

**PREDICTORS OF INSECT DIVERSITY AND ABUNDANCE  
IN A FRAGMENTED TALLGRASS PRAIRIE ECOSYSTEM**

by

Kody Micah Shane Unstad

A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Master of Science

Major: Natural Resource Sciences

Under the Supervision of Professor Craig R. Allen

Lincoln, Nebraska

April, 2012

# **PREDICTORS OF INSECT DIVERSITY AND ABUNDANCE IN A FRAGMENTED TALLGRASS PRAIRIE ECOSYSTEM**

Kody Unstad, M.S.

University of Nebraska, 2012

Advisor: Craig Allen

Despite providing many services, the tallgrass prairie and its ecological community is one of the most endangered ecosystems in North America. Remaining habitat exists as remnants in a highly-fragmented landscape. To make informed conservation decisions we need to better understand the effects of this fragmentation. Using the ecologically important insect groups, ants and ground beetles, this study provides baseline data on the biological diversity of southeast Nebraska prairies and investigates what management, landscape, and habitat characteristics affect them. Pitfall trap sampling was conducted in 23 tallgrass remnants scattered throughout the Southeast Prairies Biologically Unique Landscape in 2010 and 2011. Multi-model inference was used for analysis of the data.

Twenty-eight species of ants were collected with the majority being grassland-obligates. With a positive correlation, model selection results indicate that Shannon diversity of grassland ants is best predicted by the average number of grass species per m<sup>2</sup> while their abundance is positively associated with the amount of nearby haymeadow.

Most ants belonged to the Opportunist and Cold Climate Specialist functional groups. A comparison with prior studies indicates this functional group composition to be most similar to cool-temperate forests. Though different habitats, their cooler climates likely produce this similar composition.

Nineteen species of ground beetles were collected, with two species comprising nearly 95% of the collection. These two species are incapable of flight, a physiological factor that may contribute to their high abundances by leaving them hidden from predators. As with grassland ants, the strongest predictor of Shannon diversity for ground beetles was the average number of grass species per m<sup>2</sup>.

Results suggest that ants and ground beetles are non-randomly distributed in relation to landscape, habitat, and management factors. High abundances of grassland-obligate ants are associated with high amounts of haymeadow suggesting these areas may be a priority for ant conservation. Results also suggest that sites with more grass species sustain more diverse communities of ants and ground beetles, information that can be incorporated into relevant conservation decisions.

## **DEDICATION**

To my parents, for letting me play outdoors.

To my wife, for letting me continue what my parents started.

## ACKNOWLEDGEMENTS

I would first like to thank my advisor, Craig Allen, for providing me with guidance, freedom, and humor, all of which have made this an enjoyable experience. I would next like to thank Chris Helzer, for inspiring my interest in the prairie and for always thinking outside the box. I would like to thank my graduate committee members, LaReesa Wolfenbarger and Lance Meinke, as well as the many members of the Southeast Nebraska Flagship Initiative. Your wisdom and experience is greatly appreciated.

Thank you to Jim Kalisch, for patiently teaching ant identification, and to Ashley Pella, for spending countless hours in front of a microscope (even with a newborn baby). I would like to thank Jim Schalles whose commitment to working long hours on extremely hot days in July made collection of this data possible. I appreciate the support of all my fellow graduate students in the Cooperative Unit, and Chris Wood at UNO. It is nice to have others who can sympathize with your graduate school challenges.

Thank you to Stephen Winter, for being an excellent roommate for three summers and sharing your ecological knowledge, charcoal grill, and fine beers. I also thank the Salem United Church of Christ in Steinauer, NE for providing us with housing and being great landlords and great people. I am especially indebted to the landowners of southeast Nebraska for allowing me access to their haymeadows. I hope my study contributes to the conservation of this beautiful and unique landscape.

I am thankful for the funding provided by the Nebraska Game and Parks Commission and the United States Geological Survey that made this research possible. The Nature Conservancy also provided partial support for this work through the Nebraska Chapter's J.E. Weaver Competitive Grants Program.

Lastly, I would like to thank my family, especially my parents, for their love and support of all my various endeavors over the years. Climbing trees, building forts, running barefoot through cornfields, making backyard parody nature documentaries...the childhood you gave me has made me who I am today. And most importantly, I would like to thank my wonderful wife, Amanda, for her love and prayers, for allowing me to be away the better part of two summers, for not freaking out when bags of insects appeared in the freezer, and for standing by me through all of life's challenges.

## TABLE OF CONTENTS

ABSTRACT.....	ii
DEDICATION.....	iv
ACKNOWLEDGEMENTS.....	v
TABLE OF CONTENTS.....	vii
LIST OF TABLES.....	xii
LIST OF FIGURES.....	xx
Chapter 1: INTRODUCTION.....	1
THE TALLGRASS PRAIRIE.....	1
<i>Historical Background</i> .....	1
<i>The Southeast Prairies Biologically Unique Landscape</i> .....	3
<i>Arthropod Communities</i> .....	5
ANTS (HYMENOPTERA: FORMICIDAE).....	6
<i>Taxonomy</i> .....	6
<i>Morphology</i> .....	7
<i>Life Cycle</i> .....	8
<i>Colony Life Cycle</i> .....	9
<i>Eusociality</i> .....	10
<i>Functional Groups</i> .....	12
<i>Ecology and Ecosystem Services</i> .....	13
GROUND BEETLES (COLEOPTERA: CARABIDAE).....	14
<i>Taxonomy</i> .....	14
<i>Morphology</i> .....	15
<i>Life Cycle</i> .....	16
<i>Ecology and Ecosystem Services</i> .....	17
THESIS OVERVIEW .....	19
LITERATURE CITED.....	21

Chapter 2: DIVERSITY AND ABUNDANCE OF GRASSLAND, WOODLAND, AND HABITAT-GENERALIST ANTS (HYMENOPTERA: FORMICIDAE) IN REMNANT TALLGRASS PRAIRIE HAYMEADOWS.....	29
<i>Abstract</i> .....	29
INTRODUCTION.....	31
METHODS AND MATERIALS.....	32
STUDY SITES.....	32
STUDY DESIGN.....	34
<i>Pitfall Trap Sampling</i> .....	34
<i>Sample Processing</i> .....	35
<i>Habitat Characteristics</i> .....	36
<i>Landscape Characteristics</i> .....	38
<i>Management</i> .....	39
STATISTICAL ANALYSES.....	41
<i>Habitat Preference</i> .....	41
<i>Diversity, Abundance, and Species Richness</i> .....	41
<i>Multi-model Inference</i> .....	42
RESULTS.....	43
<i>Grassland-obligate Ants</i> .....	44
<i>Habitat-generalist Ants</i> .....	45
<i>Woodland-obligate Ants</i> .....	46
DISCUSSION.....	46
<i>Grassland-obligate Ants</i> .....	48
<i>Habitat-generalist Ants</i> .....	49
<i>Woodland-obligate Ants</i> .....	50
<i>Conclusion</i> .....	50
LITERATURE CITED.....	52
TABLES AND FIGURES.....	56



Chapter 3: FUNCTIONAL GROUP COMPOSITION OF ANTS (HYMENOPTERA: FORMICIDAE) IN A GRASSLAND ECOSYSTEM.....	75
<i>Abstract</i> .....	75
INTRODUCTION.....	77
METHODS AND MATERIALS.....	79
STUDY SITES.....	79
STUDY DESIGN.....	80
<i>Pitfall Trap Sampling</i> .....	80
<i>Sample Processing</i> .....	80
<i>Habitat Characteristics</i> .....	81
<i>Landscape Characteristics</i> .....	82
<i>Management</i> .....	83
STATISTICAL ANALYSES.....	84
<i>Functional Groups</i> .....	84
<i>Abundance</i> .....	84
<i>Multi-model Inference</i> .....	84
RESULTS.....	86
<i>Functional Groups</i> .....	86
<i>Model Selection</i> .....	87
DISCUSSION.....	88
<i>Functional Groups</i> .....	89
<i>Biogeographical Comparison</i> .....	90
<i>Model Selection</i> .....	92
<i>Conclusion</i> .....	94
LITERATURE CITED.....	96
TABLES AND FIGURES.....	99
Chapter 4: DIVERSITY AND ABUNDANCE OF GROUND BEETLES (COLEOPTERA: CARABIDAE) IN REMNANT TALLGRASS PRAIRIE HAYMEADOWS.....	119
<i>Abstract</i> .....	119
INTRODUCTION.....	120

METHODS AND MATERIALS.....	121
STUDY SITES.....	121
STUDY DESIGN.....	122
<i>Pitfall Trap Sampling</i> .....	122
<i>Sample Processing</i> .....	123
<i>Habitat Characteristics</i> .....	124
<i>Landscape Characteristics</i> .....	126
<i>Management</i> .....	126
STATISTICAL ANALYSES.....	127
<i>Physiological Functional Groups</i> .....	127
<i>Diversity and Abundance</i> .....	128
<i>Multi-model Inference</i> .....	128
RESULTS.....	130
FUNCTIONAL GROUPS.....	130
MULTI-MODEL INFERENCE.....	131
<i>Diversity and Abundance</i> .....	131
<i>Cyclotrachelus sodalis colossus and Pasimachus elongatus</i> .....	132
<i>Fliers</i> .....	133
<i>Climbers</i> .....	134
<i>Strong Burrowers</i> .....	134
<i>Runners</i> .....	134
DISCUSSION.....	135
<i>Diversity, Abundance, Species Richness</i> .....	137
<i>Physiological Functional Groups</i> .....	138
<i>Conclusion</i> .....	139
LITERATURE CITED.....	141
TABLES AND FIGURES.....	144
Chapter 5: SYNTHETIC SUMMARY.....	168
LITERATURE CITED.....	174

Appendix A: SUPPLEMENTAL TABLES FOR LANDSCAPE, HABITAT, AND MANAGEMENT DATA.....	175
Appendix B: SUPPLEMENTAL TABLES FOR ANT PITFALL TRAPPING RESULTS.....	182
Appendix C: SUPPLEMENTAL TABLES FOR GROUND BEETLE PITFALL TRAPPING RESULTS.....	206

## LIST OF TABLES

### Chapter 2.

Table 1.	Models used for analyses of Shannon diversity, abundance, species richness, or presence. “Month” was included as a fixed factor and “siteyear” as a random factor in all models.....	63
Table 2.	Table 2. Number of each ant species collected in June and July of 2010 and 2011 on 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. ....	64
Table 3.	Ant abundance, species richness, and Shannon Diversity for every sampling event at each of 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.....	65
Table 4.	Taxa of the Formicidae with number collected and corresponding habitat group (grassland-obligate, habitat-generalist, or woodland-obligate).....	66
Table 5.	Results of model selection for grassland-obligate ants. Shannon diversity and abundance use linear mixed models while species richness uses a generalized linear mixed model with a Poisson distribution. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	67
Table 6.	Estimates of parameters affecting grassland-obligate ant Shannon diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	69

Table 7.	Results of model selection for habitat-generalist ants. Shannon diversity and abundance use linear mixed models while species richness uses a generalized linear mixed model with a Poisson distribution. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	70
Table 8.	Estimates of parameters affecting habitat-generalist ant Shannon diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	71
Table 9.	Results of model selection for woodland-obligate ants. For presence/absence, generalized linear mixed models with a binomial distribution were used. Models were evaluated using program R. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	73
Table 10.	Estimates of parameters affecting woodland-obligate ant presence. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	74

### **Chapter 3.**

Table 1.	Models used for analyses of Shannon diversity, abundance, species richness, or presence. “Month” was included as a fixed factor and “siteyear” as a random factor in all models.....	110
----------	--	-----

Table 2.	Total number of each ant species collected in 2010 and 2011 and habitat preference. Habitat preference includes three categories: grassland-obligate, habitat-generalist, and woodland-obligate.....	111
Table 3.	Functional group ant abundance for every sampling event at each of 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.....	112
Table 4.	Taxa of the Formicidae with their abundance and the functional group to which they belong (Andersen 1997).....	114
Table 5.	Results of model selection for functional groups of ants. Opportunists, Cold Climate Specialists, Generalized Myrmicinae, and Cryptic species use linear mixed models to predict abundance. Dominant Dolichoderinae and Subordinate Camponotini use a generalized linear mixed model with a binomial distribution to predict presence. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	116
Table 6.	Table 6. Estimates of parameters affecting abundance of ant functional groups. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	117

#### **Chapter 4.**

Table 1.	Models used for analyses of Shannon diversity, abundance, and species richness. “Month” was included as a fixed factor and “siteyear” as a random factor in all models.....	151
----------	---	-----

Table 2.	Total number of each ground beetle species collected in June and July of 2010 and 2011 on 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.....	152
Table 3.	Taxa of Carabidae with total number collected and physiological abilities. Flying ability is either capable (x) or incapable (-); climbing ability is occasional, regular, frequent, or non-climber (-); burrowing ability is strong or not strong (-); running ability is slow, moderate or fast.....	153
Table 4.	Results of model selection for ground beetles. The response variables of Shannon diversity and abundance use linear mixed models while species richness uses a generalized linear mixed model with a Poisson distribution. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	155
Table 5.	Estimates of parameters affecting ground beetle Shannon Diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	156
Table 6.	Results of model selection for the abundance of <i>Cyclotrachelus sodalis colossus</i> and <i>Pasimachus elongatus</i> . Linear mixed models were evaluated using program R. Results displayed include any model whose weight is above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	158

Table 7.	Estimates of parameters affecting abundance of <i>Cyclotrachelus sodalis</i> <i>colossus</i> and <i>Pasimachus elongatus</i> . Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	159
Table 8.	Results of model selection for the abundance of ground beetles grouped by flying ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	160
Table 9.	Estimates of parameters affecting abundance of flying ground beetles. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	161
Table 10.	Results of model selection for the abundance of ground beetles grouped by climbing ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	162
Table 11.	Estimates of parameters affecting abundance of climbing ground beetles. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	163



Table 12.	Results of model selection for the abundance of ground beetles grouped by burrowing ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	164
Table 13.	Estimates of parameters affecting abundance of climbing ground beetles. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	165
Table 14.	Results of model selection for the abundance of ground beetles grouped by running ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.....	166
Table 15.	Estimates of parameters affecting ground beetle Shannon Diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).....	167

## Appendix A.

Table 1.	Landscape data for study sites in the Southeast Prairies Biologically Unique Landscape. Includes the latitude and longitude of the center pitfall trap, the size of sites, and the percentage of land within a 250 m radius of the center trap covered by each of six classes (haymeadow, cattle pasture, CRP, trees, cropland, and other) .....	176
Table 2.	Vegetation structural data from 2010 and 2011 for study sites in the Southeast Prairies Biologically Unique Landscape. Includes date of sampling, average litter depth (cm), average vegetation density (Robel measurement to nearest $\frac{1}{4}$ decimeter), and vertical heterogeneity of the vegetation (Shannon diversity index of every plant touching the Robel pole every $\frac{1}{4}$ decimeter). For data collection details see chapter 2.....	177
Table 3.	Plant diversity of study sites in the Southeast Prairies Biologically Unique Landscape. Includes average number of plant species, grass species, and forb species per m <sup>2</sup> . See chapter 2 for a description of data collection.....	179
Table 4.	Percentage of each study site in the Southeast Prairies Biologically Unique Landscape comprised of five soil classes (loam, clay loam, silty loam, silty clay loam, and other) .....	180
Table 5.	Haying dates of study sites in the Southeast Prairies Biologically Unique Landscape and corresponding “haying” values. Values are based on date hayed with July 15 = 1, July 16 = 2, etc. In 2010, sites CB, EN, ES, and R were hayed at an unknown date after September 21; therefore the 2011 value was used as the average value.....	181

## **Appendix B.**

Table 1.	June 4-7, 2010 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.....	182
Table 2.	June 29-July 2, 2010 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.....	188
Table 3.	June 3-6, 2011 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.....	194
Table 4.	June 28-July 1, 2011 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.....	200

## **Appendix C.**

Table 1.	June 4-7, 2010 pitfall trap sampling results for ground beetles. Includes the number of each species captured in every trap at every site.....	206
T able 2.	June 29-July 2, 2010 pitfall trap sampling results for ground beetles. Includes the number of each species captured in every trap at every site.....	212
Table 3.	June 3-6, 2011 pitfall trap sampling results for ground beetles. Includes the number of each species captured in every trap at every site.....	218
Table 4.	June 28-July 1, 2011 pitfall trap sampling results for ground beetles. Includes the number of each species captured in every trap at every site.....	224

## LIST OF FIGURES

### Chapter 2.

- Figure 1. Map showing the Biologically Unique Landscapes of southeast Nebraska (The Nature Conservancy 2012), including the Southeast Prairies BUL which includes most of Pawnee as well as portions of Johnson, Richardson, and Gage counties..... 56
- Figure 2. Location of the 23 study sites within the counties of the Southeast Prairies Biologically Unique Landscape..... 57
- Figure 3. Sampling design used in study sites. Nine pitfall traps were arranged in a 3 x 3 grid spaced 25 m apart. Twelve Robel pole locations were arranged in a 4 x 4 grid spaced evenly between and outside the pitfall traps..... 58
- Figure 4. Total number of ants captured in 2010 and 2011 at each of the 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. Site CC had the fewest with 109 and site G had the most with 1,188. Most sites remained fairly consistent between the two years. The most notable exception was site BE which had 746 more ants in 2011 than 2010. Sites HBE and WA also had relatively large increases in 2011..... 59
- Figure 5. Percentage of ants from 2010 and 2011 belonging to each habitat group. The grassland-obligate ants dominated the remnant haymeadows, followed by habitat-generalists, and very few woodland-obligate species..... 60

Figure 6. Plot of the collection frequency vs. the log of the abundance for (a) *Lasius neoniger* and (b) *Myrmica americana*. There is a strong correlation between the two variables ( $r^2=0.85$  and  $r^2=0.97$  respectively) indicating that abundance is not driven by large numbers due to pheromone trails or close proximity of traps to nests..... 61

Figure 7. Linear regression of grassland-obligate ants with relevant habitat, landscape, and management factors in 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. Regression includes: (a) Shannon diversity of ants vs. mean number of grass species per  $m^2$ ; (b) Log of the abundance of ants vs. percentage of haymeadow with a 250 m radius; (c) Species richness of ants vs. mean number of grass species per  $m^2$ ; (d) Species richness of ants vs. averaging haying date (July 15=1, July 16=2, etc.). Data from June and July are combined to give a single value for each site for each year..... 62

### Chapter 3.

Figure 1. Map showing the Biologically Unique Landscapes of southeast Nebraska (The Nature Conservancy 2012), including the Southeast Prairies BUL which includes most of Pawnee as well as portions of Johnson, Richardson, and Gage counties..... 100

Figure 2. Location of the 23 study sites within the counties of the Southeast Prairies Biologically Unique Landscape..... 101

- Figure 3. Sampling design used in study sites. Nine pitfall traps were arranged in a 3 x 3 grid spaced 25 m apart. Twelve Robel pole locations were arranged in a 4 x 4 grid spaced evenly between and outside the pitfall traps..... 102
- Figure 4. Total number of ants captured in 2010 and 2011 at each of the 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. Site CC had the fewest with 109 and site G had the most with 1,188. Most sites remained fairly consistent between the two years. The most notable exception was site BE which had 746 more ants in 2011 than 2010. Sites HBE and WA also had relatively large increases in 2011..... 103
- Figure 5. Percentage of ants from 2010 and 2011 belonging to each functional group. The Opportunists and Cold Climate Specialists dominated the remnant haymeadows, followed by Generalized Myrmicinae and Cryptic Species. Only about 1% of the collection consisted of Dominant Dolichoderinae and Subordinate Camponotini..... 104
- Figure 6. Percentage of the total ant abundance belonging to each functional group for 2010 and 2011 combined. Includes the sum total abundance and abundance using a 6-point scale (Andersen 1997). Opportunists are dominant using both methods, but Generalized Myrmicinae are nearly even with Cold Climate Specialists using the 6-point scale method..... 105
- Figure 7. Proportion of total ants comprised of each functional group for all study sites, 2010 and 2011 combined..... 106

- Figure 8. Percentage of ants belonging to each functional group in arid desert, temperate woodland, and cool-temperate forest (Andersen 1997) compared to southeast Nebraska grassland. The 6-point scale method of abundance was used for comparison. The functional group composition in the grassland was most similar to cool-temperate forests in that both are dominated by Opportunists and Cold Climate Specialists..... 107
- Figure 9. Plot of the log abundance of Cold Climate Specialists vs. (a) the mean grass species richness per m<sup>2</sup> and (b) the mean forb species richness per m<sup>2</sup>. Grasses have a positive correlation while forbs have a negative correlation..... 108
- Figure 10. Plot of the log abundance of (a) Generalized Myrmicinae vs. Opportunists and (b) Cold Climate Specialists vs. Opportunists. Grasses have a positive correlation while forbs have a negative correlation. Opportunists have a negative correlation with the more aggressive Generalized Myrmicine, but a positive correlation with Cold Climate Specialists..... 109

#### **Chapter 4.**

- Figure 1. Map showing the Biologically Unique Landscapes of southeast Nebraska (The Nature Conservancy 2012), including the Southeast Prairies BUL which includes most of Pawnee as well as portions of Johnson, Richardson, and Gage counties..... 144
- Figure 2. Location of the 23 study sites within the counties of the Southeast Prairies Biologically Unique Landscape..... 145

Figure 3.	Sampling design used in study sites. Nine pitfall traps were arranged in a 3 x 3 grid spaced 25 m apart. Twelve Robel pole locations were arranged in a 4 x 4 grid spaced evenly between and outside the pitfall traps.....	146
Figure 4.	Total number of ground beetles captured at each site for 2010 and 2011. Sites HBW and WA had the fewest with 38 and 39 respectively. Site CB had the most with 391. Most sites were relatively similar in collection numbers over the two years.....	147
Figure 5.	The average number of ground beetles captured at each site with error bars representing the 95% confidence interval.....	148
Figure 6.	Proportion of (a) individual ground beetles and (b) species belonging to each functional group. Although those incapable of flying and climbing dominate numerically, they are comprised of relatively few species.....	149
Figure 7.	Linear regression of the log of the abundance of <i>Cyclotrachelus sodalis colossus</i> vs. the density of the vegetation as measured with a Robel pole.....	150

## **Appendix A.**

Figure 1.	Comparison of sites between 2009 and 2010 using the Floral Quality Assessment Index (FQI). At the 95% confidence interval, FQI values were consistent between the two years.....	175
-----------	--	-----



## **Chapter 1: INTRODUCTION**

### **THE TALLGRASS PRAIRIE**

#### *Historical Background*

The Great Plains once covered an estimated 162 million hectares of central North America, extending north into Canada, south into Texas, west into Wyoming, and east into Ohio (Samson and Knopf 1994, Samson et al. 1998). This vast grassland is subdivided into three major prairie types: tallgrass, mixed grass, and shortgrass. Although all three types have been significantly reduced since European settlement, the reduction of tallgrass prairie surpasses that of any other major North American ecosystem (Samson and Knopf 1994, Samson et al. 2004).

