were refrigerated in 70% ethanol at 4°C until they could be analyzed (Pinotti *et al.* 2011). The protocol for mouse sampling was approved by the Iowa State University Animal Care and Use Committee (ID # 5-12-7369-W).

Stomach Content Analysis

Before analysis we weighed the mouse stomachs and ceca. Using a scalpel, an incision was made along the greater curvature of each stomach and the contents were emptied into a petri dish. The contents of each stomach were then mixed with 1 mL of deionized water to homogenize the sample. Using a stereoscope, we then observed the contents of each stomach at 3X (Pinotti *et al.* 2011). We then randomly sampled 10 fields of view (FOV) and assessed the presence or absence of invertebrate parts (1/0) as well as the approximate percent cover of invertebrate parts in the FOV. Percent cover was grouped into four categories <25%, 25-50%, 50-75% and >75%. Due to the amount of maceration of animal matter in the stomach we did not attempt to classify various particles to specific invertebrate orders. Additionally, fine taxonomic resolution was not necessary to answer our general question about how different prey types (broadly invertebrates, weed seeds and waste grain) in the diet varied temporally. The petri dishes were then sealed and stored in the freezer for future reference.

Analysis

We used generalized linear models (GLMs) determine how the proportion of invertebrates in the stomachs of deer mice changed over time and how their use of this resource compares to the temporal change in availability (Gregg *et al.* 2008). The proportion of invertebrates in each stomach, measured by presence of invertebrates in 10 FOV, was

highly correlated ($R^2 = 0.7022$) with the estimated percent cover of invertebrates in the FOV so all analyses were done using the more objective measure (the proportion of invertebrates). Using PROC GENMOD in SAS 9.3 (binomial distribution and logit link function) we modeled the probability of finding invertebrates in the stomach ($x/10$ FOV) of a mouse by date, field (random effect), sex, invertebrate abundance (pitfall traps), as well as the date*invertebrate abundance and sex*invertebrate abundance interactions. The first interaction term modeled how the proportion of invertebrates in a mouse's stomach for a given invertebrate abundance changes over time (i.e., are use and availability proportional over time?). The second interaction term modeled how the proportion of invertebrates for a given sex changes with invertebrate abundance (i.e., do males and females have different probabilities of consuming invertebrates given availability?). Analysis of the residuals showed no violation of the assumptions. We ran a total of three models (Model 1: does not include sex, Model 2: includes sex, Model 3: includes sex and the sex-invertebrate abundance interaction) which were ranked using AIC (Burnham and Anderson, 2002).

Results

A total of 164 deer mice were collected during the course of the summer. We captured 103 males and 60 females. We were unable to sex one mouse because it was partially eaten while in the trap, however we were still able to recover its stomach for analysis.

During the course of the study, a total of 1588 invertebrates were collected of which 57% belonged to four orders: coleoptera (24%), orthoptera (18%), diplopoda (9%), and

opilliones (6%). The relative abundance of invertebrates within the corn fields increased from June to late July and then decreased for the remainder of the study (Figure 1). Invertebrates occupied the majority of the stomachs during the beginning of the study in June (Figure 2). However, seed endosperm increased in frequency and amount towards the end of the study in November. We suspect that the majority of the seed endosperm was from corn waste grain, but without molecular analyses, we were unable to accurately distinguish it from other seed endosperm. We ran three GLM models to determine which model best predicted the probability of observing invertebrates in a mouse's stomach (Table 1). The best model was Model 3 (lowest AIC, > 2 AIC units from next best model), which included all of the predictor variables as well as both interactions (Table 2). The proportion of invertebrates in the diets of mice living within these corn fields decreased over the course of the study, with a significantly greater probability of consuming invertebrates earlier in the season (Wald $\chi^2 = 79.16$, $p < 0.0001$). We detected the presence of invertebrates in 90% of the stomachs analyzed and the 10% in which we did not detect invertebrates occurred with greater frequency towards the end of the study (we detected invertebrates in all mouse stomachs before July 30th). The relative abundance of invertebrates captured in the field significantly ($\alpha = 0.1$) influenced the probability of observing invertebrates in a mouse's stomach (Wald $\chi^2 = 3.47$, $p = 0.0627$). Additionally, the relative abundance of invertebrates also significantly ($\alpha = 0.1$) influenced the probability of observing invertebrates in a mouse's stomach given the sample date (interaction: Wald $\chi^2 = 3.46$, $p = 0.0630$). Figure 2 shows that, early in the season, mice had a high probability of consuming invertebrates regardless of availability. As the season progressed, the probability of consuming invertebrates depended on availability (i.e., lower probability when availability was low; higher probability when