Since 1830 the original area of tallgrass prairie has declined by 99% in some states (Samson et al. 1998), a decline primarily due to agricultural conversion (Samson et al. 2004). The loss of grasslands may lead to a loss in many important ecosystem services such as soil formation, nutrient cycling, and water regulation (Safriel and Adeel 2005). The roots of tallgrass prairie plants descend deep into the ground trapping moisture, preventing erosion, and enriching the soil with organic matter (Whiles and Charlton 2006). Converting prairie to agriculture may result in pesticide use and tillage, reduced decomposition, reduced soil moisture, impaired nutrient cycling, and reduced soil organic carbon with associated nutrients (Safriel and Adeel 2005). This results in a loss of soil fertility in addition to increased soil erosion and decreased water quality (Safriel and Adeel 2005).

Loss of grasslands endangers the persistence of many species. Of bird species that breed in the United States, over 75% have been documented to breed in the Great Plains

(Samson and Knopf 1994). These grassland birds have been experiencing population declines in North America for decades due to prairie fragmentation and rangeland deterioration (Brennan and Kuvlesky 2005). This enormous decline may be unfolding into a wildlife management crisis (Brennan and Kuvlesky 2005). Although habitat loss has already eliminated much of the Great Plains' grasslands, other factors threaten what remains.

Fire control, along with fragmentation of the prairie by roads, crops, and other artifacts of civilization, has reduced or eliminated fire in most of the remaining prairie (Samson and Knopf 1996). Tallgrass prairie, which historically occupied 60 million ha and the eastern third of the Great Plains (Samson and Knopf 1994), receives the most precipitation of the three prairie types (Samson et al. 1998). This precipitation allows domination by large grass species such as big bluestem (*Andropogon gerardii*), indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and rough dropseed (*Sporobolus asper*) (Samson and Knopf 1996), but also makes the prairie susceptible to woody invasion in the absence of frequent fires (Bragg and Hulbert 1976, Briggs et al. 2002).

Fragmentation may isolate prairie remnants so that migrants or propagules of species cannot reach additional food or habitat. Individual fragments may therefore lose biodiversity and fail to produce the same services they would with a larger area or an accessible network of fragments (Saunders et al. 1991). Fragmenting prairie into small, irregularly shaped remnants increases the edge to interior ratio, thus strengthening the influence of edge effects (Saunders et al. 1991, Ewers et al. 2007). This allows non-native species greater access to the prairie and increases the potential for biological invasions.

Competition with non-native invaders may negatively affect native species. One study of 54 tallgrass prairie remnants found that 8 to 60 percent of native plants were lost over a 32- to 54- year period (Leach and Givnish 1996).

### *The Southeast Prairies Biologically Unique Landscape*

An important source pool for much of the Great Plains biodiversity, some experts have specified native grasslands as a priority for urgent conservation action (Ricketts 1999). Nebraska is no exception. Of the pre-settlement 6,100,000 ha of tallgrass prairie, only 123,000 ha remain (Samson and Knopf 1994). The Nebraska Natural Legacy Project was developed in 2003 as a comprehensive wildlife conservation strategy for the state. The Project identifies biologically unique landscapes (BULs) as priorities for conservation based on the greatest known assemblages of biological diversity, including many populations of at-risk species (Schneider et al. 2005). One such landscape, the Southeast Prairies BUL, was selected for its remaining tallgrass prairie habitat.

The Nebraska Natural Legacy Project formed the Southeast Nebraska Flagship Initiative in 2007. This partnership of organizations works collaboratively to promote research-driven conservation within the Southeast Prairies and neighboring Sandstone Prairies BULs (Prairie Nebraska 2011). The Nature Conservancy is the designated lead agency for research and monitoring with partners from the Northern Prairies Land Trust, Nebraska Game and Parks Commission, the University of Nebraska at Omaha, and the Nebraska Cooperative Fish and Wildlife Research Unit at the University of Nebraska at Lincoln.

The landscape of the Southeast Prairies BUL, once contiguous tallgrass prairie, is now a fragmented mosaic of crops, trees, roads, cattle pastures, and haymeadows.

Though modified by decades of annual mowing, haymeadows contain much of the remaining local, native plant diversity. Understanding how fragmentation affects these remnants is critical for developing conservation practices for the tallgrass prairie.

The impacts of fragmentation are inherently complex and act at multiple scales (McGarigal and Cushman 2002). How fragmentation is manifest depends on how a particular organism interacts with its environment. The landscape matrix may strongly influence what species are able to survive in a given habitat by subsidizing resources in fragments (Rand and Louda 2006), providing additional, lower-quality habitat, or allowing passage to other suitable fragments (Andren 1994). Thus composition and spatial arrangement of the landscape mosaic are critical factors to consider when evaluating fragmentation effects. Local (within-fragment) habitat characteristics, such as plant community and structure, also influence species richness and abundance (Stoner and Joern 2004). Models investigating how species are affected by fragmentation should include both local and landscape characteristics (Mazerolle and Villard 1999, Stoner and Joern 2004).

Most tallgrass prairie fragments in the Southeast Prairies BUL are currently managed for hay production. Although management is similar on all sites, there are some important differences. Some sites have been over-seeded with non-native species such as red clover (*Trifolium pratense*) and smooth brome (*Bromus inermis*), directly changing plant composition. Other sites possess treeline borders which increase shade, decrease wind, and potentially increase woodland species in the fragment.

Another important difference in management is time of haying, which ranges from mid-July to late September. This difference can affect vegetation composition and structure, altering the habitat for other prairie organisms. Haying before plants are able to produce viable seed limits their reproduction, potentially eliminating populations from sites that are hayed early; this may particularly affect annuals or short-lived perennials whose populations depend on frequent reproduction. Vegetation structure is altered when, in some sites, perennials are mowed annually at the peak of their aboveground production, weakening them over time and decreasing height and biomass.

### *Arthropod Communities*

Arthropods play a crucial role in ecosystem functioning of the tallgrass prairie. Worldwide, the phylum Arthropoda contains an estimated 2 million (Hodkinson and Casson 1991) to 50 million or more species (Erwin 1988). Their extraordinary species diversity, abundance, rapid growth rates, functional roles, and wide range of body sizes led some experts to suggest including arthropods with plants and vertebrates as an essential component when making conservation decisions (Kremen et al. 1993, Oliver and Beattie 1993). Their rapid responses to changes in the environment make terrestrial arthropods potentially good bioindicators (Kremen et al. 1993), yet their use as such remains largely untapped.

Herbivorous arthropods, particularly those of the class Insecta, have been the focus of many studies due to their potential for economic damage as pests. Their consumption of plants threatens crops as well as the livestock they directly compete with for food (Branson et al. 2006). Hewitt and Onsanger (1983) estimated that grasshoppers

annually remove 21-23% of available vegetation on 262 million ha of rangeland in the western United States.

Compared to herbivores, the role of arthropod predators in the tallgrass prairie is relatively understudied (Whiles and Charlton 2006). Predators may be providing many underappreciated ecosystem services, namely reducing insect pest populations. By maintaining natural habitat such as tallgrass prairie within an agricultural landscape, predator arthropods may provide natural control of pests, thus reducing the costs associated with pesticides (Landis et al. 2000). Herbivore-reduction due to predators may increase plant biomass in grasslands through a top-down trophic cascade (Moran and Hurd 1998). Predatory arthropods also affect the diversity of other invertebrate guilds. In fact, predator and parasite diversity can have more influence on herbivore diversity than plant diversity (Siemann et al. 1998). Two of the most important predatory insect groups in the tallgrass prairie are ants (Hymenoptera: Formicidae) and ground beetles (Coleoptera: Carabidae).

### **ANTS (HYMENOPTERA: FORMICIDAE)**

#### *Taxonomy*

Ants, like wasps and bees, fall within the order of Hymenoptera, but maintain a separate family classification, the Formicidae. The Formicidae is subdivided into 21 subfamilies comprising 290 genera and more than 12,500 extant species (Bolton et al. 2006). As taxonomic knowledge of ants expands, some of these species will undoubtedly prove to be redundant; despite these redundancies, the current rate of discovery of new ants suggests their total species diversity could easily exceed 25,000 (Ward et al. 2010).

Although most of these species occur in tropical bioregions, approximately 580 species have been described in the Nearctic region (North America north of Mexico) (Hölldobler and Wilson 1990).

In the past, ant morphology served as the principal source for delimiting species; as DNA sequencing has advanced it has supplanted morphology as the main source of evidence for determining species and their phylogenetic relationships (Ward et al. 2010). Consequently, ant taxa are frequently being reclassified based on new information. Although ant taxonomy remains unresolved, there still exists a relatively strong taxonomic base on which to perform biodiversity studies.

### *Morphology*

Ants, like all insects, have a hard external exoskeleton. The exoskeleton protects the soft interior of the ant, provides a place for muscular attachment, and prevents desiccation. The ant's body is divided into three parts: head, thorax, and abdomen. Ants possess a petiole toward the front of the abdomen, a feature unique only to certain members of Hymenoptera. The petiole consists of one or two constricted abdominal segments creating a narrow tube that separates the body into the mesosoma (composed of the thorax fused together with one abdominal segment) and the gaster (the hind body composed of several more abdominal segments). The mesosoma can be further subdivided into the pronotum, mesonotum, and propodeum.

Other morphological structures in ants have evolved differently enabling species to fill a variety of niches. Ants can vary in size from less than two millimeters to over 248 (Pfeiffer and Linsenmair 1998). Eyes can be absent, vestigial, or well-developed

compound eyes with several hundred ommatidia (Depickere et al. 2004). Additionally, some species possess ocelli, light-responsive simple eyes, arranged in a triangle on the top of the head. Ants possess variously-shaped mandibles which hinge on the front of the head in such a way that they can be closed tightly together or opened wide (Brian 1977). The sharply serrate margins of the mandibles enable them to grip or pierce objects (Brian 1977).

Arguably the most important sense organs all ants possess are the distinctly elbowed antennae (Brian 1977). The antennae allow ants to detect a wide variety of chemicals important in communication, to sense sounds and vibrations in the substratum, and to understand the size and shape of objects in their environment (Brian 1977). Antennae typically consist of six to twelve segments and in some species the terminal segments are enlarged to form a distinct club.

Alates, the reproductive male and female ants, differ from workers in that they typically possess four membranous wings located on the mesosoma. Female alates, or queens, lose their wings after mating but are still distinguishable from other females due to their relatively large body size, particularly the size of their gaster.

### *Life Cycle*

Ants are holometabolous insects, undergoing a complete metamorphosis that includes four stages of development: egg, larva, pupa, and adult. Larvae emerge from oval-shaped eggs that are laid by the queen and transported by workers. These larvae are white, legless grubs that can do little more than arch their bodies and consume the food workers bring them (Brian 1977). The larvae will go through a number of instars, molting



several times in order to expand (Brian 1977). During the final instar, larvae cease feeding in preparation for pupation (Fraser et al. 2001).

The pupal stage begins when the prepupal exuvium is shed (Bruder and Gupta 1972). The pupa is often naked, resembling a white adult with the antennae and legs pressed close to the body. In some species the larvae spin silk and the pupal stage occurs inside a cocoon (Wheeler 1915). Eventually a pale adult emerges from the pupa; it will darken to its final color as the exoskeleton hardens over the next several days. The development from egg to adult varies based on species, environmental factors, and whether or not it is part of the incipient brood, but takes between approximately 36-63 days (Bruder and Gupta 1972).

### *Colony Life Cycle*

The life cycle of an ant colony can be divided into three stages: founding, ergonomic (growth), and reproductive (Oster and Wilson 1978, Kaspari 2000). The founding stage initiates with the nuptial flight of the alates. Typically, males aggregate in a swarm above the landscape and females enter the swarm, mating in flight. In contrast to male-aggregation, some species use female-calling for reproduction. With female-calling, wingless queens release pheromones from the ground or low-lying vegetation to attract males to them (Hölldobler and Bartz 1985). In the case of these wingless queens, new colonies are usually not founded independently but with the help of workers who leave the natal colony with the queen, a process known as budding (Peeters and Molet 2010). In either case, the males soon die after mating while the female queens will locate a suitable nest site in the soil and construct a first nest cell (Hölldobler and Wilson 1990).

The queen will shed her wings (if she has them) and, if she is founding the colony independently, will rear the new colony's first brood of workers using only her tissue reserves (Hölldobler and Wilson 1990). Some smaller, non-claustral queens contain insufficient tissue reserves and will therefore forage outside their nesting cell in order to rear the first generation of workers (Peeters and Molet 2010). After workers reach the adult stage they will take over foraging, nest enlargement, and brood care (Hölldobler and Wilson 1990).

Over the coming weeks and months the colony transitions to the ergonomic stage in which the focus is exclusively on colony growth. During the ergonomic stage the population of workers grows, the average size of workers increases, and the queen is confined only to egg-laying (Hölldobler and Wilson 1990). After a period that can range from a single season to several years (Hölldobler and Wilson 1990), the colony enters the reproductive stage when it begins to produce alates. These alates will eventually venture out on their nuptial flights beginning the life cycle of a new colony.

### *Eusociality*

Ant colonies are societies of conspecific individuals (Steiner et al. 2010) characterized by cooperative care of the young, overlapping generations within the same nest, and a specialization of tasks by reproductive and non-reproductive castes (Hölldobler and Wilson 1994). Cooperation within the colony is the foundation for the ecological success of these eusocial insects (Wilson 1987, Hölldobler and Wilson 1990, Bourke and Franks 1995).

A caste system exists within ant colonies and consists of three primary forms:

workers (sterile females), queens (reproductive females), and drones (reproductive males). The function of queens is egg-laying while the only function of drones is mating. The worker caste, which makes up the vast majority of the colony (Steiner et al. 2010), can be further subdivided by the specialized tasks they perform, known as polyethism. In age polyethism tasks vary based on the age of the individual worker. Although less common, if workers are enabled to perform specialized tasks by possessing distinctly different anatomical sizes and shapes it is called physical polymorphism (Oster and Wilson 1978, Bourke and Franks 1995).

Whether the roles of workers are specialized or general depends upon the species (Steiner et al. 2010), but typical tasks include brood care, nest construction, nest hygiene, foraging, and defense (Hölldobler and Wilson 1990). In the case of foraging and defense, social behavior is a great advantage; if an item of food or a nest intruder is too large for an individual to handle, groups of workers can be swiftly assembled through recruitment or alarm signals (Hölldobler and Wilson 1990). Such signals are part of a necessary component that allows eusocial organisms to flourish: communication.

Much of the communication in an ant colony is transmitted chemically (Steiner et al. 2010). In fact, Hölldobler and Wilson (1990) found that pheromones, produced by a number of different exocrine glands, play the central role in the organization of ant societies. Pheromone signals are detected by olfactory receptors located in antennal sensilla (Kleineidam et al. 2005). Pheromones can indicate a worker's task to other workers and inform whether or not a certain task should be performed (Greene and Gordon 2003). Ants of a single colony share a particular chemical with one another through trophallaxis, giving them a distinct colony odor (Dahbi et al. 1999). The colony

odor allows ants to recognize members of their own colony and respond hostilely toward ants of other colonies and species (Hölldobler and Wilson 1990). Other important chemical communication responses include: alarm, simple attraction, recruitment, grooming, exchange of solid food particles, control of reproductives, territory and nest marking, and sexual communication (Hölldobler and Wilson 1990).

### *Functional Groups*

It is often useful to group species into functional groups for analyses. Functional groups allow predictability in the member species' reactions to stress and disturbance. Many ant species perform multiple functions (e.g., predation, scavenging, aphid-tending) making them difficult to group. Andersen, however, identified several functional groups of ants in Australia (Andersen 1995, Andersen 2000). These functional groups have since been extrapolated to include North American species (Andersen 1997). They are Dominant Dolichoderinae, Subordinate Camponotini, Cold Climate Specialists, Hot Climate Specialists, Tropical Climate Specialists, Cryptic Species, Opportunists, Generalized Myrmicinae, and Specialist Predators.

Dominant Dolichoderinae inhabit hot, open areas of low disturbance. In North America, Dominant Dolichoderinae are absent in most habitats. Subordinate Camponotini are usually behaviorally submissive to Dominant Dolichoderinae. Cryptic Species are small ants that nest and forage primarily in soil, litter, and rotting logs. Opportunists are poorly competitive and predominate at highly disturbed sites where behavioral dominance by other ants is low. Generalized Myrmicinae are among the most abundant ants in warm areas and predominate in environments experiencing moderate

levels of stress or disturbance. They are often competitive with Dominant Dolichoderinae. Outside of direct predation, Specialist Predators have little interaction with other ants (Andersen 2000).

### *Ecology and Ecosystem Services*

Ants have been dubbed “ecological engineers” due to their ability to modify the structure of their environment in ways that affect other organisms (Lawton 1994, Kaspari 2000). One example is the movement and enrichment of soil while excavating nests. The significant amounts of displaced soil increases aeration and drainage while incorporating litter from the surface (Kaspari 2000). Ants also change the chemical nature of the soil by transforming organic matter and incorporating nutrients as they bring food from throughout their foraging territory and concentrate it in their nest (Folgarait 1998, Kaspari 2000); these nutrients are eventually recycled by the plant community (Kaspari 2000).

The reproduction of certain plants (at least 3,000 species in 90 genera) is adapted for seed-dispersal by ants (Rico-Gray and Oliveira 2007). As ants transport seeds into their nest they not only disperse the seeds but place them in an area appropriate for germination: below ground, away from predators, and in enriched soil (Culver and Beattie 1978).

Ants are one of the foremost predators in their size range. Possessing the ability to hunt in groups, ants consume vast quantities of prey arthropods (Trager 1998). Although some ants specialize as herbivores or scavengers, most prairie ants function as generalist predators (Trager 1998). The primary prey items are soft-bodied, protein-rich, immature

insects which mostly go toward feeding the growing ant larvae (Trager 1998). With such high abundances of ants in many ecosystems this predation can significantly affect populations of other insects, including the reduction of pest species. Because of their voraciousness some experts have suggested ants as a biological control for pest insects (Way and Khoo 1992).

### **GROUND BEETLES (COLEOPTERA: CARABIDAE)**

#### *Taxonomy*

Coleopterans, or beetles, are the most speciose and widespread order of insects (Erwin 1997). With the exception of the deep sea, beetles are found on every part of the earth (Erwin 1997). Three to four-hundred thousand or more species have already been described (Hammond 1992), suggesting that beetles comprise 25% of all animal species (Erwin 1997, Liebherr and McHugh 2003). Of the estimated 140 families of beetles, most are found worldwide and provide a number of ecological services wherever they occur (Erwin 1997). One such family is the Carabidae, otherwise known as carabids, or ground beetles.

The Carabidae contain 40,000 described species (Erwin 1985, Riddick 2008), making it the most speciose group belonging to the suborder Adephaga. In North America, ground beetles are estimated to contain over 2,000 species (Riddick 2008). Many taxonomic problems remain to be solved with ground beetles. In spite of cladograms with new phylogenetic hypotheses, different authorities continue to divide the family into different subfamilies (Lövei and Sunderland 1996). For instance, tiger beetles have been placed in their own family, Cicindelidae, their own subfamily,

Cicindelinae, or an existing subfamily, Carabinae. Although most commonly placed in their own subfamily, there seems to be no consensus classification for this group.