availability was high) (Figure 3). Sex itself was not significant (Wald $\chi^2 = 0.02$, $p=0.8985$). However, the sex-invertebrate abundance interaction was significant (Wald $\chi^2 = 4.41$, $p=0.0358$). Figure 4 shows this interaction and indicates that there was a greater probability of observing invertebrates in a mouse's stomach when availability was high if the mouse was female. There was about the same probability of observing invertebrates in male mouse stomachs when invertebrate abundance was low or high (Figure 4).

Discussion

Invertebrates, such as crickets (*Orthoptera*) and ground beetles (*Coleoptera*), are important prey items for prairie deer mice living in conventional corn fields during the summer months (Clark & Young 1986). A variety of invertebrate fragments were observed in various amounts in 142 out of 158 mouse stomachs during the course of this study. Thus, during the crop-growing period when there are fewer seeds (such as weed seeds or waste-grain) but seasonally abundant invertebrates, deer mice consume a large amount of this alternative food source.

The strong seasonal trend in invertebrate consumption suggests that mice show a strong bias towards consuming invertebrates regardless of their availability early on in the season. This suggests that the availability of other food items in the field was low and, thus, the relative abundance of invertebrates was high with regards to all potential food items. Alternatively, these results may indicate that mice are forgoing opportunities to capture other food items in their search for invertebrates or simply caching other prey items for consumption at another time. Unlike invertebrates, seeds are highly cacheable, and therefore, mice may adjust their foraging to reflect these properties.

The interaction between date and invertebrate availability may be a result of the increased availability of other food items, such as weed seeds and corn waste grain, and thus the decreased relative abundance of invertebrates and/or a switch in the mouse's foraging strategy from high protein foods to easily cacheable high energy foods. Westerman *et al.* (2006) showed that weed-seed dispersal starts towards the end of August with the majority of seeds being dropped between September and harvest, at which time waste-grain also becomes available. This may provide an explanation for our results, which essentially show that mice eat a large proportion of invertebrates in the spring (most likely the onset of reproductive activity) regardless of their abundance and then less during the fall leading up to winter when easily cacheable high energy prey become available.

As with many other generalist small rodents, invertebrate prey items most likely play an important role during summer reproduction (especially the onset of reproduction) due to their higher protein content (McAdam & Millar 1999; Von Blanckenhagen *et al.* 2007; Tabacaru *et al.* 2010) whereas high-energy prey (such as corn) are more important during the winter months. In our study, there was a higher probability of observing invertebrates in female mouse stomachs than in male stomachs, especially when invertebrate abundance was high. Females often require more protein rich food items during pregnancy and lactation than do males or non-reproductive females (Sadleir *et al.* 1973; Millar 1979). Additionally, several other investigators have found that despite higher abundances of alternative food types, females will select and consume resources of higher quality over resources of higher quantity (McAdam & Millar 1999; Tabacaru *et al.* 2010). Although we were unable to include pregnancy as a factor in our study, we assume that the majority of adult females in this system were reproductively active during the course of our study.

From a population perspective, invertebrates may play an important role in the growth of mouse populations living within these fields. As of yet, we can only speculate about the factors that influence the population growth of deer mice living in conventional crop fields. However we have found that the addition of corn waste grain (a highly preferred and energy-rich resource) during the winter does not influence the numerical response of mice living within these same fields (Flick & Danielson in prep), suggesting that overwinter food resources do not limit population growth. Following this same idea, we expect that food resources would most likely be a more important factor in regulating population growth during the summer months when the majority of individuals are reproductively active. McAdam & Millar (1999) showed that northern deer mice (*Peromyscus maniculatus borealis*) were protein limited (as opposed to just being energy/food limited). Their study shows that by supplementing these populations with a high protein food source resulted in more young of the year females to breed in the summer of their birth resulting in higher population growth (McAdam & Millar 1999).