Despite the disagreements in ground beetle systematics, the abundance, species richness, and colorful exoskeletons of many ground beetle species have made them popular study subjects for both professional and amateur entomologists (Lövei and Sunderland 1996). Relative to many other insects, ground beetle taxonomy is well documented.

### *Morphology*

As with all insects, ground beetles possess a three-part body consisting of the head, thorax, and abdomen. Morphological features unique to ground beetles and other members of Adephaga include several abdominal ventrites (hard plates that form the exoskeleton), defense glands on the terminal tergite, and liquid-feeding mouthparts in the larvae (Lawrence and Britton 1991).

Overall, ground beetles possess an easily recognizable, non-specialized body plan (Lövei and Sunderland 1996). Adults are well-proportioned with long slender legs, striate elytra, and pronounced mandibles (Riddick 2008). Despite this generalist body plan, the shapes of their bodies and legs are characteristically modified for various functions that include running, digging, burrowing, climbing, and swimming (Evans 1977, Riddick 2008). Other morphological characteristics that differentiate ground beetles include: mandibles specialized for hunting specific prey, eating seeds, or consuming an omnivorous diet; fully functional wings and elytra (hard, external wing-coverings) that

allow for flight or missing wings with elytra that are fused together (Lövei and Sunderland 1996). There exists flight dimorphic species in which some individuals possess wings while others of the same species do not (Lövei and Sunderland 1996).

Adult ground beetles range in size from 2 mm to 80 mm (Will 2003). Many species are dark black or brown while other species tend to be iridescent and brightly colored or patterned. Ground beetles typically have long legs (Lövei and Sunderland 1996) which allow them to move rapidly when capturing prey and avoiding predators.

### *Life Cycle*

Ground beetles, like ants, are holometabolous insects (Lövei and Sunderland 1996, Liebherr and McHugh 2003) experiencing a complete metamorphosis that includes four distinct stages of growth: egg, larva, pupa, and adult. Female ground beetles carefully choose the oviposition site, sometimes excavating a chamber in which to lay the eggs (Lövei and Sunderland 1996). The selection of the oviposition site is critical due to the relatively soft bodies and limited mobility of the larvae which are vulnerable to predators and starvation. Eggs are laid singly and some species may lay several hundred in a season (Ernsting and Isaaks 1997).

The larval stage typically consists of three instars (Crowson 1981, Lövei and Sunderland 1996, Liebherr and McHugh 2003) and is spent beneath the soil surface. Most larval ground beetles are carnivorous with a campodeiform body that is flattened, elongated, and contains well-developed legs and antennae (Lawrence and Britton 1991, Liebherr and McHugh 2003). After the larval stages are complete, pupation takes place underground in a specially constructed pupal chamber (Lövei and Sunderland 1996). The



whitish pupa lies on its back where it is supported by dorsal hairs (Lövei and Sunderland 1996). After eclosion, the adult begins to sclerotize; it usually takes weeks for the exoskeleton to fully harden and develop its color (Lövei and Sunderland 1996).

The process of development from egg to adult generally takes less than a year but may take up to four years for individuals lacking sufficient food resources or living in harsh environmental conditions (Lövei and Sunderland 1996). After reaching adulthood, ground beetles typically reproduce a single time before dying (Lövei and Sunderland 1996). The adult life spans tend to be longer with larger species and species that overwinter as larvae (autumn breeders) (Lövei and Sunderland 1996).

#### *Ecology and Ecosystem Services*

Ground beetles are considered to be mostly opportunistic feeders that consume a variety of foods including aphids, lepidopteron pests, slugs, the eggs and larvae of dipterans and coleopterans (Holland 2002), as well as carrion and plant materials (Lövei and Sunderland 1996). Although some food preferences exist, laboratory experiments have demonstrated that ground beetles will generally eat almost everything offered (Tooley and Brust 2002). The quality of these foods ranges from essential to purely supplementary (Toft and Bilde 2002). A few species are phytophagous (Thiele 1977); of particular interest are granivores which feed almost entirely on plant seeds (Toft and Bilde 2002). This “seed predation” may provide an ecological service to humans when it controls weeds within an agricultural system (Tooley and Brust 2002). With relatively few studies investigating phytophagous ground beetles, some scientists suggest that

ground beetle herbivory and granivory may be largely underestimated (Tooley and Brust 2002).

Although a few phytophagous species exist, the majority of species have been observed as primarily predatory (Toft and Bilde 2002). Some of these predatory ground beetles specialize on one food source, such as snails or slugs (Hengeveld 1980), but most are generalists with the potential to reduce a wide range of agricultural pest insects (Sunderland 2002). Because they are voracious feeders that daily consume close to their own mass (Kromp 1999), some have suggested ground beetles as biological controls. Although some field studies have demonstrated their potential (Clark et al. 1994), it is likely that ground beetles contribute the most to pest reduction when they are part of an assemblage of generalist predators (Sunderland 2002), thus making their individual role difficult to distinguish.

Ground beetles have been used as bioindicators due to their cost-effective collection methods, sensitivity to environmental factors, and wide range of habitat requirements (Rainio and Niemela 2003). The presence or lack of certain species, particularly specialists, may indicate the state of a particular habitat (Rainio and Niemela 2003). In a study comparing tallgrass prairie to several other habitats, Larsen et al. (2002) discovered that most specialist ground beetles were found in the prairie. This suggests that few of these specialists can survive in other habitats and highlights the importance of conservation and proper management of prairie fragments for insect biodiversity preservation (Larsen et al. 2002).

## THESIS OVERVIEW

Once a dominant landscape feature of North America, tallgrass prairie has been reduced to one of the most endangered ecosystems. That which remains is threatened by further habitat loss and the negative effects of fragmentation. Aside from the aesthetic value of preserving our natural heritage, conservation of the tallgrass prairie will preserve its ecosystem services such as soil formation, nutrient cycling, biodiversity production, and pest control. Large, contiguous preserves may be ideal for conservation, but relatively small, isolated fragments are the reality in the Southeast Prairies BUL. To make informed decisions about conserving this endangered resource, we need to better understand the effects of fragmentation and how to mitigate their negative impacts.

This study investigates how biological diversity and ecological functions of the tallgrass prairie are affected by broad-scale landscape characteristics, within-fragment habitat characteristics, and management actions. Biological diversity and ecosystem functioning are assessed using the key insect groups, ants and ground beetles. These insects play important functional roles in the tallgrass prairie and have been recognized as good potential bioindicators (Andersen et al. 2002, Larsen et al. 2002, Rainio and Niemela 2003), yet few studies have investigated them in Nebraska. Results of this study may be insightful for guiding conservation in the Southeast Prairies BUL as well as other fragmented tallgrass systems.

This thesis is presented in five chapters. In a detailed literature review, the first chapter introduces the tallgrass prairie, the importance of ants and ground beetles within it, and gives an overview of the study. The second and third chapters present analyses of ants in the Southeast Prairies BUL grouped by habitat preference and functional group

respectively. The fourth chapter reports the results of ground beetle analyses, and the fifth chapter presents a synthetic summary of the findings.

## LITERATURE CITED

- Andersen, A.N. 1995. A classification of Australian ant communities based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* **22**:15-29.
- Andersen, A.N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography* **24**:433-460.
- Andersen, A.N. 2000. Global ecology of rainforest ants: functional groups in relation to environmental stress and disturbance. Pages 25-34 *in* D. Agosti, J.D. Majer, L.E. Alonso, and T.R. Schultz, editors. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington and London.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355-365.
- Bolton, B., G. Alpert, P.S. Ward, and P. Naskrecki. 2006. Bolton's catalogue of ants of the world. Harvard University Press, Cambridge, MA. CD-ROM.
- Bourke, A.F.G. and N.R. Franks. 1995. *Social evolution in ants*. Princeton University Press, Princeton, New Jersey.
- Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management* **29**:19-24.
- Brian, M.V. 1977. *Ants*. William Collins Sons & Co Ltd, Glasgow.
- Briggs, J.M., A.K. Knapp, and B.L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *The American Midland Naturalist* **147**:287-294.

- Bruder, K.W. and A.P. Gupta. 1972. Biology of the pavement ant, *Tetramorium caespitum* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **65**:358-367.
- Clark, M.S., J.M. Luna, N.D. Stone and R.R. Youngman. 1994. Generalist predator consumption of armyworm (Lepidoptera: Noctuidae) and effect of predator removal on damage in no-till corn. *Environmental Entomology* **23**:617-622.
- Crowson RA. 1981. *The Biology of the Coleoptera*. Academic Press, London.
- Culver, D.C. and A.J. Beattie. 1978. Myrmecochory in viola: dynamics of seed-ant interactions in some West Virginia species. *Journal of Ecology* **66**:53-72.
- Dahbi, A., A. Hefetz, X. Cerdá, and A. Lenoir. 1999. Trophallaxis mediates uniformity of colony odor in *Cataglyphis iberica* ants (Hymenoptera, Formicidae). *Journal of Insect Behavior* **12**:559-567.
- Depickere S., D. Fresneau, and J. Deneubourg. 2004. The influence of red light on the aggregation of two castes of the ant, *Lasius niger*. *Journal of Insect Physiology* **50**:629-635.
- Ernsting, G. and J.A. Isaaks. 1997. Effects of temperature and season on egg size, hatchling size and adult size in *Notiophilus biguttatus*. *Ecological Entomology* **22**:32-40.
- Erwin, T.L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Pages 437-472 in G.E. Ball, editor. *Taxonomy, phylogeny and zoogeography of beetles and ants*. Junk Publishers, Dordrecht.

- Erwin, T.L. 1997. Biodiversity at its utmost: tropical forest beetles. Pages 27-40 *in* M.J. Reaka-Kudla, D.E. Wilson, and E.O. Wilson, editors. Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, D.C.
- Evans, M.E. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. *Journal of Zoology* **181**:189-226.
- Ewers, R.M., S. Thorpe, and R.K. Didham. 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* **88**:96-106.
- Folgarait, P.J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* **7**:1221-1244.
- Fraser, A.M., A.H. Axén, and N.E. Pierce. 2001. Assessing the quality of different ant species as partners of a myrmecophilous butterfly. *Oecologia* **129**:452-460.
- Greene, M.J. and D.M. Gordon. 2003. Cuticular hydrocarbons inform task decisions. *Nature* **423**:32.
- Hammond, P. 1992. Species inventory. Pages 17-39 *in* B. Groombridge, editor. Global biodiversity: status of the earth's living resources. Chapman and Hall, London.
- Hengeveld, R. 1980. Polyphagy, oligophagy, and food specialization in ground beetles (Coleoptera: Carabidae). *Netherland Journal of Zoology* **30**:564-584.
- Holland, J.M. 2002. Carabid beetles: ecology, survival and use. Pages 1-40 *in* J.M. Holland, editor. The agroecology of carabid beetles. Intercept Limited, Hampshire, UK.
- Hölldobler, B. and S.H. Bartz. 1985. Sociobiology of reproduction in ants. *Fortschritte der Zoologie* **31**:237-257.

- Hölldobler, B. and E.O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge, Massachusetts.
- Hölldobler, B. and E.O. Wilson. 1994. *Journey to the ants: a story of scientific exploration*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Kaspari, M. 2000. Primer on ant ecology. Pages 9-24 *in* D. Agosti, J.D. Majer, L.E. Alonso, and T.R. Schultz, editors. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington and London.
- Kleineidam, C.J., M. Obermayer, W. Halbach, and W. Rossler. 2005. A macroglomerulus in the antennal lobe of leaf-cutting ant workers and its possible functional significance. *Chemical Senses* **30**:383-392.
- Kremen, C., R.K. Colwell, T.S. Erwin, D.D. Murphy, R.F. Noss and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**:796-808.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment* **74**:187-228.
- Larsen, K.J., T.T. Work, and F.F. Purrington. 2002. Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia* **47**:288-299.
- Lawrence J.F. and E.B. Britton. 1991. Coleoptera. Pages 543-683 *in* *The insects of Australia: a textbook for students and research workers*, 2<sup>nd</sup> Edition. Cornell University Press, Ithaca, New York.
- Lawton, J. 1994. What do species do in ecosystems? *Oikos* **71**:364-374.



- Leach, M.K. and T.J. Givnish. 1996. Ecological determinants of species loss in prairie remnants. *Science* **273**:1555-1558.
- Liebherr, J.K. and J.V. McHugh. 2003. Coleoptera (beetles, weevils, fireflies). Pages 209-230 *in* V.H. Resh and R.T. Carde, editors. *Encyclopedia of insects*. Academic Press, San Diego, California.
- Lövei, L.G. and K.D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**:231-256.
- Oster, G.F. and E.O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton University Press, Princeton, New Jersey.
- Peeters, C. and M. Molet. 2010. Colonial reproduction and life histories. Pages 159-176 *in* L. Lach, C. L. Parr, and K.L. Abbott, editors. *Ant ecology*. Oxford University Press Inc., New York.
- Pfeiffer, M. and K.E. Linsenmair. 1998. Polydomy and the organization of foraging in a colony of the Malaysian giant ant *Camponotus gigas* (Hym./Form.). *Oecologia* **117**:579-590.
- Mazerolle, M.J., and M.A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience* **6**:117-124.
- McGarigal, K., and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12**:335-345.
- Prairie Nebraska. The Southeast Nebraska Flagship Initiative.  
<<http://prairienebraska.org/initiatives>>. Accessed 2012 January 27.

- Rainio, J. and J. Niemela. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* **12**:487-506.
- Rand, T.A. and S.M. Louda. 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conservation Biology* **20**:1720-1729.
- Ricketts, T.H., D.M. Olson, C.J. Loucks, W. Eichbaum, D. Della-Sala, K. Kavenagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abell, and S. Walters. 1999. *Terrestrial ecoregions of North America: a conservation assessment*. Island Press, Washington, D.C.
- Rico-Gray, V. and P.S. Oliveira. 2007. *The ecology and evolution of ant-plant interactions*. The University of Chicago Press, Chicago and London.
- Riddick, E.W. 2008. Ground beetle (Coleoptera: Carabidae). Pages 1742-1752 *in* J.L. Capinera, editor. *Encyclopedia of entomology*; Volume 2: D-K, 2<sup>nd</sup> Edition. Springer Science+Business Media, New York.
- Safriel, U. and Z. Adeel. 2005. Dryland systems. Pages 623-662 *in* R. Hassan, R. Scholes, and N. Ash, editors. *Ecosystems and human well-being: current state and trends*. The millennium ecosystem assessment, Vol. 1. Island Press, Washington, D.C.
- Samson, F.B., and F.L. Knopf. 1994. Prairie conservation in North America. *BioScience* **44**:418-421.
- Samson, F.B, and F.L. Knopf, editors. 1996. *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press. Washington, D.C.

- Samson, F.B., Knopf, F.L. and Ostlie, W.R. 1998. Grasslands. Pages 437-472 *in* M.J. Mac, P.A. Opler, C.E. Puckett Haecker, and P.D. Doran, editors. Status and trends of the nation's biological resources, Volume 2. United States Department of the Interior, United States Geological Survey, Reston, VA.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* **32**:6-15.
- Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18-32.
- Schneider, R., M. Humpert, K. Stoner, G. Steinauer. 2005. The Nebraska Natural Legacy Project. The Nebraska Game and Parks Commission, Lincoln, NE.
- Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist* **152**:738-750.
- Steiner, F.M., R.H. Crozier, and B.C. Schlick-Steiner. 2010. Colony structure. Pages 177-193 *in* L. Lach, C. L. Parr, and K.L. Abbott, editors. *Ant ecology*. Oxford University Press Inc., New York.
- Stoner, K.J.L. and A. Joern. 2004. Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecological Applications* **14**:1306-1320.
- Sunderland, K.D. 2002. Invertebrate pest control by carabids. Pages 1-40 *in* J.M. Holland, editor. *The agroecology of carabid beetles*. Intercept Limited, Hampshire, UK.

- Thiele, H.U. 1977. Carabid Beetles in their environments: a study on habitat selection by adaptations in physiology and behaviour. Springer-Verlag, New York.
- Toft, S. and T. Bilde. 2002. Carabid diets and food values. Pages 81-110 *in* J.M. Holland, editor. The agroecology of carabid beetles. Intercept Limited, Hampshire, UK.
- Tooley, J. and G. E. Brust. 2002. Weed seed predation by carabid beetles. Pages 215-230 *in* J.M. Holland, editor. The agroecology of carabid beetles. Intercept Limited, Hampshire, UK.
- Trager, J. C. 1998. An introduction to ants (Formicidae) of the tallgrass prairie. Missouri Prairie Journal **18**:4-8.
- Ward, P.S. 2010. Taxonomy, Phylogenetics, and Evolution. Pages 3-17 *in* L. Lach, C. L. Parr, and K.L. Abbott, editors. Ant ecology. Oxford University Press Inc., New York.
- Way, M.J., and K.C. Khoo. 1992. Role of ants in pest management. Annual Review of Entomology **37**:479-503.
- Wheeler, W.M. 1915. On the presence and absence of cocoons among ants, the nest-spinning habits of the larvie and the significance of the black cocoons among certain Australian species. Annals of the Ent. Society of America **8**:323-342.
- Whiles, M.R., and R.E. Charlton. 2006. The ecological significance of tallgrass prairie arthropods. Annual Review of Entomology **51**:387-412.
- Will, K.W. 2003. Review and cladistic analysis of the generic-level taxa of Morionini Brulle (Coleoptera: Carabidae). Pan-Pacific Entomologist **79**: 212-229.
- Wilson, E.O. 1987. Causes of ecological success: the case of the ants. Journal of Animal Ecology **56**:1-9.

**Chapter 2: DIVERSITY AND ABUNDANCE OF GRASSLAND, WOODLAND,  
AND HABITAT-GENERALIST ANTS (HYMENOPTERA:  
FORMICIDAE) IN REMNANT TALLGRASS PRAIRIE  
HAYMEADOWS**

*Abstract:*

Tallgrass prairie habitat continues to decline making its conservation increasingly important. In southeast Nebraska, most remaining tallgrass remnants exist as privately-owned haymeadows in a highly-fragmented landscape. To make informed decisions about conserving this endangered resource better understanding of the effects of fragmentation is needed. Although many conservation decisions are made with plants and vertebrates in mind, invertebrates are increasingly recognized as essential components of the ecosystem. One of the most functionally important groups of tallgrass prairie invertebrates is ants (Hymenoptera: Formicidae). I investigated how the abundance and diversity of grassland-obligate, woodland-obligate, and habitat-generalist ants respond to landscape, habitat, and management characteristics. In 2010 and 2011, ants were collected with pitfall traps in twenty-three haymeadows of the Southeast Prairies Biologically Unique Landscape. Twenty-eight species from eighteen genera were collected with the majority belonging to grassland-obligates, followed by habitat-generalists, with very few woodland-obligates. I tested multiple models consisting of relevant landscape, habitat, and management factors with data collected across the two years. I put these models at risk using multi-model inference to determine which were most plausible in predicting Shannon diversity, abundance, and species richness for each group. Models containing the average number of grass species per m<sup>2</sup> were the best

predictors of Shannon diversity and species richness of grassland-obligate ants; both Shannon diversity and species richness increased with increasing grass species. The model containing the proportion of haymeadow in the nearby landscape was the best predictor of grassland ant abundance; abundance increased as the proportion of haymeadow increased. This suggests that priority should be given to sites with more haymeadow in the landscape and with high grass species richness to maximize abundance and diversity of grassland ants. The abundance of habitat-generalist ants was negatively correlated with the proportion of haymeadow. The presence of woodland-obligate ant species at a site was predicted by low amounts of cattle-pasture in the nearby landscape. Results indicate that landscape, habitat, and management factors influence ants and all three should be incorporated into conservation decisions.

## INTRODUCTION

The reduction of tallgrass prairie since European settlement surpasses that of any other major North American ecosystem (Samson and Knopf 1994) making it a globally endangered resource (Ricketts et al. 1999). Remaining prairie exists as relatively small, isolated remnants scattered throughout its former geographic range. Habitat loss and fragmentation continue to threaten these remnants and their associated ecosystem services. Because they are source pools of biodiversity, some experts consider native grasslands a priority for urgent conservation action (Ricketts 1999).

The Nebraska Natural Legacy Project identifies the Southeast Prairies Biologically Unique Landscape (BUL) as an area for priority conservation in Nebraska. The landscape of the Southeast Prairies BUL, once contiguous tallgrass prairie, is now a fragmented mosaic of haymeadows, crops, trees, roads, and cattle pastures. The majority of the remaining historic biodiversity is contained within those remnants serving as haymeadows. Understanding what landscape, habitat, and management factors affect the ecology of these fragments is critical for developing conservation practices for the tallgrass prairie. One method for accomplishing this goal is adaptive management.

Adaptive management involves using management practices to probe the functioning of an ecosystem. By monitoring the results and learning from the outcomes of management actions one can assess their effectiveness. Practices can then be altered to more effectively meet goals and the process is repeated with the new management techniques. In the case of the Southeast Prairies BUL, the goal is conservation of historic tallgrass prairie communities. Although most of the tallgrass prairie in the region is privately owned and managed, the effects of current management can be assessed as the

first step in the adaptive management process. Based on this assessment, educated recommendations can be given to landowners for the benefit of both conservation and agriculture, and future research can continue the process by studying the effects of new practices.

The impacts of fragmentation are inherently complex and act at multiple scales (McGarigal and Cushman 2002). How fragmentation's effects manifest depends on how a particular organism interacts with its environment. Arthropods have important functions in grassland communities and contribute significantly to their biodiversity (Arenz and Joern 1996, Panzer and Schwartz 1998). Their extraordinary diversity, abundance, rapid growth rates, functional roles, and wide range of body sizes make them useful in ecosystem monitoring and have led some experts to suggest including arthropods with plants and vertebrates as an essential component when making conservation decisions (Kremen et al. 1993, Oliver and Beattie 1993).

This study uses ants (Hymenoptera: Formicidae) to investigate biological diversity of the tallgrass prairie. Ants perform key ecological functions in the prairie and have been recognized as potential bioindicators (Andersen et al. 2002), yet few studies have investigated them in Nebraska. Results may be insightful for guiding conservation both in the Southeast Prairies BUL as well as other fragmented tallgrass systems.

## **METHODS AND MATERIALS**

### **STUDY SITES**

This study was conducted in the Southeast Prairies BUL which consists of Pawnee County as well as portions of Richardson, Johnson, and Gage Counties in



southeast Nebraska (Fig. 1). The dominant landscape feature is cattle pasture, but the area contains considerable amounts of cropland, trees, and other types of grasslands. The specific study sites were 23 privately-owned haymeadows scattered throughout the BUL (Fig. 2). All of these sites are cut annually for hay. As a consequence, none of these sites have ever been plowed and remain as tallgrass prairie habitat. Although some cattle pastures in the region have never been plowed and could arguably also be considered tallgrass prairie, many have been overgrazed or sprayed with selective herbicides to remove forb species. Consequently, the majority of the historic biodiversity of the region is retained only in these remnant tallgrass haymeadows.

Management is fairly consistent across all sites with a couple important differences: first, some are hayed significantly earlier in the summer (mid-July) and some are hayed later (late September); second, some appear to have been over-seeded with non-native species such as smooth brome (*Bromus inermis*) and red clover (*Trifolium pratense*). These differences have likely altered the plant community and habitat structure over time.

Study sites were identified during a 2009 pilot study by searching the BUL for grassland fragments that had never been farmed (i.e., lacked terraces), that possessed key tallgrass species easily identifiable from the road (e.g., compass plant (*Silphium aconitum*) and wild alfalfa (*Psoralea tenuiflora*)), and had high, apparent plant diversity. Ownership was discerned through plat maps of the area and permission was obtained for use of the land. The edges of the fragments were closely correlated with the edges of annual mowing, typically running up against treelines, roads, crops, or cattle pastures and

often divided from these by barbed-wire fencing. Sites varied in size from approximately 1.75 to 26.9 ha and in shape from highly-irregular to near-perfect squares.

## STUDY DESIGN

### *Pitfall Trap Sampling*

Pitfall traps were determined to be the best collection method for sampling ants in this study. Although some have noted biases with the use of pitfall traps (Thomas and Sleeper 1977, Topping and Sunderland 1992), they remain the most common, inexpensive, and convenient way to sample for ground-dwelling invertebrates. Pitfall traps sample 24 hours a day, collecting both diurnal and nocturnal species, and do not select for rare or against common species (Esau and Peters 1975). Most studies place pitfall traps along transect lines or grids with even intervals between the traps (New 1998). Although 10 meter intervals appear to be common for studies of ants (Esau and Peters 1975, Andersen et al. 2002), Digweed et al. (1995) found that spacing of 25 meters or greater captured more rare insect species than 10 meter spacing.

With relatively large sites, the pitfall traps in this study were able to be spaced 25 meters apart in a 3 x 3 grid, a total of nine traps per site (Fig. 3). The center of the grid was haphazardly selected near the center of each fragment; the remaining traps in the grid were arranged to coincide with the cardinal directions based on the selected center point. As the Southeast Prairies BUL is rather hilly, grid-placement was kept primarily to upland areas at all sites, avoiding lower, often wetter areas where the vegetation changes dramatically.

The pitfalls consisted of test tubes in conduit pipe sleeves as described by New (1998). Holes were dug in the soil with a 1" diameter soil corer and 6" long,  $\frac{3}{4}$ " diameter PVC pipes were placed in the hole. These pipe sleeves remained in the ground throughout the duration of each summer, and were corked to prevent debris or insects from falling in. Corks were spray-painted with bright orange to assist in locating them, and each trap's location was recorded with GPS and marked with flagging tape on nearby vegetation. Keeping pipe sleeves in the ground allowed for repeated sampling at the exact same location. PVC sleeves were inserted at least a week before sampling, allowing time for the disturbed soil around the trap to recover (New 1998).

Sampling was conducted by removing the corks and placing test tubes in the PVC pipe sleeves. The test tubes contained propylene glycol (antifreeze) to serve as the killing agent; propylene glycol was chosen over ethylene glycol because it captures as efficiently but is less toxic to non-target wildlife (Weeks and McIntyre 1996). Tubes were filled halfway to give leeway in the event of precipitation and displacement of the liquid by insects. Traps were placed in the ground at all sites on the same day to minimize differences in collection due to changes in weather rather than site characteristics. Traps were left in the ground for 72 hours, a time observed in the pilot study to collect insects without getting so many that some traps fill entirely. Sampling occurred in early June and early July of both 2010 and 2011.

### *Sample Processing*

Following collection, samples were poured through a fine mesh strainer to filter them from the propylene glycol and dirt particles. They were then rinsed with 70% ethyl

alcohol to remove all remaining propylene glycol. Ants were separated from leaves, twigs, and other arthropods and placed in a vial of 70% ethyl alcohol labeled with the collection date, site, and sample number. Ants were initially counted for preliminary abundance numbers and later identified to species using *The Ants of Ohio* (Covert 2005) and other keys (Fisher and Cover, 2007, Trager et al. 2007).

### *Habitat Characteristics*

Compared to other types of habitat in the Southeast Prairies BUL, the haymeadows in this study are strikingly similar to one another in terms of structure and composition. However, their habitat characteristics vary widely between sites. The floral composition, vegetation structure, depth of lying litter, and type of soil are all factors that may directly or indirectly influence the species composition and abundance of ants for each site.

Data on floral composition was gathered at 50 sampling locations along transects arranged to cover the breadth of each site. At each location, all plant species were identified within a square meter quadrat. By averaging the 50 samples together, mean estimates of plant species richness per m<sup>2</sup> were obtained. Floral composition data collection began in 2009 and was completed in 2010. Data on four sites were collected for both years to confirm that plant composition remained consistent from year to year (see Appendix A: Fig. 1).

The structure of vegetation includes the above-ground biomass, the vertical structure/canopy cover, and the amount of litter. These factors are important to ants in that they may change shade and moisture levels at the ground's surface. Thus habitat

structural data was gathered using a Robel pole (Robel et al. 1970) at twelve locations in each site. The locations were kept local to the pitfall trap sampling area by spacing them halfway between the traps, and 12.5 meters to the east and west of the outer traps (Fig. 3). Vegetation sampling was conducted following each pitfall collection round and completed for all sites within a week to minimize temporal changes in vegetation.

The Robel pole was read from each of the cardinal directions and averaged together for a relative estimate of vegetation density at each location. Litter depth to the nearest 0.5 cm was also measured at each point the Robel pole was read. To estimate vertical structure, the height of every plant touching the Robel pole was recorded. This data was analyzed using a Shannon diversity index for an estimate of vertical heterogeneity, and a simple sum of the number of touches for an estimate of canopy cover. Both of these estimates were rather highly correlated ( $r^2 > 0.5$ ) with the vegetation density, however, and consequently eliminated from the analysis.

Ants, which often nest in the soil, can be influenced by soil texture (Bestelmeyer and Wiens 2001, Boulton et al. 2005). The Web Soil Survey (2012) was used to determine the percentage of each site covered by loam, clay loam, silty loam, and silty clay loam. Because these soil classes are similar and in some cases highly correlated, clay loam was the only soil class used for the analysis. Whereas other soil types were often lacking, clay loam was present in almost every site to varying degrees. Additionally, prior studies have shown clay content to alter abundance, species richness, and community composition of ants (Bestelmeyer and Wiens 2001, Boulton et al. 2005). The term loam refers to soil composed of relatively equal parts clay (small particles), silt (medium particles) and sand (large particles). Clay loam consists of all three particle types but has

a greater proportion of clay than the other two. (See the tables in Appendix A for more data concerning habitat factors.)

### *Landscape Characteristics*

The historical landscape of the prairie was relatively homogenous, with gradual transitions to other habitats. Fragmentation has resulted in very abrupt changes to dramatically different kinds of habitat. The type, amount, and distance to these other habitats can influence ant composition by isolating the fragments, by subsidizing ants with additional resources, or by harming ants with additional predators.

Two different methods of determining isolation in fragmentation studies are the buffer index and the connectivity index (Öckinger 2012). The buffer index determines the proportion of habitat within a certain radius; the connectivity index weights the areas of surrounding patches based on their distance to the fragment of interest. The buffer index approach of analyzing landscape composition was used in this study. Use of this approach eliminated issues such as determining fragment edges. For instance, in some areas tallgrass haymeadow habitat was divided by a treeline or road. It is difficult to determine if the treeline or road would be enough of an ant barrier to warrant classification as two separate haymeadows. The buffer index eliminates this decision and yet often remains highly-correlated with the connectivity index approach (Moilanen and Nieminen 2002).

Landscape composition around fragments was determined by digitizing the surrounding landscape in a Geographic Information System (GIS). Each polygon of the digitized landscape was classified as: cattle pasture, haymeadow, trees, cropland, and

Conservation Reserve Program (CRP) grass. An “other” classification was used for areas that did not fit these major categories. Roads may potentially serve as fragmenting agents to insects, but due to their high variability (e.g. grassy field paths, gravel roads, or paved streets) they were included in the “other” category. This category was not analyzed directly in the analyses, but was included implicitly via its proportionate contribution to the total area. Based on the foraging ability of some ant species (Brian 1955), a 250 meter radius buffer was created in GIS around the center pitfall trap for each site and the percentage of each landscape type was determined within each buffer (Dauber et al 2003). The proportion of different land-use types ranged from 0 to 64% for cattle pasture, 14 to 82% for grassland, 1 to 75% for trees, 0 to 63% for cropland, and 0 to 58% for CRP or other low diversity grassland (Appendix A: Table 1).

The size and shape of sites can influence ant composition by varying the edge to interior ratio and associated edge effects. In this study, however, both size and perimeter to interior ratio were highly correlated with the percentage of haymeadow within a 250 meter buffer and therefore eliminated as factors. (See the tables in Appendix A for more data concerning landscape factors.)

### *Management*

Although over-seeding with new species and planting of treeline edges are management actions affecting these sites, they occur infrequently and are likely reflected in the habitat and landscape factors. When unsatisfied with hay production, owners or managers of sites may on occasion experiment with techniques such as fertilizer

application or burning, but this is uncommon (site CA was sprayed with fertilizer in early spring, 2010; site HO was unintentionally burned in early spring, 2011.)

The predominant management tool is haying. Most haymeadows in this region, including all of the study sites, are cut for hay once a year. The time of haying, which ranges from mid-July to late September, can affect vegetation composition and structure. Haying before plants are able to produce viable seed limits their reproduction, potentially eliminating populations from sites that are hayed early; this may particularly affect annuals or short-lived perennials whose populations depend on frequent reproduction. Vegetation structure is altered when, in some sites, perennials have been mowed annually at the peak of their aboveground production, weakening them over time and decreasing height and biomass. The amount of litter is also affected by the time of haying. Although vegetation density, litter, and plant species richness are undoubtedly influenced to some degree by haying time, because their correlation with haying time was relatively low ( $r^2 < 0.17$ ), this warrants their consideration as separate factors.

The time each site is hayed varies year to year based on factors such as weather, but remains fairly consistent (i.e., within two to three weeks). Generally, owners who want to maximize the quality of the hay cut early while owners who want to maximize production cut late (Pfeiffer, personal communication). Sites were monitored every two to three days starting in mid-July and the date of haying events was recorded. To quantify haying time, a value was assigned to each day (i.e., July 15=1, July 16=2, etc.) and the average was taken between 2010 and 2011 for each site (Appendix A: Table 5). Thus larger values correspond with later average haying time.



## STATISTICAL ANALYSIS

### *Habitat Preference*

The individual species that comprise the ant community in a given tallgrass prairie ecosystem have a wide range of functions and requirements. Thus it is often useful to categorize ants into relevant groups; this allows for predictability of the member species' reaction to and effect on various environmental factors. For this study, ants were categorized as grassland-obligates, habitat-generalists, or woodland-obligate species by interpreting descriptions of their habitat from *The Ants of Ohio* (Coover 2005).

Grassland-obligate species are those found almost exclusively in open fields or grasslands; habitat-generalists are species that commonly inhabit woodlands and grasslands, as well as other habitats; woodland species are found almost exclusively in or near woody areas, sometimes spilling over into the edges of grasslands.

### *Diversity, Abundance, and Species Richness*

For the analyses of grassland-obligate and habitat-generalist ants, a value for Shannon diversity, abundance, and species richness was calculated for each sampling event. The Shannon diversity index (diversity) is a commonly used method to characterize species diversity in a community. It accounts for both abundance and number of species. It will have a higher value when many species contain similar numbers of individuals. Although diversity is useful in that it accounts for evenness, some ecosystems may contain certain species that naturally have low or high populations. In that case, lower diversity may not necessarily indicate a less natural state for that community. Thus, to obtain the most complete picture, it is important to look at

abundance and species richness in addition to diversity. In this study, abundance is the sum of the total number of ants collected in all nine pitfall traps at each site. It is intended to be a relative measure between sites and not an absolute estimate of all ants at a site. Species richness (richness) is the total number of species collected at a site. Because there were few woodland-obligate ant species collected, presence/absence at a site was used in place of diversity, abundance, or richness.

### *Multi-model Inference*

In ecological studies that contain several likely predictors with multiple expected combinations it is useful to employ information-theoretical model selection. This approach weighs evidence among multiple competing hypotheses predicting ant diversity, abundance, richness, or in the case of woodland-obligate ants, presence/absence. If at least one woodland species was collected at a site during a given sampling event they were considered present; if no woodland species were collected they were considered absent.

This study was limited to a suite of 16 *a priori* models with individual variables corresponding to the landscape, habitat, and management data collected for each fragment (Table 1). The candidate models include a landscape model, a plant composition model, a habitat structure model, a soil model, and a management model. Additionally, a null model (no effects) and a global model (all variables) were included along with models that test each explanatory variable independently. Using Program R (R Development Core Team 2012), Akaike's Information Criterion adjusted for small sample size (AICc) was calculated to rank the candidate models. From the AICc values,

Akaike weights ( $w_i$ ) were calculated to determine the most parsimonious models (i.e., the best fits for the empirical data) (Anderson et al. 2000). The confidence set includes any model with an Akaike weight within 10% of the highest ranked model; this is comparable to the minimum cutoff point suggested by Royall (1997).

For normalization, the abundance data was log-transformed for use as the response variable. For abundance and diversity, the models were analyzed as linear mixed models; for species richness, the models were analyzed as generalized linear mixed models with a Poisson distribution. Logistic regression was used for presence/absence data (i.e., generalized linear mixed model with a binomial response distribution). Site and year sampled were combined into a single “site-year” variable and included as a random factor in all models; all other variables were fixed. Because the month sampled had a large impact on the response variables, it was included in every model to allow the environmental and management factors to drive the model selection.

## RESULTS

A total of 9,171 ants were collected in 2010 and 2011 representing 28 species from 18 genera. This included 3,840 individuals and 28 species in 2010 and 5,331 individuals and 24 species in 2011 (Table 2). Consisting of 69.4% of the collection, the three most abundant species captured were *Myrmica americana*, *Lasisus neoniger*, and *Tapinoma sessile*. The total number of ants collected at a single site ranged from 109 (CC) to 1,188 (G) (Fig. 4). The fewest species collected at a site for given sampling event was 3 (EN, July 2010 and WA, June 2010) and the most was 12 (ES, July 2011 and KS,

July 2011); the Shannon diversity at sites ranged from 0.402 (CB, June 2010) to 2.161 (M, June 2011) (Table 3).

Species were assigned to one of the three habitat groups (Table 4). Nine species comprising 61.7% of the total collection were categorized as grassland-obligates; 12 species comprising 36.8% were habitat-generalists; and 7 species comprising 1.6% were woodland-obligates (Fig. 5).

#### *Grassland-Obligate Ants*

The model containing the average number of grass species per m<sup>2</sup> has a positive association with the Shannon diversity of grassland-obligate ants and a weight of 67%, (Tables 5). With 23% of the weight, the second model, which includes the average number of forb and grass species at a site, has the first model nested within it. Thus the grass variable may be driving selection of the second model as well as the top model. Because additional parameters in models are heavily penalized, however, this is unclear.

The model selection results are very clear for the abundance of grassland-obligate ants. The percentage of haymeadow within a 250 m radius from the center trap appears to positively influence the abundance of ants. This is the only model in the confidence set and it comprises 92% of the weight (Table 5). In contrast, the species richness of grassland-obligate ants has several models in the confidence set (Table 5). As with diversity, the top model indicates a positive relationship with mean grass species richness, and has a weight of 32%. The second model follows closely with a weight of 25% and indicates a negative relationship with annual haying time. In other words, the later in the year sites are hayed the fewer grassland ant species they are likely to contain.

The third model is the floral composition model, which has the top model nested within it, and possesses a weight of 14%. The percentage of cattle pasture and trees within 250 m both have negative associations with grassland ant species richness; their model weights are 9% and 4% respectively. The model involving the depth of lying litter has a positive effect with 6% of the weight. Model-averaged parameters estimates indicate that at the 95% confidence interval grasses, pasture, and litter all have a positive effect on species richness (Table 6).

#### *Habitat-generalist Ants*

Only weak inference was possible for modeling the diversity of habitat generalist ants, and 13 models were in the confidence set (Table 7). With a weight of 21%, the highest model indicates the percentage of a site composed of clay loam has a negative association with Shannon diversity. The second model, with 14% of the weight, shows a positive correlation with annual haying date; sites hayed later had higher diversity. The third model selected was the global model indicating that many of the factors considered have a comparable influence on the diversity of ants. It is therefore not surprising that the confidence set contains an additional 10 models with similar weights (3%-9%). Model-averaged parameter estimates do not indicate any of the parameters to have a positive or negative effect at the 95% confidence level (Table 8).

Concerning abundance of habitat-generalist ant species, the inference is much stronger. As with grassland-obligate ant abundance, there is only one top model: the percentage of haymeadow within a 250 m radius (Table 7). Unlike grassland ants, however, habitat-generalist abundance was negatively correlated with haymeadow. Thus

with more haymeadow in the near vicinity, the fewer habitat-generalist ants are present. For species richness of habitat-generalist ants, the top model was the null model, with a weight of 28% (Table 7). This indicates that none of the models were very good predictors of species richness for this group.

### *Woodland-obligate Ants*

The results have relatively strong inference with a single top model that garnered 85% of the weight (Table 9). This model involves a negative association with the percentage of cattle pasture within a 250 m radius (Table 10). In other words, the more cattle pasture in the nearby landscape, the less likely a woodland species was to be present at a site.

## **DISCUSSION**

The wide range of abundances (109 to 1,188) and number of species (5 to 15) clearly demonstrates there are differences between these sites in the factors that affect ant communities. With the notable exception of site BE, and to a lesser extent sites HBE and WA, most sites remained relatively consistent in the number of ants collected each year (Fig. 4). Anecdotal observations of these sites did not reveal any major changes in habitat between the years that would explain the difference. A potential bias of pitfalls may occur because of the social nature of ants: ants may create pheromone trails that can potentially lead vast numbers of individuals directly to a trap, particularly if the trap is placed close to a nest. In site BE, the majority of ants in 2011 were *Lasius neoniger* collected from two traps in July; these traps were 50 meters apart. It is possible the count

was misleadingly high because the traps were placed near pheromone trails. However, it is logical that with a greater abundance of ants there is a greater chance a pheromone trail would be created near a trap. This makes it unclear if the increase at BE in 2011 was due to a greater abundance of ants, pheromone trails, or close proximity to ant nests.

An alternative measurement to abundance is collection frequency. By dividing the number of traps with a particular species by the total number of traps at the site (9), one can obtain a frequency value of 0 to 1. Because species with more individuals at a site are expected to fall into more pitfall traps, the frequency value reflects how common a species is but remains independent of how many individuals are in a given trap, eliminating the aggregation bias. Comparing frequency values to the log of the abundance values of the two most abundant species, *Lasisus neoniger* and *Myrmica americana*, we find the two variables to be very highly correlated (Fig. 6). This indicates that the abundance is not driven by captures of great numbers of individuals due to their social tendencies.