There was a significant seasonal trend in the abundance of invertebrates collected within our study fields over the course of the study. Not surprisingly, we found that invertebrates were lower in abundance earlier in the spring as well as in late fall. Unexpectedly, invertebrate abundance peaked around July 30, 2012 which is much earlier than we anticipated (late August) and based on previous observations in the area (O'Rourke *et al.* 2006). Two factors that may have contributed to this abnormal temporal variation in invertebrate abundance could be the record drought conditions experienced in the Midwest during the summer of 2012 as well as the occurrence of a large windstorm just prior to the July 30th sample date. The windstorm resulted in a large amount of the previously standing

corn to be knocked down in several of the fields resulting in more open canopy but also more corn biomass on the surface of the soil in these fields.

Our data showed that there was a substantial amount of variation in the stomach contents of individual mice within each sampling period. Much of this variation may be attributed to the fact that we were unable to control the amount of time a mouse spent foraging before encountering our traps. In addition to the overall seasonal patterns, variation between individuals suggests that these mice are, in fact, very generalist foragers and, in many cases, may opportunistically feed on a variety of prey items as they encounter them where as others (such as females, or more specifically reproductive females) may forgo attacking other prey types until they encounter a protein rich invertebrate. Additionally, some of the variation we observed between individuals may be a result of the fact that we were unaware of the availability of other resources within these fields. However, this would not significantly influence/alter the interpretation our results based on the premise that the profitability of potential prey items within these fields is similar across all corn fields (i.e., the inclusion of invertebrates in the mouse's diet should depend on profitability not encounter rate) (Stephens and Krebs 1986).

Although some invertebrates have been shown to contribute to weed-seed predation during the late summer and fall (Harrison *et al.* 2003; Heggenstaller *et al.* 2006; O'Rourke *et al.* 2006; Westerman *et al.* 2008), studies have also shown that other invertebrates are the primary source of crop seedling damage in the spring (Clark & Young 1986). Our data suggests that deer mice may benefit farmers in yet another way, by removing invertebrates from the field early in the spring, indirectly increasing crop seedling. As an example, Parmenter & MacMahon (1988) showed that excluding foraging by four rodent species (one

of which was the deer mouse) allowed for beetle (Carabidae) abundances to be 111% higher than when these rodents were present. If the deer mice living in these crop fields had even a fraction of the magnitude of this effect on beetles and other crop eating invertebrates within these fields, we can see that Parmenter & McMahon's (1988) predictions concerning seedling predation may also be supported in our system. Additionally, reduced consumption of invertebrates later in the summer allows for the invertebrate populations to increase and, therefore, provide additional weed-seed predation services towards the fall.

Some agronomists have stated that these mice are one of the "many little hammer's" that can combine to ecologically manage agricultural weeds (Liebman & Gallandt 1997). We would like to take that a step further and suggest that these mice not only play a key role in ecological weed management but also in the control of other pests such as volunteer corn (resulting from waste grain) and invertebrates in the spring, acting as the perfect tool for all of these situations, somewhat like an ecological Swiss Army knife.

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Table 1. Generalized linear models relating the probability of observing invertebrates in a mouse’s stomach to the measured predictor variables and their resulting AIC values.

Model #	Predictor Variables	AIC
1	Date, field, invertebrate abundance, invertebrate abundance*date	828.37
2	Date, field, invertebrate abundance, sex, invertebrate abundance*date	821.62
3	Date, field, invertebrate abundance, sex, invertebrate abundance*date, invertebrate abundance*sex	818.97

Table 2. Analysis of the maximum likelihood parameter estimates and their associated standard error used to predict the probability of observing invertebrates in a mouse’s stomach based on Model #3, which included the variables date, field, invertebrate abundance, and mouse sex as well as two interaction terms.

Parameter	Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq
Intercept	432.5312	48.6042	79.19	<0.0001
Field 1	0.1936	0.1936	1.03	0.3112
Field 2	-0.0091	0.2005	0	0.9639
Field 3	-0.2045	0.1807	1.28	0.2578
Field 4	0.3165	0.2043	2.4	0.1214
Field 5	0.0000	0	-	-
Invertebrate Abundance	-2.9388	1.5786	3.47	0.0627
Date	-0.0225	0.0025	79.16	<0.0001
Sex - female	-0.0298	0.2334	0.02	0.8985
Sex - male	0.0000	0	-	-
(Invertebrate Abundance)*(date)	0.0002	0.0001	3.46	0.063
(Invertebrate Abundance)*(female)	0.0092	0.004	4.41	0.0358
(Invertebrate Abundance)*(male)	0.0000	0	-	-