Concerning habitat preference, the vast majority of ants collected (61.7%) were grassland-obligates while very few were woodland-obligates (1.6%). This is not surprising considering these sites are grassland habitats. The abundance of habitat-generalists is harder to predict because they can utilize both grassland and woodland habitat. Of collected ants, 36.8% were habitat-generalists indicating that, although they can use haymeadow habitat, their presence within it is much smaller than grassland-obligate species. The results of the model selection give some insight into what might be causing these differences.

*Grassland-obligate Ants*

Unlike the woodland or habitat-generalist groups, grassland-obligate ants are dependent specifically on grasslands for survival. The factors that affect grassland ants should therefore receive more consideration in terms of conserving tallgrass prairie biodiversity. Both the Shannon diversity and species richness of grassland-obligate ants appear to be positively influenced by the mean number of grass species at a site (Fig. 7). Mutualism has been observed between certain species of prairie grasses and ants, although the mechanisms for promoting these associations remain unclear (Petersen 2002). Grasses provide food in the form of tissues and honey-dew produced by aphids; it is possible that more species of grasses, with their varying above and below ground structures, may provide more niches for more species of ants.

The later sites are hayed appears to have a negative effect on grassland-obligate ant richness (Fig. 7). Whereas sites hayed early have time for plant regrowth, sites hayed toward the end of the growing season remain cut, virtually to the ground, until the start of the next growing season. Some species may require the extra cover or resources provided by the standing litter through the fall and winter and therefore may not be present in sites that are hayed late.

Other factors negatively affecting species richness, albeit to a smaller degree, include the percentage of the landscape covered by cattle pasture or trees. Because these are grassland-obligate species, it is not surprising that more trees would have a negative impact. However, it is interesting that cattle pasture is negatively correlated with grassland ants because it is a type of grassland habitat. It may be that because the structure and composition of pastures is less diverse it provides fewer niches for fewer



grassland ant species. It is also possible that the trampling by cattle may compact the soil thereby decreasing the ability of ants to nest there. Or perhaps cattle pastures are inhabited by a different community of grassland-obligate ants than the haymeadows.

The most important factor affecting the abundance of grassland-obligate ants is the percentage of haymeadow in the nearby landscape, a value that includes the fragment itself. The high diversity habitat of haymeadows may provide more resources for greater numbers of ants. Lower diversity grasslands, such as pastures or CRP, do not appear to have the same effect. Larger sites, or divided sites that are near to one another, may be the best option when seeking to benefit the abundance of grassland ants.

#### *Habitat-generalist Ants*

The Shannon diversity results for habitat-generalist ants show a great deal of uncertainty. There are 13 parsimonious models, with the third highest being the global model. This may indicate that many of the factors are having a small impact on predicting diversity rather than a few having a large impact. A different set of predictor variables may be better suited for modeling habitat-generalist Shannon diversity.

The abundance of habitat-generalist ants is strongly affected by one factor: the amount of haymeadow in the nearby landscape. Unlike grassland ants, the relationship with haymeadow is negative. The grassland-obligate ants that dominate haymeadows may compete with habitat-generalist ants for nesting space or food resources; this may decrease their abundance at these sites.

### *Woodland-obligate Ants*

Increasing cattle pasture decreases the likelihood of finding woodland species at a site. It is logical that with more grassy areas fewer woodland species would be in the vicinity, but why the response only to pasture and not haymeadows or other grassland types? Although this study only investigates the landscape within a 250 m radius, cattle pastures tend to be very large, extending far beyond this area. It is possible that when the landscape within the 250m radius is dominated by other grassland types, these grassland fragments may end not far beyond the edge of the analysis, potentially leaving more areas of trees nearby. In contrast, large pastures may extend far beyond the 250m area, leaving fewer areas in the vicinity of the site for trees that may support woodland ant species.

It is also possible that habitat-generalist ants, which can use both woodland and grassland habitat, may have the advantage of being supplemented by the resources of the cattle pasture and are therefore outcompeting woodland ants in areas of trees. Consequently, even as areas of trees increase, if they are being dominated by habitat-generalist species the number of woodland species may remain low and therefore would be less likely to be present in the nearby haymeadows.

### *Conclusion*

Ants have many important functional roles in the tallgrass prairie and should be considered when making conservation decisions. As shown in this study, landscape, habitat, and management factors all influence the composition of ant communities in tallgrass prairie fragments. By analyzing ants according to habitat preferences, more meaningful assumptions can be derived from the results. Because of their reliance

specifically on grasslands, grassland-obligate ants are the most important group in terms of tallgrass prairie conservation. Their abundance is positively associated with the amount of haymeadow in the nearby landscape. Conservation with these species in mind should therefore focus on individual large sites or smaller sites that are near to one another. To maximize species diversity of grassland-obligate ants, sites with high overall grass species richness should be the priority. Tallgrass prairie restorations should place more emphasis on high numbers of grass species to benefit grassland ant diversity. Managing sites by haying earlier, such as in July or August, may also serve to increase grassland ant species richness.

Further research should investigate the landscape matrix between these sites. Trees, cropland, and particularly the cattle pastures that comprise the majority of the landscape of the Southeast Prairies BUL. Investigating the community composition of ants in pastures may reveal whether or not grassland-obligate species are primarily dependent on the haymeadows, as this study suggests, or if they thrive in other types of grassland as well. Such studies may discover if other grassland species benefit from cattle pasture and whether habitat-generalists or grassland-obligate species dominate these pastures. Additional investigations may also help determine what characteristics of a habitat allow woodland-obligate or habitat-generalist species to become dominant.

## LITERATURE CITED

- Andersen, A.N., B.D. Hoffmann, W.J. Muller and A.D. Griffiths. 2002. Using ants as bioindicators in inland management: simplifying assessment of ant community responses. *Journal of Applied Ecology* **39**:8-17.
- Anderson, D.R., K.P. Burnham and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence and an alternative. *The Journal of Wildlife Management* **64**:912-913.
- Arenz, C.L. and A. Joern. 1996. Prairie legacies-invertebrates. Pages 91-110 *in* F.B. Samson and F.L. Knopf, editors. *Prairie conservation: Preserving North America's most endangered ecosystem*. Island Press, Covello.
- Bestelmeyer, B.T. and J.A. Wiens. 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. *Ecological Applications* **11**:1123-1140.
- Boulton, A.M., K.F. Davies, and P.S. Ward. 2005. Species richness, abundance, and composition of ground-dwelling ants in Northern California grasslands: role of plants, soil, and grazing. *Environmental Entomology* **34**:96-104.
- Brennan, L.A. and W.P. Kuvlesky Jr. 2005. Invited paper: North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* **69**:1-13.
- Brian, M.V. 1955. Food collection by a Scottish ant community. *Journal of Animal Ecology* **24**:336-351.
- Coover, G.A. 2005. *The ants of Ohio (Hymenoptera: Formicidae)*. Ohio Biological Survey, Inc., Columbus, Ohio.

- Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment* **98**:321-329.
- Digweed, S.C., C.R. Currie, H.A. C'arcamo, and J.R. Spence. 1995. Digging out the 'digging-in effect' of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* **39**:561-76.
- Esau, K.S. and D.C. Peters. 1975. Carabidae collected in pitfall traps in Iowa cornfields, fencerow, and prairies. *Environmental Entomology* **4**:509-513.
- Fisher, B.L. and S.P. Cover. 2007. *Ants of North America: a guide to the genera*. University of California Press, Berkeley and Los Angeles, California.
- Kremen, C., R.K. Colwell, T.S. Erwin, D.D. Murphy, R.F. Noss and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**:796-808.
- McGarigal, K., and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12**:335-345.
- Moilanen, A and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* **83**:1131-1145.
- New, T.R. 1998. *Invertebrate surveys for conservation*. Oxford University Press, Oxford.
- Öckinger, E., K.-O. Bergman, M. Franzen, T. Kadlec, J. Krauss, M. Kuussaari, J. Poyry, H.G. Smith, I. Steffan-Dewenter, and R. Bommarco. 2012. The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology* **27**:121-131.

- Oliver, I. and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* **7**:562-568.
- Panzer, R. and M.W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. *Conservation Biology* **12**:693-702.
- Petersen, C.E., D.G. Dave, C.L. Parker, and R.E. Petersen. 2002. Ant-plant relationships in a re-created tallgrass prairie. *The Great Lakes Entomologist* **35**:27-32.
- Pfeiffer, Kent. 2012. Personal communication. January 27, 2012.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.  
<<http://www.R-project.org>>. Accessed 2012 February.
- Ricketts, T.H., E. Dinerstein, D.M. Olson, C.J. Loucks, W. Eichbaum, D. Della-Sala, K. Kavenagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abell, and S. Walters. 1999. Terrestrial ecoregions of North America: A conservation assessment. Island Press, Washington, D.C.
- Robel, R.J., J.N. Briggs, A.D. Dayton and L.C. Hulbert. 1970. Relationship between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* **23**:295-298.
- Royall, R.M. 1997. Statistical evidence: a likelihood paradigm. Chapman and Hall, New York.
- Samson, F.B. and F.L. Knopf. 1994. Prairie conservation in North America. *BioScience* **44**:418-421.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* **32**:6-15.

- The Nature Conservancy. <<http://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/nebraska/howwework/senebmap.pdf>> Accessed 2012 March.
- Thomas, D.B., Jr. and E.L. Sleeper. 1977 The use of pit-fall traps for estimating the abundance of arthropods, with special reference to the Tenebrionidae (Coleoptera). *Annals of the Entomological Society of America* **70**:242-248.
- Topping, C.J. and K. D. Sunderland. 1992. Limitations to the Use of Pitfall Traps in Ecological Studies Exemplified by a Study of Spiders in a Field of Winter Wheat. *Journal of Applied Ecology* **29**: 485-491.
- Trager, J. C., MacGown, J. A., Trager, M. D. 2007. Revision of the Nearctic endemic *Formica pallidefulva* group. Pages 610-636 in Snelling, R.R., B.L. Fisher, and P.S. Ward, editors. *Advances in ant systematics (Hymenoptera: Formicidae): homage to E.O. Wilson - 50 years of contributions*. *Memoirs of the American Entomological Institute*, 80.
- Web Soil Survey. United States Department of Agriculture: Natural Resource Conservation Service. <<http://websoilsurvey.nrcs.usda.gov>>. Accessed 2012 February.

## TABLES AND FIGURES



Figure 1. Map showing the Biologically Unique Landscapes of southeast Nebraska (The Nature Conservancy 2012), including the Southeast Prairies BUL which includes most of Pawnee as well as portions of Johnson, Richardson, and Gage counties.



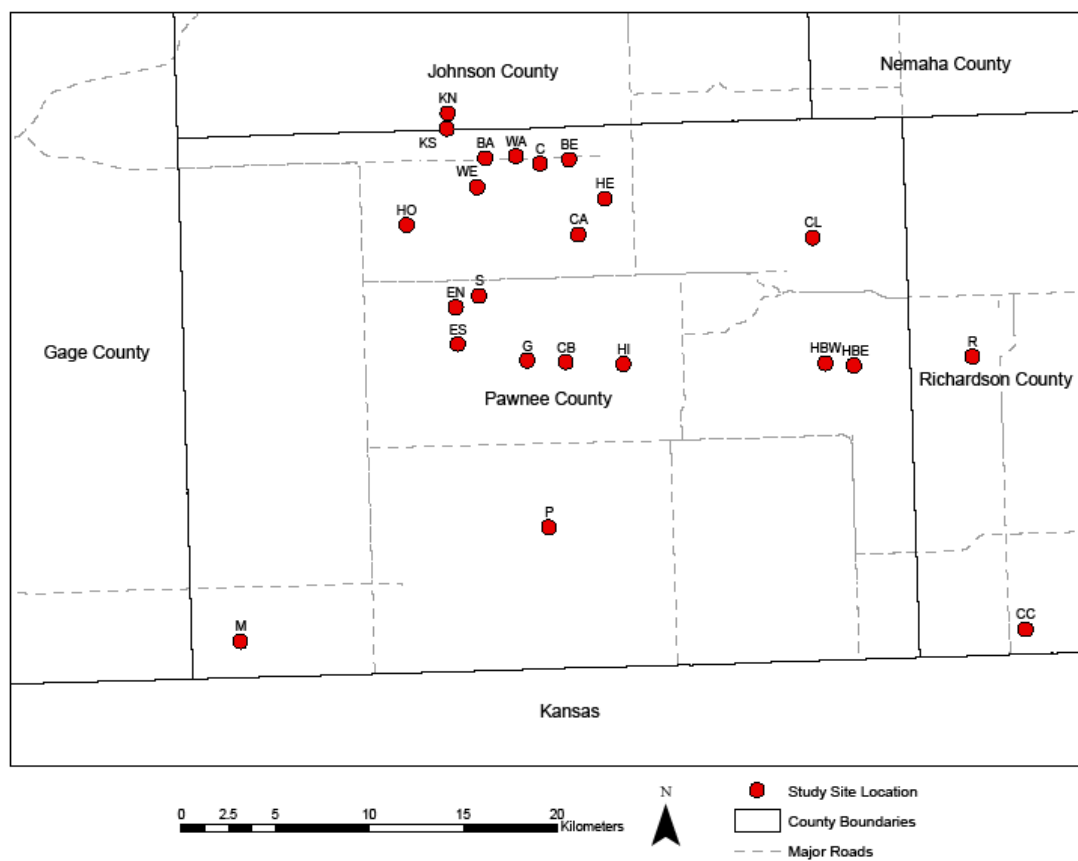


Figure 2. Location of the 23 study sites within the counties of the Southeast Prairies Biologically Unique Landscape.

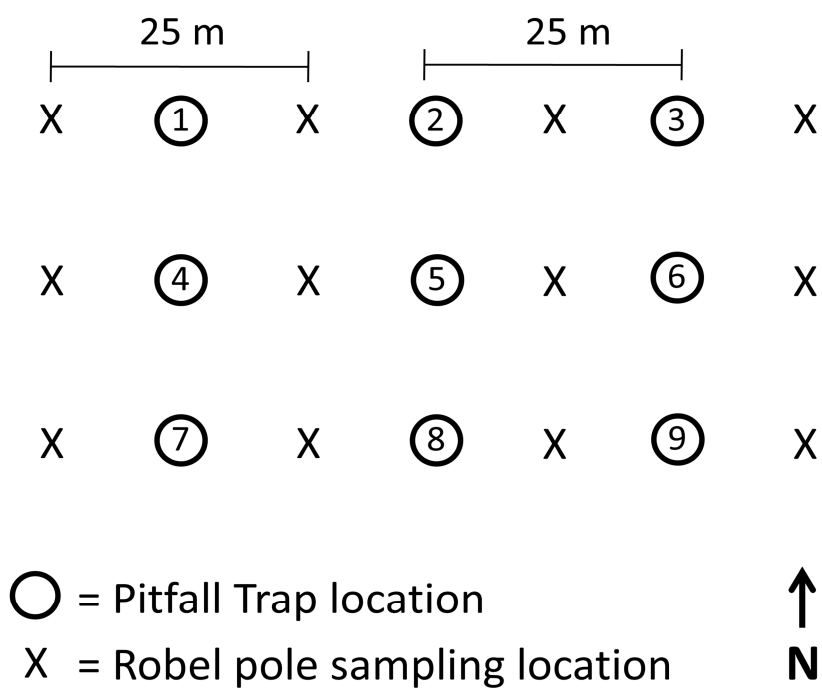


Figure 3. Sampling design used in study sites. Nine pitfall traps were arranged in a 3 x 3 grid space 25 m apart. Twelve Robel pole locations were arranged in a 4 x 4 grid spaced evenly between and outside the pitfall traps.

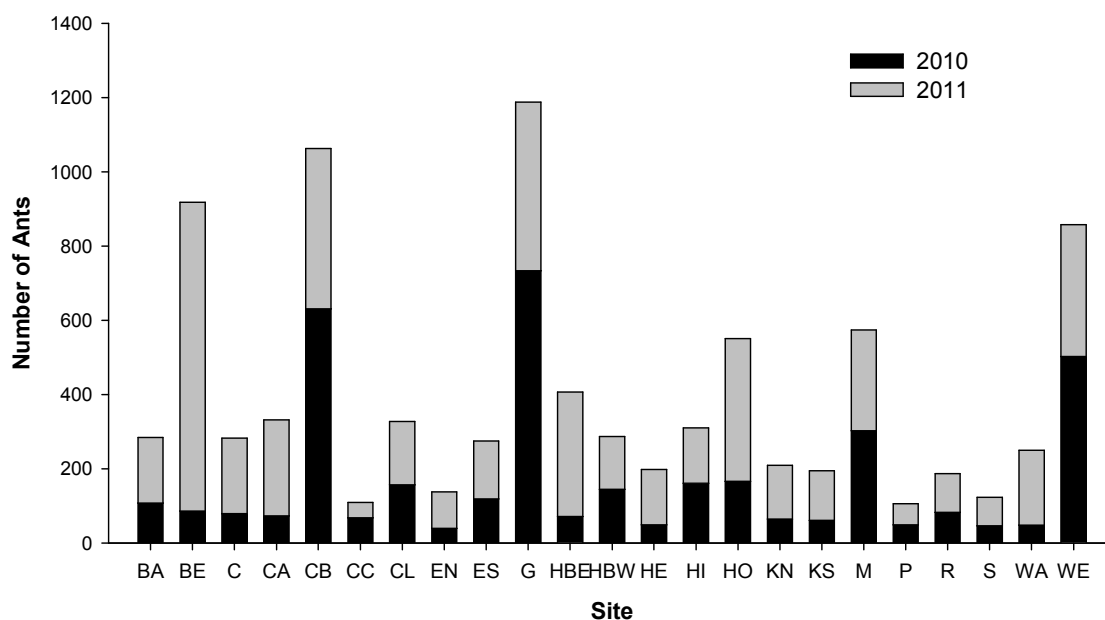


Figure 4. Total number of ants captured in 2010 and 2011 at each of the 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. Site CC had the fewest with 109 and site G had the most with 1,188. Most sites remained fairly consistent between the two years. The most notable exception was site BE which had 746 more ants in 2011 than 2010. Sites HBE and WA also had relatively large increases in 2011.

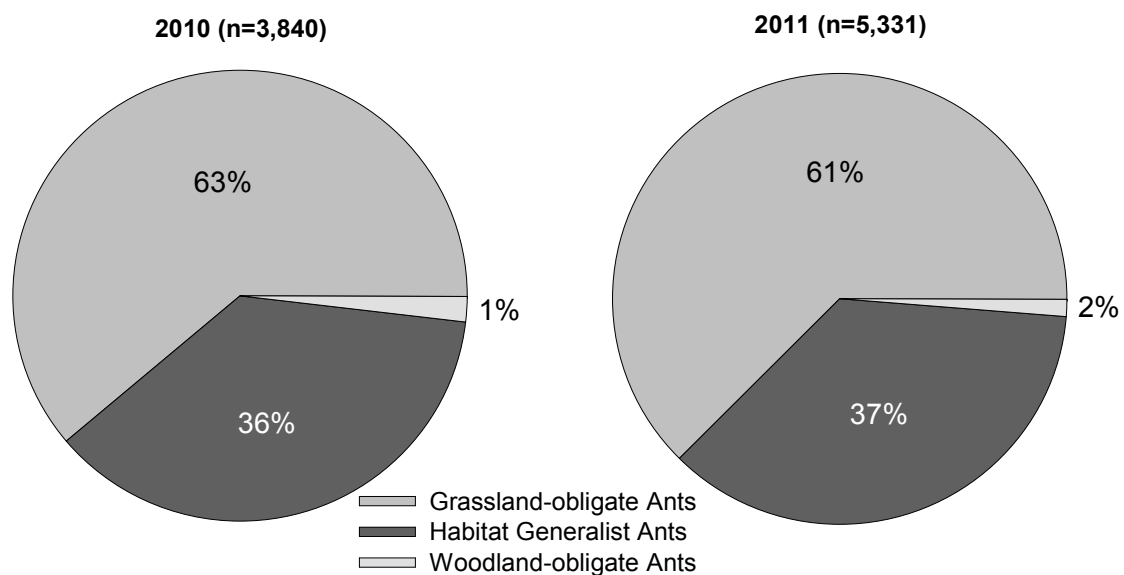


Figure 5. Percentage of ants from 2010 and 2011 belonging to each habitat group. The grassland-obligate ants dominated the remnant haymeadows, followed by habitat-generalists, and very few woodland-obligate species.