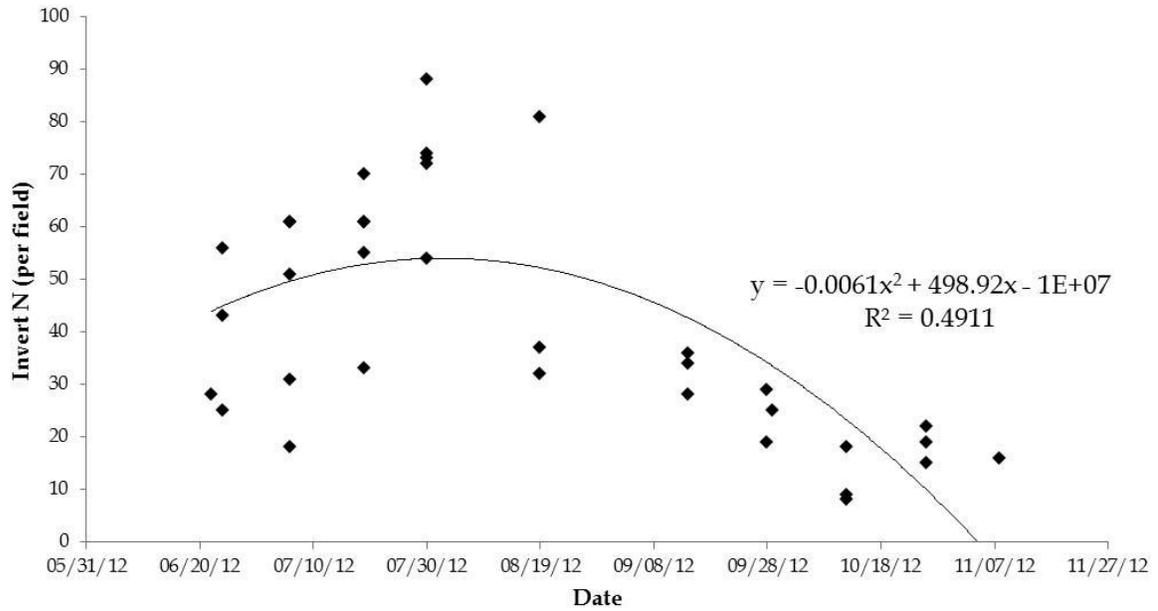


Figure 1. Seasonal trend in total invertebrate abundance from June 2012 to November 2012 in conventional corn fields in Ames, Iowa, USA. Invertebrate abundance was measured using pitfall trapping.