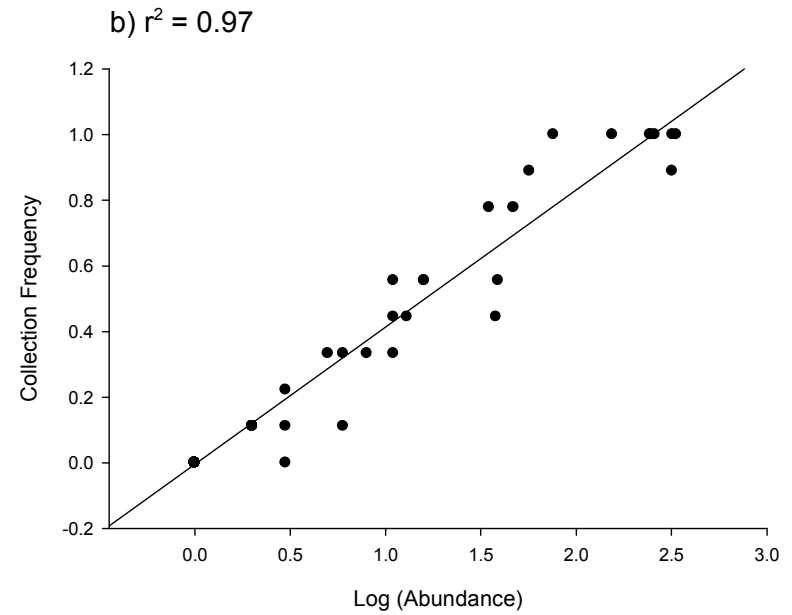
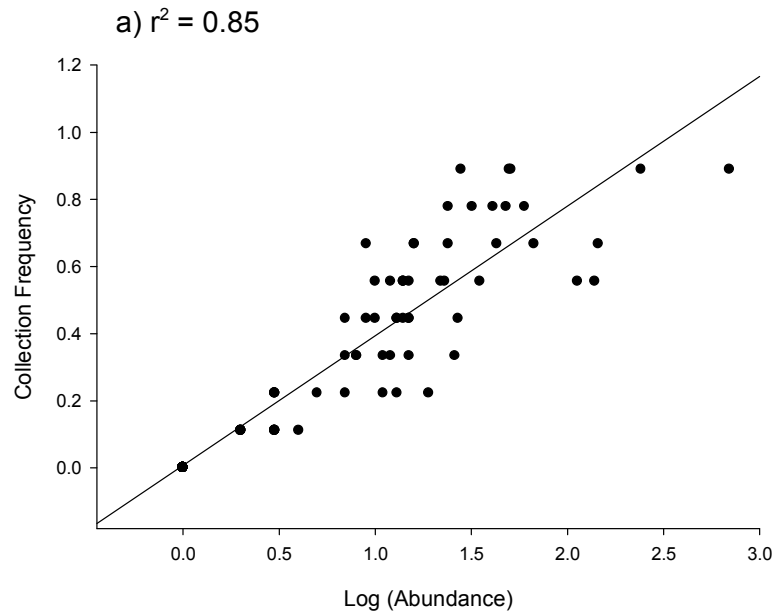


Figure 6. Plot of the collection frequency vs. the log of the abundance for (a) *Lasius neoniger* and (b) *Myrmica americana*. There is a strong correlation between the two variables ( $r^2=0.85$  and  $r^2=0.97$  respectively) indicating that abundance is not being driven by large numbers due to pheromone trails or close proximity of traps to nests.

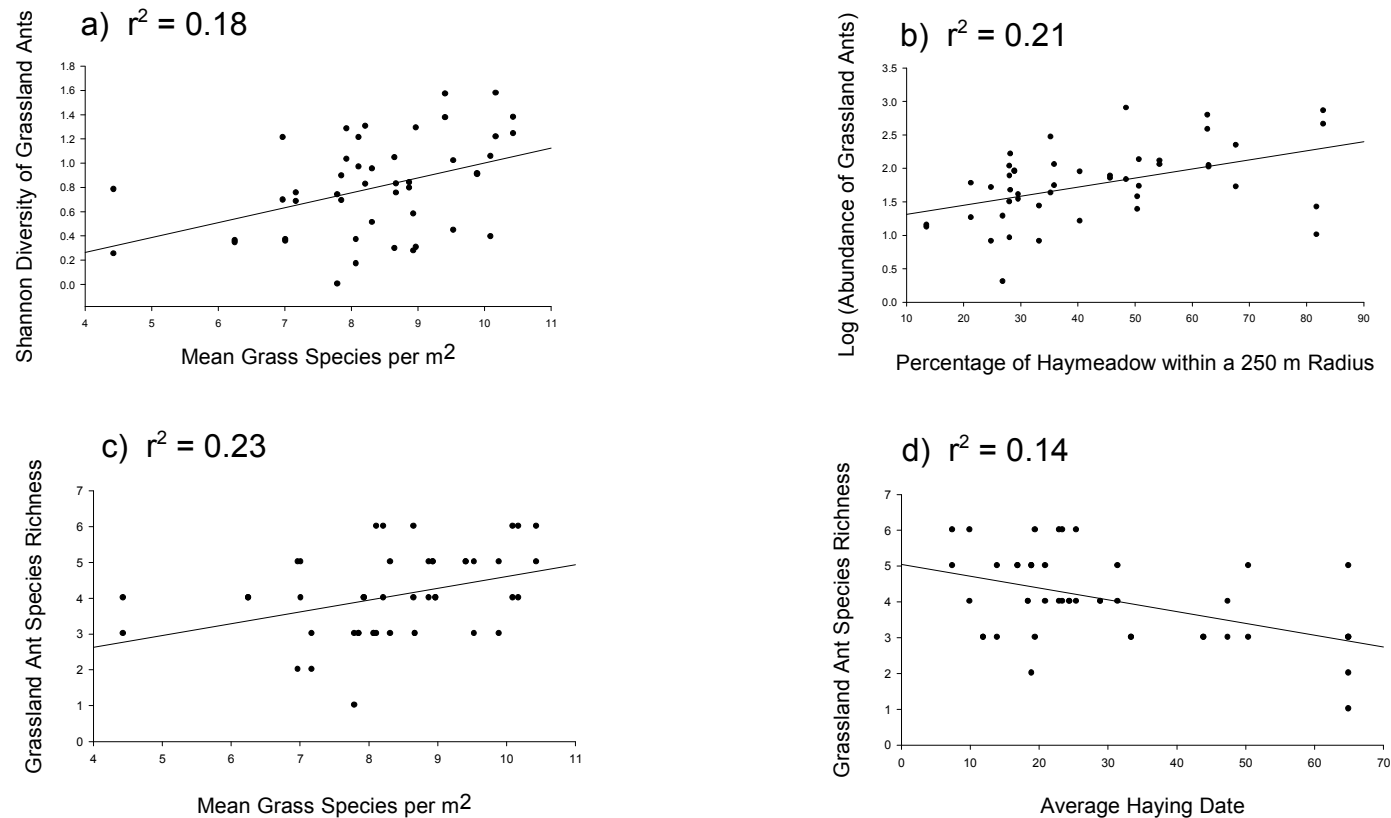


Figure 7. Linear regression of grassland-obligate ants with relevant habitat, landscape, and management factors in 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. Regression includes: (a) Shannon diversity of ants vs. mean number of grass species per m<sup>2</sup>; (b) Log of the abundance of ants vs. percentage of haymeadow with a 250 m radius; (c) Species richness of ants vs. mean number of grass species per m<sup>2</sup>; (d) Species richness of ants vs. averaging haying date (July 15=1, July 16=2, etc.). Data from June and July are combined to give a single value for each site for each year.

Table 1. Models used for analyses of Shannon diversity, abundance, species richness, or presence. “Month” was included as a fixed factor and “siteyear” as a random factor in all models (not shown below).

Models	Type
<b>Combination</b> forbs + grasses density+litter haymeadow + pasture + crop + CRPgrass + trees	floral composition vegetation structure landscape composition
<b>Single Variable</b> haying clayloam forbs grasses density litter haymeadow pasture crop CRPgrass trees	management soil texture floral composition floral composition vegetation structure vegetation structure landscape composition landscape composition landscape composition landscape composition landscape composition
<b>Other</b> all factors no factors	global model null model

forbs = mean number of forb species/m<sup>2</sup>

grasses = mean number of grass species/m<sup>2</sup>

density = Robel pole readings of vegetation density

litter = average depth of lying litter

haymeadow = % haymeadow within 250m of center pitfall trap

pasture = % cattle pasture within 250m of center pitfall trap

crop = % cropland within 250m of center pitfall trap

CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center pitfall

Trees = % trees within 250m of center pitfall trap

haying = average annual haying day

clayloam = % of site covered in clay loam soil

Global model = all covariates

Table 2. Number of each ant species collected in June and July of 2010 and 2011 on 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.

Species	2010		2011		Total
	June	July	June	July	
<i>Myrmica americana</i>	706	649	295	615	2265
<i>Lasius neoniger</i>	363	247	150	1487	2247
<i>Tapinoma sessile</i>	173	572	227	897	1851
<i>Crematogaster lineolata</i>	75	124	86	341	626
<i>Solenopsis molesta</i>	121	154	117	190	482
<i>Monomorium minimum</i>	121	116	157	83	477
<i>Formica incerta</i>	32	52	73	144	301
<i>Forelius pruinus</i>	8	43	73	63	187
<i>Leptothorax pergandei</i>	20	44	38	66	168
<i>Formica pallidefulva</i>	30	21	29	80	160
<i>Formica dolosa (schaufussi)</i>	2	12	24	50	88
<i>Formica argentea</i>	20	19	13	32	84
<i>Nylanderia (Paratrechina) parvula</i>	15	16	14	24	69
<i>Crematogaster cerasi</i>	15	34	2	3	54
<i>Aphaenogaster rudis</i>	2	3	21	18	44
<i>Myrmecina americana</i>	4	0	4	10	18
<i>Tetramorium caespitum</i>	0	8	2	3	13
<i>Camponotus americanus</i>	1	2	3	3	9
<i>Leptothorax ambiguus</i>	2	1	1	2	6
<i>Camponotus castaneus</i>	1	2	0	2	5
<i>Camponotus pennsylvanicus</i>	0	1	3	0	4
<i>Dorymyrmex insanus</i>	0	2	0	2	4
<i>Formica rubicunda</i>	0	2	0	1	3
<i>Ponera pennsylvanica</i>	0	1	0	1	2
<i>Acanthomyops interjectus</i>	1	0	0	0	1
<i>Formica difficilis</i>	0	1	0	0	1
<i>Nylanderia (Paratrechina) faisonensis</i>	1	0	0	0	1
<i>Pheidole pilifera</i>	0	1	0	0	1



Table 3. Ant abundance, species richness, and Shannon Diversity for every sampling event at each of 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.

Site	Abundance				Species Richness				Shannon Diversity			
	2010		2011		2010		2011		2010		2011	
	June	July	June	July	June	July	June	July	June	July	June	July
BA	40	68	77	99	5	10	9	8	0.9942	1.5575	1.5368	1.1608
BE	30	56	71	761	5	6	8	9	1.4585	1.4114	1.8477	0.4428
C	22	57	60	144	7	6	8	10	1.5100	1.1499	1.5417	1.6449
CA	47	26	65	194	6	5	8	8	1.3595	1.5097	1.5096	1.0125
CB	363	268	108	324	9	6	9	9	0.4020	0.4201	1.1838	0.8640
CC	36	32	21	20	5	4	5	9	1.1256	0.9984	1.1428	1.9865
CL	65	92	25	145	5	9	6	6	1.4159	1.4104	1.6449	0.7510
EN	17	22	31	68	6	3	5	5	1.3813	0.7560	1.2448	1.1370
ES	42	77	40	116	7	5	7	12	0.8170	0.9557	1.5494	1.8185
G	392	341	179	276	6	7	7	5	0.6037	0.3298	0.5921	0.2907
HBE	35	36	35	301	7	8	8	11	1.5210	1.7997	1.7817	0.9152
HBW	49	96	37	105	5	9	5	6	1.0745	0.9857	0.6589	1.1004
HE	20	29	44	105	6	5	8	11	1.5382	1.2731	1.4776	1.9331
HI	86	75	27	122	6	6	6	6	1.0418	1.1810	1.3203	1.0311
HO	39	127	163	222	4	9	7	10	0.9787	1.2122	0.9845	1.2253
KN	13	51	19	126	3	8	9	6	0.5360	1.5787	1.9133	0.7275
KS	17	44	39	95	5	8	8	12	1.3130	1.6849	1.7534	1.6748
M	176	126	65	207	7	10	10	11	0.8651	1.1781	2.1611	1.6341
P	22	27	19	38	8	8	7	8	1.5868	1.6627	1.8546	1.6281
R	31	52	53	51	5	7	6	5	1.1374	1.5786	1.5506	1.2824
S	20	26	37	40	5	9	6	4	1.1634	1.7179	0.6963	0.8970
WA	5	43	34	168	3	7	9	9	1.0549	0.7023	1.8335	1.1043
WE	146	356	83	272	9	10	8	11	1.2125	0.7703	1.3546	1.0096

Table 4. Taxa of the Formicidae with number collected and corresponding habitat group (grassland-obligate, habitat-generalist, or woodland-obligate).

Subfamily	Genus	Species	Number Collected	Habitat Group
Dolichoderinae	<i>Forelius</i>	<i>Forelius pruinosus</i> (Roger)	187	grassland
	<i>Doryrmex</i>	<i>Doryrmex insanus</i> (Buckley)	4	grassland
	<i>Tapinoma</i>	<i>Tapinoma sessile</i> (Say)	1851	generalist
Formicinae	<i>Camponotus</i>	<i>Camponotus americanus</i> Mayr	9	generalist
		<i>Camponotus castaneus</i> (Latreille)	5	woodland
		<i>Camponotus pennsylvanicus</i> (De Geer)	4	woodland
	<i>Formica</i>	<i>Formica argentea</i> Wheeler	84	generalist
		<i>Formica difficilis</i> Emery	1	generalist
		<i>Formica dolosa (schaufussi)</i> Wheeler	88	generalist
		<i>Formica incerta</i> Emery	301	grassland
		<i>Formica pallidefulva</i> Latreille	160	grassland
		<i>Formica rubicunda</i> Emery	3	woodland
	<i>Lasius</i>	<i>Lasisus neoniger</i> Emery	2247	grassland
	<i>Acanthomyops</i>	<i>Acanthomyops interjectus</i> (Mayr)	1	generalist
	<i>Nylanderia (Paratrechina)</i>	<i>Nylanderia faisonensis</i> (Forel)	1	woodland
		<i>Nylanderia parvula</i> (Mayr)	69	woodland
Myrmicinae	<i>Aphaenogaster</i>	<i>Aphaenogaster rudis</i> (Enzmann)	44	woodland
	<i>Crematogaster</i>	<i>Crematogaster cerasi</i> (Fitch)	54	generalist
		<i>Crematogaster lineolata</i> (Say)	626	generalist
	<i>Leptothorax (Temnothorax)</i>	<i>Leptothorax ambiguus</i> Emery	6	generalist
		<i>Leptothorax pergandei</i> Emery	168	generalist

Myrmicinae (cont'd)	<i>Monomorium</i>	<i>Monomorium minimum</i> (Buckley)	477	grassland
	<i>Myrmecina</i>	<i>Myrmecina americana</i> Emery	18	woodland
	<i>Myrmica</i>	<i>Myrmica Americana</i> Weber	2265	grassland
	<i>Pheidole</i>	<i>Pheidole pilifera pilifera</i> (Roger)	1	grassland
	<i>Solenopsis</i>	<i>Solenopsis molesta molesta</i> (Say)	482	generalist
	<i>Tetramorium</i>	<i>Tetramorium caespitum</i> (Linnaeus)	13	grassland
Ponerinae	<i>Ponera</i>	<i>Ponera pennsylvanica</i> (Buckley)	2	generalist

Table 5. Results of model selection for grassland-obligate ants. Shannon diversity and abundance use linear mixed models while species richness uses a generalized linear mixed model with a Poisson distribution. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
<b>Shannon Diversity</b>				
grasses <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	94.12	0.00	0.67
forbs <sup>h</sup> + grasses + month + siteyear	5	96.25	2.12	0.23
<b>Abundance</b>				
haymeadow <sup>i</sup> + month + siteyear	4	116.57	0.00	0.92
<b>Species Richness</b>				
grasses + month + siteyear	4	47.67	0.00	0.32
<i>haying</i> <sup>j</sup> + month + siteyear	4	48.18	0.51	0.25
<i>forbs</i> + grasses + month + siteyear	5	49.32	1.65	0.14
<i>pasture</i> <sup>k</sup> + month + siteyear	4	50.21	2.54	0.09
<i>litter</i> <sup>l</sup> + month + siteyear	4	51.11	3.43	0.06
<i>trees</i> <sup>m</sup> + month + siteyear	4	51.71	4.04	0.04

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-h</sup> grasses = mean number of grass species/m<sup>2</sup>; month = month sampled (June or July); siteyear = the site and year sampled; forbs = mean number of forb species/m<sup>2</sup>

<sup>i</sup> haymeadow = % haymeadow within 250m of center trap

<sup>j-m</sup> haying = average annual haying day; pasture = % cattle pasture within 250m of center trap; litter = average depth of lying litter; trees = % of landscape covered by trees within 250m of center trap

Table 6. Estimates of parameters affecting grassland-obligate ant Shannon diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Shannon Diversity				
Grasses	0.1261	0.0314	0.0645	0.1877
Forbs	0.0067	0.0177	-0.0280	0.0413
Month (June)	-0.1207	0.0740	-0.2657	0.0243
Intercept	-0.3509	0.2983	-0.9356	0.2338
Abundance				
Haymeadow	0.0143	0.0037	0.0071	0.0215
Month (June)	-0.2352	0.0587	-0.3504	-0.1201
Intercept	0.9077	0.1745	0.5657	1.2970
Species Richness				
Grasses	0.1200	0.0462	0.0294	0.2106
Forbs	-0.0187	0.0244	-0.0665	0.0291
Haying	-0.0092	0.0037	-0.0163	0.0020
Pasture	0.0066	0.0030	0.0007	0.0125
Litter	0.0539	0.0278	0.0007	0.1084
Trees	-0.0065	0.0038	-0.0139	0.0010
Month (June)	-0.3058	0.1188	-0.5387	-0.0729
Intercept	0.8571	0.6370	-0.3914	2.1055

Table 7. Results of information theoretical model selection for habitat-generalist ants. Shannon diversity and abundance use linear mixed models while species richness uses a generalized linear mixed model with a Poisson distribution. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
<b>Shannon Diversity</b>				
<i>clayloam</i> <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	64.53	0.00	0.21
<i>hay</i> <sup>h</sup> + month + siteyear	4	65.34	0.81	0.14
Global model	14	66.16	1.63	0.09
<i>crop</i> <sup>i</sup> + month + siteyear	4	66.16	1.63	0.09
<i>density</i> <sup>j</sup> + month + siteyear	4	66.40	1.87	0.08
<i>trees</i> <sup>k</sup> + month + siteyear	4	66.80	2.27	0.07
<i>litter</i> <sup>l</sup> + month + siteyear	4	67.00	2.47	0.06
<i>density</i> + <i>litter</i> + month + siteyear	5	67.32	2.79	0.05
<i>pasture</i> <sup>m</sup> + month + siteyear	4	67.55	3.02	0.05
CRPgrass <sup>n</sup> + month + siteyear	4	68.20	3.67	0.03
grasses <sup>o</sup> + month + siteyear	4	68.22	3.69	0.03
forbs <sup>p</sup> + month + siteyear	4	68.68	4.15	0.03
haymeadow <sup>q</sup> + month + siteyear	4	68.76	4.23	0.03
<b>Abundance</b>				
<i>haymeadow</i> + month + siteyear	4	85.38	0.00	0.72
<b>Species Richness</b>				
Null model	2	44.00	0.00	0.28

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-q</sup> *clayloam* = % of site covered in clay loam soil; *month* = month sampled (June or July); *siteyear* = the site and year sampled; *hay* = average annual haying day; *crop* = % cropland within 250m of center trap; *density* = Robel readings of vegetation density; *trees* = % of landscape covered by trees within 250m of center trap; *litter* = average depth of lying litter; *pasture* = % cattle pasture within 250m of center trap; *CRPgrass* = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center trap; *grasses* = mean number of grass species/m<sup>2</sup>; *forbs* = mean number of forb species/m<sup>2</sup>; *haymeadow* = % haymeadow within 250m of center trap

Table 8. Estimates of parameters affecting grassland-obligate ant Shannon diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Shannon Diversity				
Grasses	0.0444	0.0381	-0.0303	0.1191
Forbs	0.0272	0.0207	-0.0133	0.0677
Density	-0.0985	0.0657	-0.2273	0.0303
Litter	0.0262	0.0186	-0.0103	0.0626
Clay Loam	-0.0023	0.0012	-0.0046	0.0000
Haying	0.0043	0.0023	-0.0001	0.0087
Haymeadow	-0.0186	0.0196	-0.0570	0.0199
Pasture	-0.0192	0.0204	-0.0593	0.0209
Crop	-0.0088	0.0189	-0.0459	0.0282
CRP Grass	-0.0185	0.0218	-0.0612	0.0241
Trees	-0.0159	0.0185	-0.0521	0.0202
Month (June)	0.1303	0.0712	-0.0093	0.2699
Intercept	0.8513	0.7808	-0.6790	2.3817
Abundance				
Haymeadow	-0.0086	0.0027	-0.0138	-0.0034
Month (June)	-0.3439	0.0579	-0.4574	-0.2304
Intercept	1.8661	0.1276	1.6160	2.1162
Species Richness				
Grasses	0.0681	0.0442	-0.0185	0.1547
Forbs	-0.0010	0.0239	-0.0479	0.0459
Density	-0.0383	0.1463	-0.3250	0.2484
Litter	0.0378	0.0275	-0.0161	0.0917
Clay Loam	0.0012	0.0016	-0.0020	0.0044
Haying	-0.0017	0.0034	-0.0083	0.0049
Haymeadow	-0.0030	0.0032	-0.0092	0.0032
Pasture	0.0001	0.0032	-0.0064	0.0061
Crop	0.0034	0.0032	-0.0029	0.0098