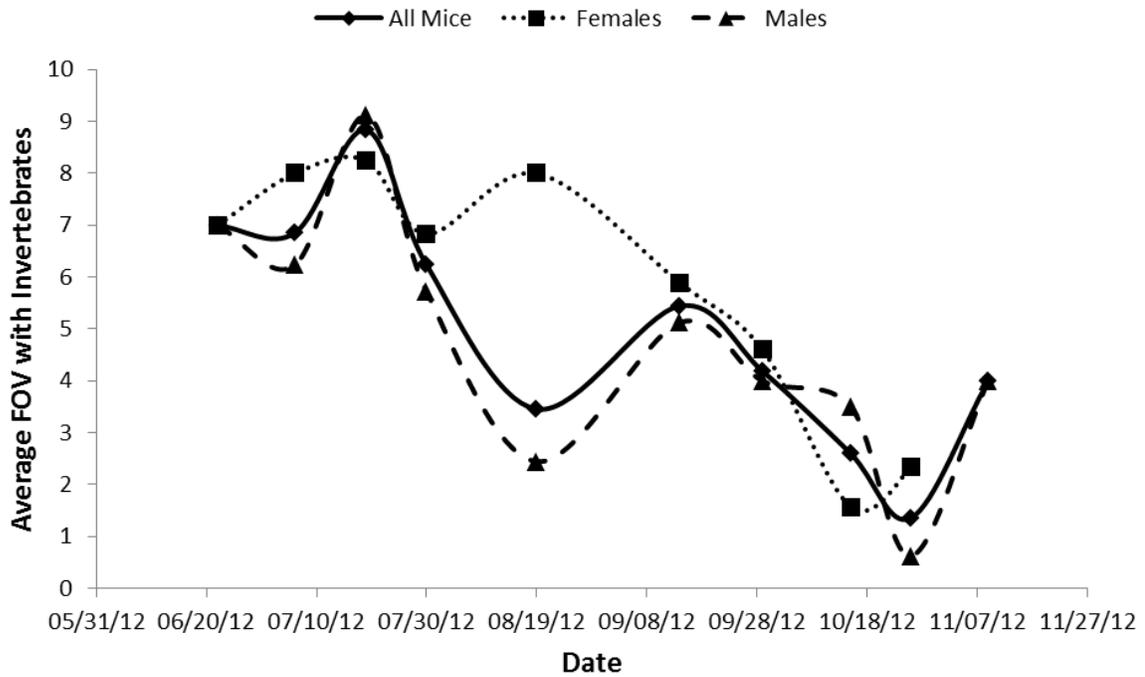


Figure 2. Average number of fields of view (FOV) out of 10 with invertebrates present in mouse stomachs from June 2012 to November 2012. The solid line shows the average for all mice captured, the dotted line shows the average for females only, and the dashed line shows the average for males only.

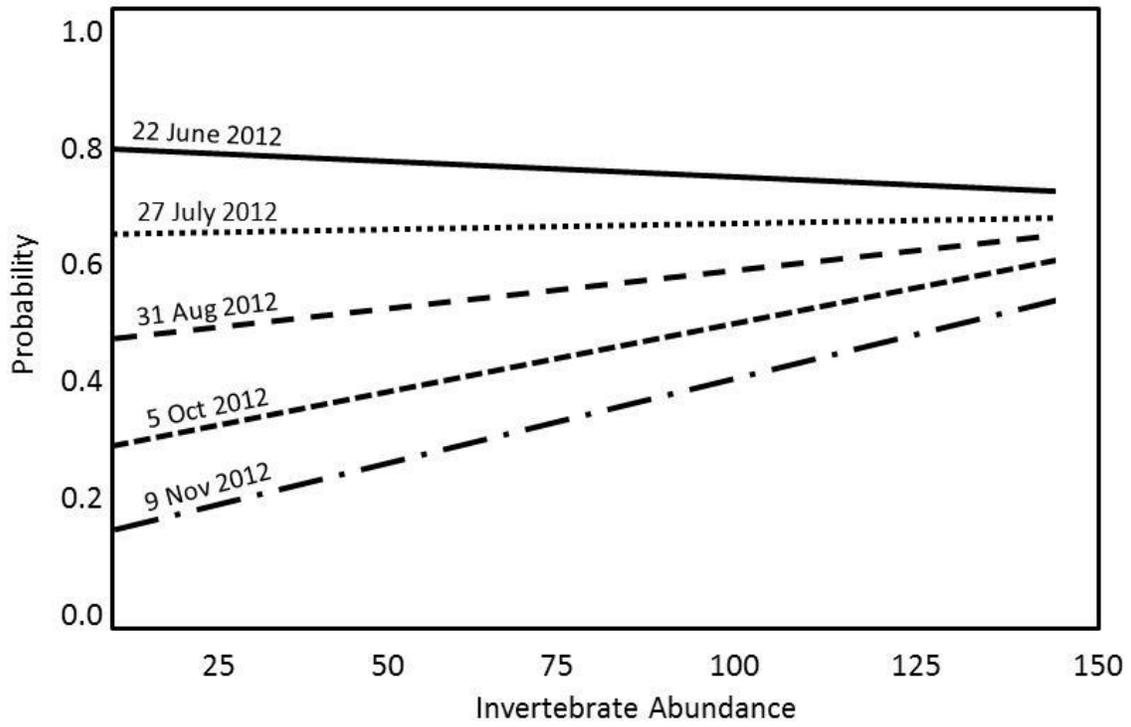


Figure 3. Predicted probabilities for observing invertebrates in a mouse's stomach showing the interaction between total invertebrate abundance and date. Interaction: Wald $\chi^2=3.46$, $p=0.0630$

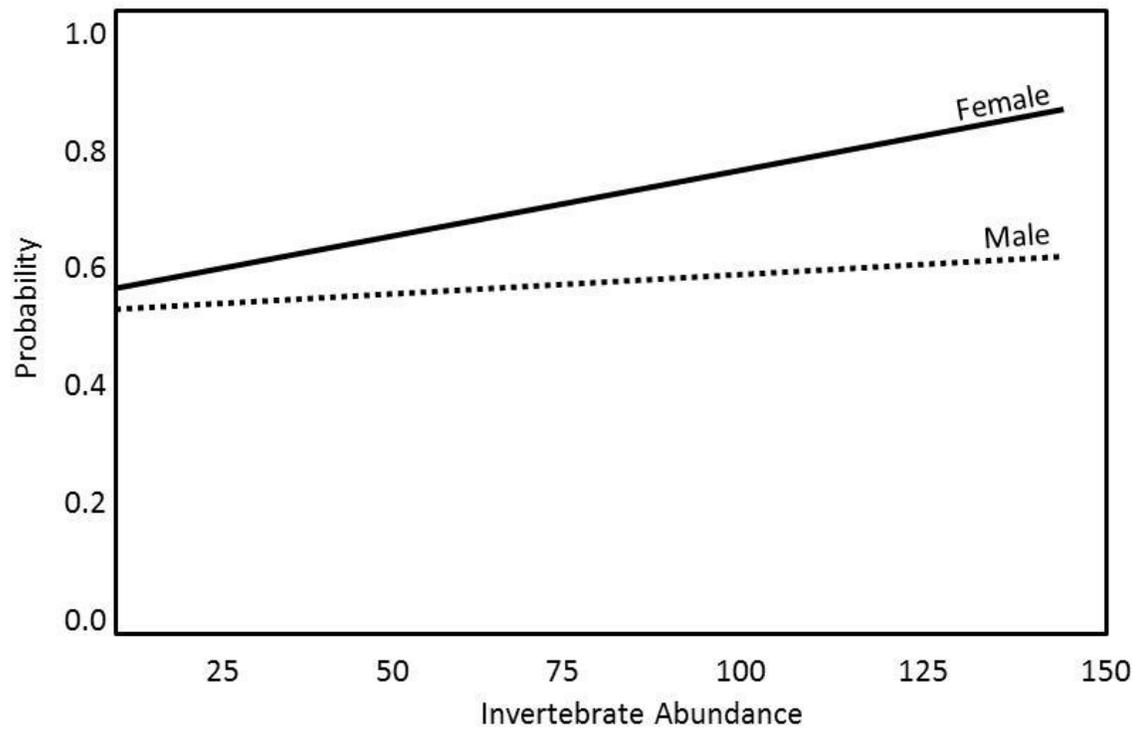


Figure 4. Predicted probabilities for observing invertebrates in a mouse's stomach showing the interaction between total invertebrate abundance and mouse sex. Interaction: Wald $\chi^2 = 4.41$, $p=0.0358$.

CHAPTER 4. GENERAL CONCLUSIONS

Conclusions

This thesis focused on understanding how the spatial distribution and temporal variability in resources influenced foraging by prairie deer mice in conventional crop fields. Additionally, the pest control implications of these findings have been highlighted.

In the first study, I found that individual deer mice showed increased foraging and, therefore, a greater functional response in large patches of waste grain. At the treatment scale, mice living in patchy environments overall may benefit from the additional resources regardless of whether or not their burrow is located within a corn patch itself. The difference in our results between the treatment with many small patches versus the treatment with a few large patches suggests that mice have greater access to resources when they are distributed in a more complex way than when the patches are larger but fewer (while holding total patch area constant). This difference in access is most likely explained by the fact that some mice in the treatment with a few large patches (FL treatment) had to travel a much longer distance to reach a patch, not only increasing the costs of foraging but also the likelihood of encountering conspecifics, which may prevent these mice from foraging within the conspecific home ranges. Surprisingly, I found that the spatial distribution of additional corn waste grain did not influence the numerical response of mice living within the studied corn fields, at least on the scale of one year. Thus, we still do not know what regulates deer mouse abundances in conventional cornfields.