## Species Richness (continued)

CRP Grass	-0.0031	0.0038	-0.0105	0.0043
Trees	0.0021	0.0032	-0.0041	0.0084
Month (June)	-0.0689	0.1208	-0.3056	0.1678
Intercept	1.1395	0.3783	0.3981	1.8809

---



Table 9. Results of information theoretical model selection for woodland-obligate ants. For presence/absence, generalized linear mixed models with a binomial distribution were used. Models were evaluated using program R. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b><math>\Delta</math>AICc<sup>c</sup></b>	<b><i>wi</i><sup>d</sup></b>
Presence/Absence				
<i>pasture</i> <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	115.79	0.00	0.85

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size;  $\Delta$ AICc = relative AICc; *wi* = Akaike weight

<sup>e-g</sup> *pasture* = % cattle pasture within 250m of center trap; *month* = month sampled (june or july); *siteyear* = the site and year sampled; *haying* = average annual haying day

Table 10. Estimates of parameters affecting woodland-obligate ant presence. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

<b>Parameter</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>95% Confidence Interval</b>	
			<b>Low</b>	<b>High</b>
Presence				
Pasture	-0.0611	0.0175	-0.0954	-0.0268
Month (June)	0.0000	0.4780	-0.9369	0.9369
Intercept	1.3560	0.4386	0.4963	2.2156

**Chapter 3: FUNCTIONAL GROUP COMPOSITION OF ANTS  
(HYMENOPTERA: FORMICIDAE) IN A GRASSLAND  
ECOSYSTEM**

*Abstract:*

I assessed composition of ant functional groups in the fragmented tallgrass prairie ecosystem of southeast Nebraska. Although prior studies have investigated these groups in desert, woodland, and forested areas of North America, little research has been conducted in grasslands. This study adds to the limited knowledge of these functional groups with a biogeographical comparison of their composition in a grassland system to other habitats. In addition to assessing composition of the broader study area, habitat, landscape, and management factors were investigated using model selection to see what might predict the abundance of a given functional group at individual sites. These groups have been used successfully in monitoring restoration success of uranium mines in Australia, and may have potential as bioindicators in North American grasslands. Six groups were represented in the collection; the three most abundant were Opportunists, Cold Climate Specialists, and Generalized Myrmicinae comprising 53.2%, 26.6%, and 12.6% of the collection respectively. This composition is most similar to the Douglas fir forests of Arizona that are dominated by Opportunists and Cold Climate Specialists. Although a much lower elevation than cool-temperate forests, the higher latitude of the grasslands in this study also produces a cool climate more similar to fir forest than the other habitats; this climate likely results in the similar functional group composition by limiting Dominant Dolichoderinae and favoring Opportunists and Cold Climate Specialists. Cold Climate Specialists are positively related to mean grass species per m<sup>2</sup>

and negatively related to mean forb species per m<sup>2</sup>. Inference for predicting many of the other functional groups was weak and produced top models that were either global or null. This suggests that prediction of functional group composition at individual sites within the larger ecosystem is limited.

## INTRODUCTION

The analysis of a biological community may produce broad results that overshadow the responses of individual species. Analyzing all individual species within a community may be too narrowly-focused for generating meaningful conclusions that can be applied to conservation and management of the larger ecosystem. Although this trade-off between precision and generality exists, functional groupings of organisms can serve as a useful middle ground for analyses. Functional groups based on ecological criteria help reduce the complexity of ecological communities and identify general patterns of community structure (Andersen 1997). These general patterns can help predict the member-species' responses to environmental stress and disturbance.

This study investigates a disturbed tallgrass prairie ecosystem. Since European settlement, the tallgrass prairie has been reduced more than any other major North American ecosystem (Samson et al. 2004). In Southeast Nebraska, relatively small and isolated fragments remain scattered in a mosaic of crops, trees, roads, and cattle pastures. Habitat loss and fragmentation continue to threaten what remains of these remnants and their associated ecosystem services.

The high diversity, biomass dominance, taxonomic knowledge base, ease of collection, sensitivity to environmental change, and relatively stationary nesting habits make ants (Hymenoptera: Formicidae) particularly good candidates for biodiversity studies (Alonso and Agosti 2000). Additionally, ants perform many important ecosystem functions such as soil aeration, nutrient cycling, and seed dispersal (Kaspari 2000). Tallgrass prairie ants fall into several basic guilds that include generalized predators, aphid-tenders, slave-raiders, and scavengers (Trager 1998). However, many species have

either not been studied in-depth or perform multiple functions and are therefore difficult to categorize.

In Australia, functional groups have been proposed based on the postulated competitive interactions, community dynamics, broad habitat requirements, and evolutionary history of ants (Andersen 1995). These groups have been used extensively as land assessment bioindicators with their composition determining the restoration success of rehabilitated uranium mine sites (Andersen 1993). Subsequent studies have confirmed that colonization patterns of ants on these sites reflect general patterns of invertebrate biodiversity and provide evidence that changes in ant communities reflect broader ecological changes (Andersen and Majer 2004). The use of ants as bioindicators in Australia is further supported by studies of the responses of functional groups to habitat disturbance with relatively consistent “increasers” or “decreasers” (Hoffmann and Andersen 2003). These studies have demonstrated the broadscale predictive capacity of functional groups in place of detailed species-level information.

Parallel studies have since applied these functional groups to North American ant species. The groups include: Dominant Dolichoderinae, Subordinate Camponotini, Cold Climate Specialists, Hot Climate Specialists, Tropical Climate Specialists, Cryptic Species, Opportunists, Generalized Myrmicinae, and Specialist Predators (Andersen 1997). Prior North American studies have focused on comparing their composition between desert, woodland, and forested areas (Andersen 1997), but there has been little research conducted in grasslands. By investigating their composition in the fragmented tallgrass prairie of southeast Nebraska, I add to our limited knowledge of these functional groups with a biogeographical comparison to these other habitats. Additionally, I assess

the relationship of each functional group to various habitat, landscape, and management factors to see what might predict their abundance at individual sites.

## METHODS AND MATERIALS

### STUDY SITES

My study area is the Southeast Prairies Biologically Unique Landscape (BUL) in southeast Nebraska (Fig. 1). The landscape is dominated by cattle pasture, but contains considerable amounts of cropland, trees, and other types of grasslands. Individual study sites are 23 privately-owned haymeadows scattered throughout the BUL (Fig. 2). All of these sites are cut annually for hay and have never been plowed. Consequently, the historic biodiversity of the region is retained largely in these remnant tallgrass prairie haymeadows.

Management is relatively uniform across all sites with the main exception being that some are cut for hay earlier in the summer (mid-July) and some later (late September). Also, some sites appear to have been over-seeded with non-native species such as smooth brome (*Bromus inermis*) and red clover (*Trifolium pratense*).

Study sites were identified by searching the BUL for grassland fragments that had never been farmed (i.e., lacked terraces), that possessed key tallgrass species easily identifiable from the road (e.g., compass plant (*Silphium aconitum*) and wild alfalfa (*Psoralea tenuiflora*)), and had high, apparent plant diversity. Sites varied in size from approximately 1.8 to 26.9 ha and in shape from highly-irregular to near-perfect squares.

## STUDY DESIGN

### *Pitfall Trap Sampling*

I assessed the abundance of ant functional groups in this landscape with pitfall traps. Pitfall traps were arrayed in a 3 x 3 grid with 25 m spacing, a total of 9 traps per site (Fig. 3). The center trap of the grid was haphazardly selected near the center of each fragment and in the upland areas at all sites to avoid lowland valleys where vegetation was sometimes different. Remaining traps were placed in the grid based on measurements from the center trap, and arranged to coincide with the cardinal directions. The traps themselves consisted of test tubes in PVC conduit pipe sleeves as described by New (1998). PVC sleeves were inserted at least a week before sampling, allowing time for the disturbed soil around the trap to recover (New 1998).

Sampling was conducted by placing test tubes containing propylene glycol (antifreeze) in the ground for a period of 72 hours. Traps were placed in the ground and collected on the same days at all sites to minimize collection differences due to variation in weather. Sampling occurred in early June and early July of both 2010 and 2011.

### *Sample Processing*

Samples were filtered with a fine mesh strainer to remove the propylene glycol and dirt particles. They were rinsed and placed in a vial of 70% ethyl alcohol labeled with the collection date, site, and sample number. Ants were initially counted for preliminary abundance numbers and later identified to species using *The Ants of Ohio* (Covert 2005) and other keys (Fisher and Cover 2007, Trager et al. 2007).



### *Habitat Characteristics*

The floral composition, vegetation structure, litter depth, and type of soil are all factors that may directly or indirectly influence the species composition and abundance of ants at a site. Data on the floral composition was gathered at 50 sampling locations along transects arranged to cover the breadth of each site. At each location, all plant species were identified within a square meter frame. The 50 samples were averaged for mean estimates of plant species richness per m<sup>2</sup>. Floral composition data collection began in 2009 and was completed in 2010. Data on four sites were collected for both years to confirm that plant composition remained consistent from year to year (see Appendix A: Fig. 1).

The structure of vegetation has been observed to influence ant communities (Petersen 2002). Structure may include the plant density/biomass, vertical heterogeneity/canopy cover of plants, and the amount of lying litter. These factors are important to ants in that they may change shade and moisture levels at the ground's surface and may shield them from predators. Habitat structural data was gathered using a Robel pole (Robel et al. 1970) at twelve locations in each site. The locations were kept local to the pitfall trap sampling area by spacing them halfway between the traps, and 12.5 m to the east and west of the outer traps (Fig. 3). Vegetation sampling was conducted following each pitfall collection round and completed for all sites within a week to avoid temporal changes in vegetation.

The Robel pole was read from each of the cardinal directions and averaged to provide a relative estimate of vegetation density for each location. Litter depth to the nearest 0.5 cm was also measured at each point the Robel pole was read. To estimate

vertical structure, the height of every plant touching the Robel pole was recorded. This data was analyzed using a Shannon diversity index for an estimate of vertical heterogeneity, and a simple sum of the number of touches for an estimate of canopy cover. Both of these estimates were highly correlated with the vegetation density, however, and consequently eliminated from the analysis.

Soil texture (i.e., particle size) can influence soil-nesting ants. The Web Soil Survey (2012) was used to determine the percentage of each site covered by clay loam. Clay loam was present in almost every site to varying degrees and studies have shown that clay content can influence ants (Bestelmeyer and Wiens 2001, Boulton et al. 2005). The term loam refers to soil composed of relatively equal parts clay (small particles), silt (medium particles), and sand (large particles). Clay loam consists of all three particle types but has a greater proportion of clay than the other two. (See the tables in Appendix A for more data concerning habitat factors.)

### *Landscape Characteristics*

Fragmentation of the prairie has resulted in very abrupt changes to different habitats. The type, amount, and distance to these other habitats can affect connectivity of the fragments, subsidize ants with resources outside a fragment, or harm ants with additional predators from outside a fragment. Landscape composition around these fragments was determined by digitizing the surrounding landscape in a Geographic Information System (GIS). Each polygon of the digitized landscape was classified as: cattle pasture, haymeadow, trees, cropland, and CRP grass. An “other” classification was used for areas that did not fit these major categories. Based on the foraging ability of

some ant species (Brian 1955), a 250 m radius buffer was created in GIS around the center pitfall trap for each site and the percentage of each landscape type was determined within each buffer (Dauber et al 2003). (See the tables in Appendix A for more data concerning landscape factors.)

### *Management*

Haying is the predominant management tool in these haymeadows. All of the study sites are cut for hay once a year, and the timing ranges from mid-July to late September. Haying before plants are able to produce viable seed may limit their reproduction and consequently their presence in sites. Vegetation structure may be altered by haying if perennials have been mowed annually at the peak of their aboveground production, weakening them over time and decreasing height and biomass. The amount of lying litter is also affected by the time of haying. Although these properties are reflected to some degree in other habitat factors (e.g., plant species richness, vegetation density), they were all relatively weakly correlated with haying time ( $r^2 < 0.17$ ).

The year-to-year timing of haying varies based on factors such as weather, but remains fairly consistent (i.e., within two to three weeks). Generally, owners who want to maximize the quality of the hay cut early while landowners who want to maximize production cut late (Pfeiffer, personal communication). Beginning in mid-July, sites were monitored and the date of haying events recorded. Haying time was quantified by assigning a value to each day (i.e., July 15=1, July 16=2, etc.) and the average was taken between 2010 and 2011 for each site (Appendix A: Table 5). Larger values correspond with later average haying time.

## STATISTICAL ANALYSIS

### *Functional Groups*

The individual species that comprise the ant community in a given tallgrass prairie ecosystem have a wide range of functions and requirements. Thus it is often useful to categorize ants into relevant groups that allow for predictability of the member species' reactions to and effects on various environmental factors. For this study, ants were categorized according to Andersen's (1995, 1997) functional groups and the proportional composition of sites individually and collectively determined.

### *Abundance*

Abundance for each functional group was determined two ways: first, the sum total of ants collected in all nine pitfall traps at each site; and second, a 6-point index of abundance (Andersen 1997). The 6-point method was used to make results more directly comparable to other studies of the same functional groups in North America (Andersen 1997) and to minimize the effect of having large numbers of ants captured in a trap due to placement near a nest or foraging trail (Andersen 1997). In the 6-point scale method, values correspond to the following abundances: 1, 1 ant; 2, 2-5 ants; 3, 6-10 ants; 4, 11-20 ants; 5, 20-50 ants; 6, >50 ants (Andersen 1997).

### *Multi-model Inference*

Information-theoretical model selection weighs evidence among multiple competing hypotheses to predict a response variable; in this case, either ant abundance or presence. This study was limited to a suite of 16 *a priori* models with covariates

corresponding to the landscape, habitat, and management data collected for each fragment (Table 1). The candidate models include a landscape model, a plant composition model, a habitat structure model, a vegetation structure model, a soil model, and a management model. Additionally, a null model (no effects) and a global model (all factors) were included along with models that measure each explanatory variable independently. Using Program R (R Development Core Team 2012), Akaike's Information Criterion adjusted for small sample size (AICc) was calculated to rank the candidate models. From the AICc values, Akaike weights ( $w_i$ ) were calculated to determine the most parsimonious models (i.e., the best fits for the empirical data) (Anderson et al. 2000). The confidence set includes any model with an Akaike weight at least 10% of the highest ranked model's weight (Royall 1997).

The abundance data was log-transformed for use as the response variable. Due to low numbers of Dominant Dolichoderinae and Subordinate Camponotini, these groups used presence/absence of individuals at each site during a sampling event for analyses. If at least one individual from a group was captured during a given sampling event that group was considered to be present; if not, it was assumed to be absent. Logistic regression was used for presence/absence data (i.e., generalized linear mixed model with a binomial response distribution).

Site and year sampled were combined into a single "site-year" variable and included as a random factor in all models; all other variables were fixed. Because the month sampled had a large impact on the response variables, it was included in every model to negate its effect and allow the environmental and management factors to drive the model selection.

## RESULTS

Total ants consisted of 9,171 individuals representing 28 species from 18 genera. This included 3,840 individuals and 28 species in 2010 and 5,331 individuals and 24 species in 2011 (Table 2). The three most abundant species captured were *Myrmica americana*, *Lasisus neoniger*, and *Tapinoma sessile*; these three species comprised 69.4% of the total collection. The total number of ants collected at a single site ranged from 109 (CC) to 1,188 (G) (Figure 1). The fewest species collected at a site for a given sampling event was 3 (EN, July 2010 and WA, June 2010) and the most was 12 (ES, July 2011 and KS, July 2011) (Table 3).

### *Functional Groups*

Of Andersen's (1997) functional groups, 6 were represented in the collection (Table 4). Using the sum total abundance approach, 11 species comprising 53.2% and the majority of the collection were Opportunists; 6 species comprising 26.6% were Cold Climate Specialists; 5 species comprising 12.6% were Generalized Myrmicinae; 2 species comprising 5.3% were Cryptic Species; 1 species comprising 2% was Dominant Dolichoderinae; and three species comprising less than 1% of the collection were Subordinate Camponotini (Figure 5).

The 6-point scale abundance gives similar, albeit slightly different results (Fig. 6). Opportunists were still the dominant group, comprising a smaller 39.8% of the total collection. Cold Climate Specialists and Generalized Myrmicinae were virtually even with one another, comprising 21.8% and 21.2% respectively. Dominant Dolichoderinae made up 4.1% and Subordinate Camponotini 1.1%. Although the collective study sites

reveal a particular functional group composition, the relative abundances of groups at individual sites vary greatly (Fig. 7).

### *Model Selection*

For Opportunists, two models are supported by the data (Table 5). The top ranked model, with an Akaike weight of 87%, is the global model, suggesting that many of the habitat, landscape, and management attributes considered have a comparable influence on the abundance of Opportunist ants. The second model, with much lower weight, is mean forb and grass species richness per m<sup>2</sup> (Table 5). This implies that forbs (negative) and grasses (positive) together may have a slightly stronger influence on Opportunist ant abundance than factors in other models. Model-averaged parameter estimates indicate that at the 95% confidence level forbs have a negative effect while haymeadow and clay loam have a positive effect (Table 6). Cold Climate Specialists again have two top models with 63% and 31% of the weight respectively (Table 5). These models also involve the factors of mean forb and grass species richness per m<sup>2</sup>, with forbs having a negative effect and grasses having a positive effect.

The abundance of Generalized Myrmicinae is predicted by a single, strong model with 97% of the weight: the global model (Table 5). As with Opportunists, many different factors may be influencing Generalized Myrmicinae abundance. Model selection for Cryptic Species chose the Null model as the top model indicating none of the models were very good predictors.

Due to the low abundance of Dominant Dolichoderinae and Subordinate Camponotini, the data was analyzed as Presence/Absence with logistic regression (Table

5). The top two models selected for Dominant Dolichoderinae both involve landscape factors. The top model (72% weight) includes the factor of CRPgrass, which is CRP and other unclassified, low diversity grassland. The second model includes all landscape composition factors and has the top model nested within it, likely driving selection of the second model. The only models selected for Subordinate Camponotini were the global and null models.

## **DISCUSSION**

To help reduce the complexity of communities and identify general patterns of community structure, ecologists may attempt to classify taxa based on ecological criteria. This approach can aid in studies of ecologically diverse organisms such as ants. Whereas functional group classification is typically concerned with the production of specific ecosystem services or functions, guild classification is primarily based on resource sharing by species in a competitive context (Blondel 2003). Due to his reliance on competitive interactions and habitat requirements (Andersen 1995), Andersen's classification of ants may be more appropriately termed as guilds. However, they have traditionally been referred to as functional groups in the literature, presumably because resource partitioning is often closely linked to ecosystem functioning, and I continue to do so here.

These functional groups, whose abundances vary predictably with disturbance and stress (Andersen 1995), have been used extensively in Australia (Andersen 1995, Andersen et al. 2002, Andersen and Majer 2004). There they have been applied to biogeographic comparisons of community structure, analyses of competitive dynamics



within communities, and land assessments as bioindicators (Andersen 1997). Although Australian ant taxa have been matched with ecologically equivalent taxa in North America (Andersen 1997), few studies have investigated these functional groups here, particularly in grasslands. Because many ants can be categorized into these groups without identification to species it makes them an attractive option for use in ecological studies.

### *Functional Groups*

Although Dominant Dolichoderinae species are highly aggressive and territorial, they thrive primarily in hot, open habitats (Andersen 1997). Thus they are absent throughout much of cool-temperate North America (Andersen 1997). In this study, only one species was present in moderate numbers, *Forelius pruinosus* (Table 4). The lack of territorial Dominant dolichoderines allows other functional groups to thrive, such as Opportunists and Cold Climate Specialists.

Opportunists are considered unspecialized because they possess the broadest environmental domain of all functional groups (Andersen 1995, Andersen 1997). They can be abundant in cool and shady habitats, hot and open habitats, habitats with heavy litter, or highly disturbed habitats (Andersen 1995). With such broad ecological requirements, it is not surprising they are the most abundant group in this study.

Cold Climate Specialists also tend to be abundant in habitats lacking Dominant dolichoderines (Andersen 1997). Their distribution is typically centered on cool, high latitude or high altitude areas (Andersen 1995, Andersen 1997). Apart from their climatic tolerances, Cold Climate Specialists, like Opportunists, are generally unspecialized in

terms of foraging ecology (Andersen 1995); this may be driving their high abundance in the haymeadows of southeast Nebraska.

Generalized Myrmicinae is the third most abundant functional group in this study. Although aggressive in terms of their mass mobilization and rapid recruitment to food resources, they differ from Dominant dolichoderines in that individuals are not highly active or aggressive and tend to have small foraging ranges (Andersen 1995, Andersen 1997). In North America, Generalized myrmicines are particularly abundant in warmer regions (Andersen 1997); this may be a limiting factor in their abundance in Southeast Nebraska.