During the winter, mice were able to remove on average between 59 – 66% (94.4 – 105.6 kg/ha) of the added corn seed from the soil surface, demonstrating that mice are

capable of removing large quantities of seeds with the potential of reducing volunteer corn densities in the following spring. Although the possibility that rodents play a role in reducing volunteer corn densities (especially in no-till) has been mentioned elsewhere (e.g., Getz & Brighty 1986; Stewart 2011), this study is the first to explicitly study this. These findings not only illustrate how deer mice are capable of contributing to volunteer corn pest control but highlight their potential as effective control agents in the face of increased use of glyphosate resistant corn varieties (Cerdeira *et al.* 2006; Green 2007). The work from this project is a new frontier in both understanding the special role that mammals play in agricultural systems, as well as the realization that they may hold the key to pest control in a future where pesticide-resistant organisms become increasingly difficult to control by conventional methods which rely heavily on pesticide application (Service 2013). Future work should continue to try and elucidate what factors regulate deer mouse populations within corn fields and what factors allow for more efficient foraging thus allowing crop managers to maximize the potential benefit from the mice living within their fields.

In my second study, I found that invertebrates play a key role in the diets of prairie deer mice especially in the spring and for female mice. There is a strong temporal trend in the diet composition of deer mice living within conventional crop fields. Deer mice had a high probability of consuming invertebrates at the beginning of the study in June and then a lower probability as the season went on. Towards the end of the season, we observed more mice that were completely lacking invertebrates in their stomach contents. Notably, females had a higher probability of consuming invertebrates than males, especially when invertebrate availability was high. This supports many other studies on small mammals that show that invertebrates are a key source of protein for reproductive females (Sadleir *et al.* 1973; Millar

1979; McAdam & Millar 1999; Von Blanckenhagen *et al.* 2007; Tabacaru *et al.* 2010), but more importantly, this suggests that invertebrates may play an important role in mouse population growth within conventional crop fields. Having said this, the use of certain insecticides in conventional crop fields may negatively influence mouse reproduction and population growth, therefore, hindering their potential to regulate pest populations.

One of the most interesting results that has come out of this study is that the specific timing in which mice prey on various resources is surprisingly ideal when viewed through the lens of pest regulation. We know from previous research that deer mice have the potential to consume a large amount of weed seeds towards the end of the summer when these seeds are being dispersed (Harrison *et al.* 2003; Westerman *et al.* 2005; Heggenstaller *et al.* 2006). We also know, however, that mice prefer other prey items such as corn waste grain or even invertebrates a great deal more than weed seeds. This indicates that weed seeds may escape predation if mice are focused on consuming other prey items during the short window of time after the weed seeds hit the ground and before they become inaccessible to the mice (either due to tillage or natural movement into the soil). Additionally, we know that although invertebrates contribute to weed seed predation in the late summer and early fall (Harrison *et al.* 2003; Heggenstaller *et al.* 2006; O'Rourke *et al.* 2006; Westerman *et al.* 2008), some invertebrates are also responsible for the majority of crop seedling damage in the spring (Clark & Young 1986). The diets of deer mice show that they can effectively combat both of these pest problems by exerting higher levels of predation pressure on invertebrates in the spring but lower predation pressure on invertebrates in general during the fall (thus allowing the invertebrates to contribute to weed seed predation). Additionally, the lower probability of consuming invertebrates during the fall suggests that these mice have switched to include

other resources such as weed seeds and eventually (after harvest) waste grain into their diets, again targeting the most problematic pests that that specific time.

Future studies should focus on understanding the interplay of mouse foraging on weed seeds and waste grain. From an applied perspective, understanding foraging on waste grain is beneficial for two reasons, the first has already been mentioned in that glyphosate resistant volunteer corn can be a major pest and then the second reason is that foraging on corn waste-grain will undoubtedly influence foraging on weed seeds. Based on what we know, I propose two alternative hypotheses; the first would be that the availability of waste grain will reduce weed-seed predation because corn is the more desirable resource. The alternative hypothesis would be that the availability of highly desirable waste-grain would draw more mice in to the vicinity (and/or increase the population size over a longer time frame) thus increasing the predation pressure on all resources (including weed seeds). Having said this, the fact that a numerical response was not observed in my first study may suggest that the first hypothesis may be more probable than the alternative, however, this cannot be said for sure since we do not know how waste grain availability or other factors for that matter influence population growth over a longer time scale.

Combining the findings from both studies, we see that spatial and temporal variation in food resources does influence deer mice living in conventional crop fields. We begin to see a remarkable picture take form, one where this common small mammal is contributing to the regulation of multiple pest species in a dynamic way. The temporal change in the composition of the mouse's diet throughout the year results in relatively heavy predation on each pest group (invertebrates, weed seeds and waste grain) at key times throughout the year. Additionally, the mouse's ability to exploit large resource patches as well as more spatially

complex areas with many small patches highlights its ability to target sessile prey such as weed seeds and waste grain that are commonly distributed patchily throughout crop fields. What has not been mentioned yet, but is important to note is that, in addition to foraging to consume seeds over winter, these mice spend a large amount of time caching seeds and thus removing even more seeds from the surface of the soil than is metabolically possible for the mouse to consume. So the fact that these mice are active year round and are able to remove more seeds than metabolically possible makes this organism unique in the sense that they can have a longer and larger impact on pest populations than other organisms that could potentially provide a similar service (e.g., wintering passerine birds).

In conclusion, these two projects have provided us with increased knowledge of some of the factors that influence mouse foraging and populations, as well as their year-round diet, which highlights their overall value in these agricultural systems. This is just the beginning as continued work looking at understanding more about prairie deer mouse ecology as well the factors that influence their foraging and populations will become increasingly important in the future of agriculture in the Midwestern United States. On a larger scale, the work we have done here provides a clear example of how wildlife living within agricultural landscapes provide pest control services. In light of the extent of agricultural land-use and the growing importance of addressing environmental and management concerns in these landscapes, my hope is that ecologists, and more specifically mammalogists, from around the world will take the next step by beginning to identify and study other similar species in their local agricultural settings.

Future Directions

The work presented in this thesis provides a stepping stone for future work on studying small mammals and their benefits in agricultural fields. Through this Masters work I have come to marvel at this system, these mice are essentially unstoppable, thriving in an environment that many other organisms avoid all together. Additionally, these mice function like little ecological Swiss army knives, uniquely equipped to target multiple different pest species (which are often pesticide resistant) at key points throughout the year. I hope that future work on this system will continue to expand, eventually leading to the development of tactics that famers could employ to manage mouse populations within their crop fields.

The forefront of future research should focus on understanding what factors regulate mouse populations over a longer temporal scale. Can farmers manage mouse populations to maximize their pest control benefits? Knowing what factors most strongly influence these populations will be the first step to answering this question. As with many other species, I expect that food resources play a key role in population regulation, but longer term studies will need to be done in order to determine how. Because agricultural systems, especially those in the Midwestern United States, are characteristically simple when compared to more natural habitats, I am a big supporter of taking advantage of this and conducting large-scale experimental manipulations to answer research questions. In Hollings classic 1959 paper in *The Canadian Entomologist*, he takes advantage of a uniform pine plantation, not unlike the conventional corn fields found in the Midwest, to answer important questions regarding predation on a pest invertebrate by small mammals. Similarly, I could envision future projects where invertebrate abundance and waste grain abundance are manipulated experimentally to create fields with contrasting combinations of high to low abundance in

these two critical resources. For example, spraying different concentrations of insecticides in the spring and summer to create treatments with low, medium, and high invertebrate densities and then also adding waste grain in the fall in low, medium and high densities in a full factorial design. From such a study, you would be able to answer a large number of questions including how the abundance of these resources influence the overall population growth and to what degree. Additionally, using this experimental design, one could measure the relative foraging (using GUDs) on weed seeds as well as waste grain throughout the year which would provide a better picture of how these resources influence the mouse predation on each other (i.e., interactions). An experiment like this could allow us to not only measure relative foraging but also the actual weed and volunteer corn densities from year to year, which would provide a more complete picture than just measuring relative foraging. Having said all this, determining the appropriate spatial and temporal scales for the questions being addressed will be a substantial challenge. Regardless of the actual size, the project would have to be on a larger scale and as a result will have many logistical constraints. However, with funding, cooperation from land managers, and lots of field support such a project would be both possible and valuable.

In addition to using large-scale manipulations, future work should also focus on measuring and better understanding the natural variation in mouse, invertebrate, weed, and waste-grain populations between fields. My studies show that in some cases fields in the same geographical area and even different areas within the same field can have very different mouse population densities, however, identifying why this was observed was beyond the scope of my studies. Understanding why this occurs will give researchers and farmers alike a starting point on which they could base expectations of potential pest control upon.

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