Cryptic Species were the fourth most abundant functional group in this study. They are typically small ants which nest and forage almost exclusively within soil and litter and may have little interaction with other ants (Andersen 1995).

Comprising less than 1% of the total collection, Subordinate Camponotini had the lowest abundance of all functional groups. They are defined by their large body size and submissive behavior toward Dominant dolichoderines (Andersen 1995, 1997). Although they can be abundant in the absence of Dominant dolichoderines, many *Camponotus* species are associated with woodlands, likely contributing to their numerically small presence in this study.

### *Biogeographical Comparison*

In Arizona, the relative abundance of functional groups has been analyzed in sites representing an environmental and elevation gradient, but consisting of three distinct habitat types: arid desert, temperate oak-juniper woodland, and cool-temperate Douglas

fir forest (Andersen 1997). Additionally, less in-depth studies looked at functional groups in deciduous forest, open shrubland, and spruce forest at Acadia National Park in Maine (Andersen 1997).

In the desert sites of Arizona, Dominant Dolichoderinae, Generalized Myrmicinae, and Hot Climate Specialists were dominant (Fig. 8); Generalized Myrmicinae and Opportunists were predominant at temperate woodland sites; and Opportunists and Cold Climate Specialists were predominant at cool-temperate forest sites (Andersen 1997). Cold Climate Specialists and Opportunists also dominated at the Maine sites (Andersen 1997).

In comparison to the Arizona results, the present study of tallgrass prairie haymeadows demonstrates they are least similar to the desert in terms of functional group composition (Fig. 8). Very few Dominant dolichoderines and no Hot Climate Specialists were collected from the prairie fragments. The ground surface at the desert sites consisted mostly of pebbles and bare soil with sparse shrub vegetation (Andersen 1997), a vast contrast from Great Plains' grasslands.

The haymeadows of this study are most comparable to the cool-temperate Douglas fir forest sites of Arizona, as both are dominated first by Opportunists and second by Cold Climate Specialists (Fig. 8). Although fir forests contain a very different vegetation structure and composition from tallgrass haymeadows, both possess relatively high amounts of litter, making them more similar to each other structurally than to deserts. However, the primary factor determining the functional composition of these sites is likely the climate and its resulting influence on competitive interactions. Although the elevation of the Southeast Prairies BUL (about 375 m above sea level) is significantly

lower than all of the Arizona study sites (1,400-2,600 m), its higher latitude makes it climatically more similar to the high altitude fir forests than to arid deserts. The increased stress due to climate (colder temperatures) may limit the Dominant dolichoderines in both habitat types, allowing Opportunists and Cold Climate Specialists to dominate.

Comparable results were found in the high latitude Maine sites, dominated by Cold Climate Specialists followed by Opportunists (Andersen 1997). One would expect other types of grassland (e.g., cattle pasture and CRP) in the Southeast Prairies BUL to follow this same climatically-based functional group distribution, but further investigation is needed to determine this.

### *Model Selection*

The relative proportions of each functional group vary widely indicating there are differences between sites in the factors affecting each group (Fig. 7). Although these functional groups are based primarily on biogeographical patterns rather than community dynamics at individual sites (Andersen 1995), results of model selection may still provide useful insight into what habitat, landscape, and management factors might predict functional group abundance on a more local scale. Close associations with any of these environmental factors may indicate the potential of these functional groups as ecological indicators in tallgrass prairie.

Of the 16 candidate models, the global model was the top model in the confidence set for Opportunists with 87% of the weight (Table 5). This indicates that many of the factors considered are having comparable effects on Opportunist abundance. Because Opportunists are the least specialized functional group, they may not be relying solely on

a few necessary factors; instead they may be affected a small amount by many different factors. The only other model in the confidence set, with 9% of the weight, is the floral composition model. This indicates the factors of mean forb and grass species richness per  $\text{m}^2$  may be slightly more important than the other factors in the global model.

Cold Climate Specialist abundance is influenced most by floral composition. Their abundance is best predicted by forb and grass species richness per  $\text{m}^2$  (Table 5). They are negatively correlated with forbs and positively correlated with grasses. With a weight of 63%, the top model involves mean forb and grass species richness per  $\text{m}^2$ . Forb richness per  $\text{m}^2$  has a negative correlation while grass has a positive correlation (Fig. 9). With 31% of the weight, the second model involves only the grass factor, a model nested within the first model. Parameter estimates indicate that at the 95% confidence level grasses have a stronger effect than forbs (Table 6). Linear regression of grasses and forbs with Cold Climate Specialist abundance further confirm this (Fig. 9). Grasses provide food in the form of tissues and honey-dew produced by aphids (Petersen 2002). Mutualism has been observed between species of prairie grasses and ants, although the mechanisms for promoting one another remain unclear (Petersen 2002). More species of grasses may provide more resources for greater numbers of ants. It is possible that many other insects benefit from higher grass species richness, increasing potential prey for Cold Climate Specialists.

CRP and other lower diversity grassland appear to have the greatest effect on the presence of Dominant Dolichoderinae (Table 5). More low diversity grassland in the nearby vicinity (within 250 m) increases the likelihood of a Dominant dolichoderine being present.

Aside from Cold Climate Specialists and Dominant Dolichoderinae, the top model for all other functional groups was either the global or null model (Table 5). It is possible that other unconsidered factors strongly influence their abundance at individual sites. Two of the main considerations for determining functional groups were climate and competitive interactions (Andersen 1995). Climate is the same across all study sites, but the competitive dynamics may vary. The abundance of each functional group was plotted against one another to search for patterns. Two of the strongest relationships include Opportunists with Generalized Myrmicinae and Opportunists with Cold Climate Specialists (Fig. 10). Opportunists are positively correlated with Cold Climate Specialists. Both are considered unspecialized in terms of foraging ecology and are not highly competitive. The abundance of one would not be expected to negatively affect the abundance of the other. In contrast, Generalized Myrmicinae are negatively correlated with Opportunists. Generalized myrmicines are more aggressive, particularly in terms of their mobilization and recruitment to food resources (Andersen 1995), and may therefore outcompete Opportunists in sites where they are abundant. Although Generalized myrmicines may be an additional factor affecting Opportunists, the selection of the global model for Generalized Myrmicinae leaves it unclear what is most affecting their abundance at particular sites.

### *Conclusion*

The dominance of Opportunists and Cold Climate Specialists coupled with the lack of Dominant Dolichoderinae in the Southeast Prairies BUL supports the notion that these functional groups are most strongly influenced by climate. The cooler climate is

likely the primary limiting factor for dominant groups such as Dominant Dolichoderinae; this allows submissive groups such as Opportunists to thrive. Although in a grassland system, the functional group composition of this study is more similar to Douglas fir forest in the high elevations of Arizona than to oak-juniper woodlands or scrub deserts. The cooler climates of the prairie and the fir forest are likely driving this composition.

Considered collectively, the study sites reveal a particular functional group composition; however, individual sites vary in their relative proportions. Model selection results indicate that the mean number of grass species per m<sup>2</sup> has a positive association with the abundance of Cold Climate Specialists. However, the top models for most of the functional groups were either global or null models; this suggests that although composition can be predicted in the broader landscape based on climate, use of habitat, landscape, and management factors to predict their composition within individual sites is limited. These functional groupings, based primarily on competitive interactions and broad habitat requirements, may be of limited use as ecological indicators in tallgrass prairie haymeadows.

Future studies should investigate other types of habitat in the Southeast Prairies BUL to determine if, as predicted by the climate, composition of functional groups is similar to haymeadows. Such studies might also determine if the species composition comprising the functional groups in other habitats is similar to or vastly different from the haymeadows. Although their use may be limited in distinguishing characteristics between individual sites of the same habitat type, functional group composition may yet have potential for distinguishing between different habitat types, such as haymeadows from cattle pasture or CRP.

## LITERATURE CITED

- Alonso, L.E. and D. Agosti. 2000. Biodiversity studies, monitoring, and ants: an overview. Pages 1-8 *in* D. Agosti, J.D. Majer, L.E. Alonso, and T.R. Schultz, editors. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington and London.
- Andersen, A.N. 1993. Ants as indicators of restoration success at a uranium mine in tropical Australia. *Restoration Ecology* **1**:156-167.
- Andersen, A.N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* **22**:15-29.
- Andersen, A.N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography* **24**:433-460.
- Andersen, A.N., B.D. Hoffmann, W.J. Muller and A.D. Griffiths. 2002. Using ants as bioindicators in inland management: simplifying assessment of ant community responses. *Journal of Applied Ecology* **39**:8-17.
- Andersen, A.N. and J.D. Majer. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* **2**:291-298.
- Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence and an alternative. *The Journal of Wildlife Management* **64**:912-913.



- Bestelmeyer, B.T. and J.A. Wiens. 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. *Ecological Applications* **11**:1123-1140.
- Blondel, J. 2003. Guilds or functional groups: does it matter? *Oikos* **100**:223-231.
- Boulton, A.M., K.F. Davies, and P.S. Ward. 2005. Species richness, abundance, and composition of ground-dwelling ants in Northern California grasslands: role of plants, soil, and grazing. *Environmental Entomology* **34**:96-104.
- Brian, M.V. 1955. Food collection by a Scottish ant community. *Journal of Animal Ecology* **24**:336-351.
- Covert, G.A. 2005. The ants of Ohio (Hymenoptera: Formicidae). Ohio Biological Survey, Inc., Columbus, Ohio.
- Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment* **98**:321-329.
- Fisher, B.L. and S.P. Cover. 2007. *Ants of North America: a guide to the genera*. University of California Press, Berkeley and Los Angeles, California.
- Hoffmann, B.D. and A.N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* **28**:444-464.
- Kaspari, M. 2000. Primer on ant ecology. Pages 9-24 *in* D. Agosti, J.D. Majer, L.E. Alonso, and T.R. Schultz, editors. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington and London.
- New, T.R. 1998. *Invertebrate surveys for conservation*. Oxford University Press, Oxford.

- Petersen, C.E., D.G. Dave, C.L. Parker, and R.E. Petersen. 2002. Ant-plant relationships in a re-created tallgrass prairie. *The Great Lakes Entomologist* **35**:27-32.
- Pfeiffer, Kent. 2012. Personal communication. January 27, 2012.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>. Accessed 2012 February.
- Robel, R.J., J.N. Briggs, A.D. Dayton and L.C. Hulbert. 1970. Relationship between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* **23**:295-298.
- Royall, R.M. 1997. *Statistical evidence: a likelihood paradigm*. Chapman and Hall, New York.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* **32**:6-15.
- The Nature Conservancy. <<http://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/nebraska/howwework/senebmap.pdf>> Accessed 2012 March.
- Trager, J. C. 1998. An introduction to ants (Formicidae) of the tallgrass prairie. *Missouri Prairie Journal* **18**:4-8.
- Trager, J. C., MacGown, J. A., Trager, M. D. 2007. Revision of the Nearctic endemic *Formica pallidefulva* group. Pages 610-636 in Snelling, R.R., B.L. Fisher, and P.S. Ward, editors. *Advances in ant systematics (Hymenoptera: Formicidae): homage to E.O. Wilson - 50 years of contributions*. *Memoirs of the American Entomological Institute*, 80.

Web Soil Survey. United States Department of Agriculture: Natural Resource  
Conservation Service. <<http://websoilsurvey.nrcs.usda.gov>>. Accessed 2012  
February.

## TABLES AND FIGURES



Figure 1. Map showing the Biologically Unique Landscapes of southeast Nebraska (The Nature Conservancy 2012), including the Southeast Prairies BUL which includes most of Pawnee as well as portions of Johnson, Richardson, and Gage counties.

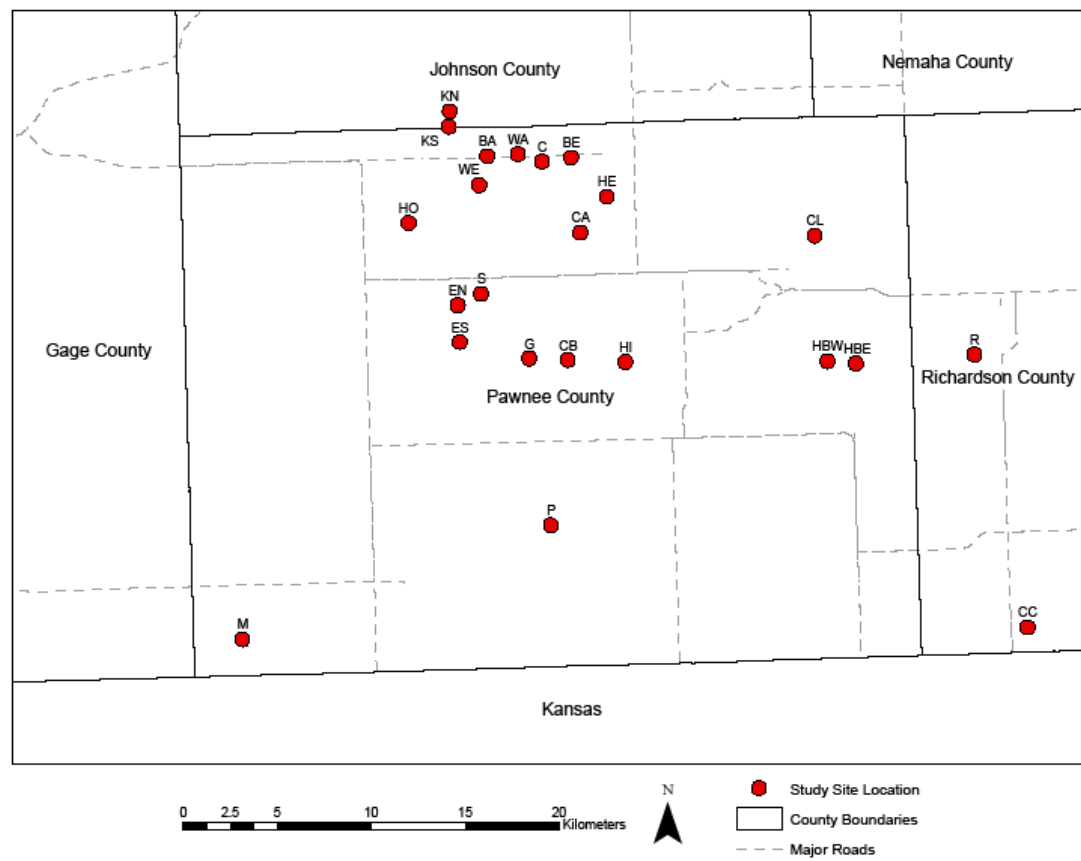


Figure 2. Location of the 23 study sites within the counties of the Southeast Prairies Biologically Unique Landscape.

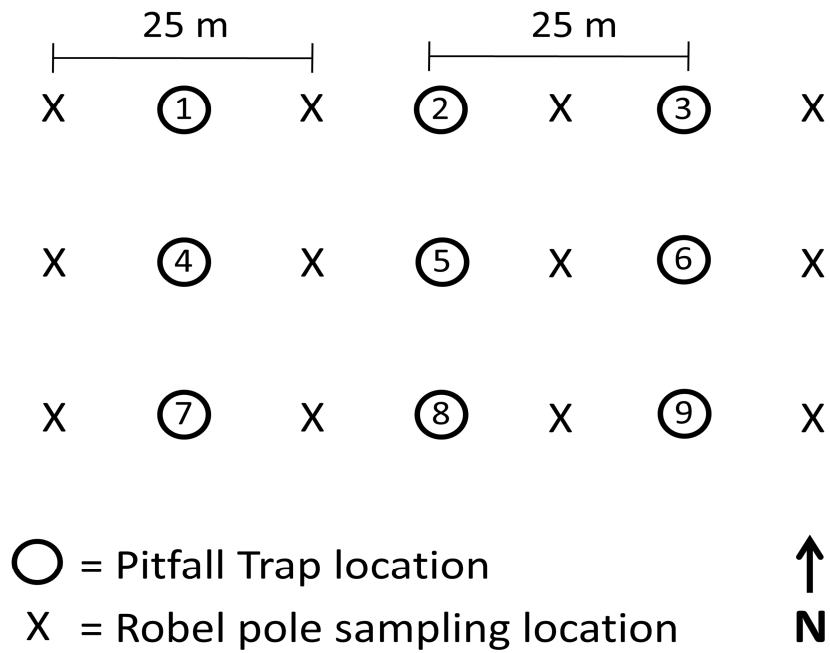


Figure 3. Sampling design used in study sites. Nine pitfall traps were arranged in a 3 x 3 grid spaced 25 m apart. Twelve Robel pole locations were arranged in a 4 x 4 grid spaced evenly between and outside the pitfall traps.

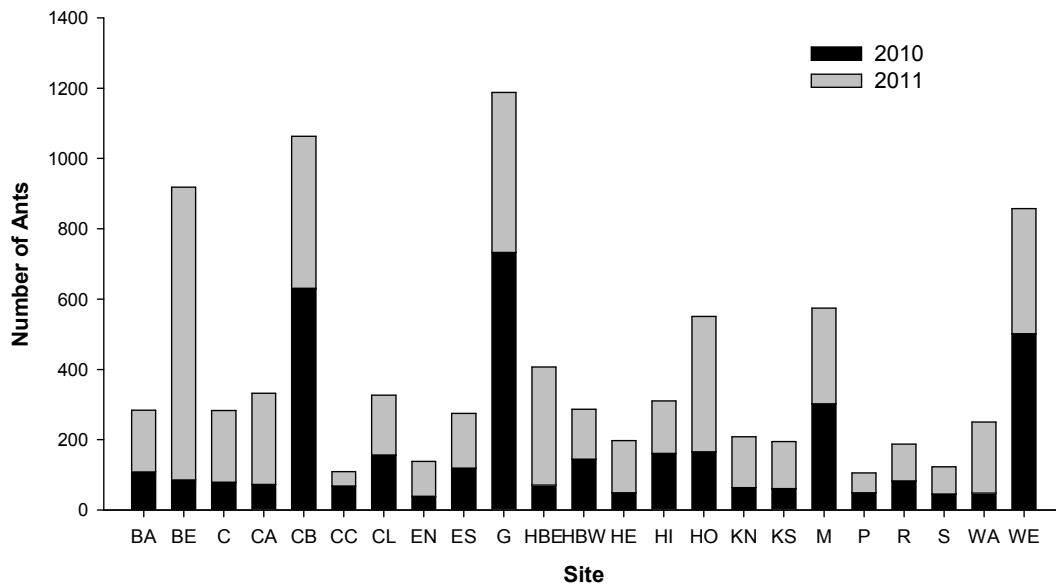


Figure 4. Total number of ants captured in 2010 and 2011 at each of the 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape. Site CC had the fewest with 109 and site G had the most with 1,188. Most sites remained fairly consistent between the two years. The most notable exception was site BE which had 746 more ants in 2011 than 2010. Sites HBE and WA also had relatively large increases in 2011.

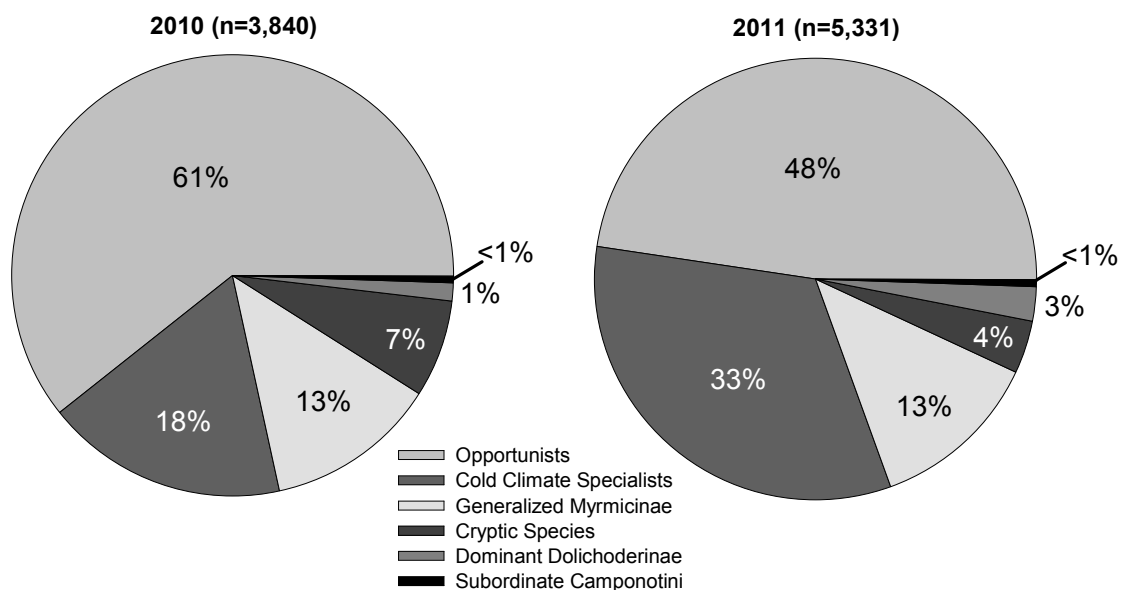


Figure 5. Percentage of ants from 2010 and 2011 belonging to each functional group. The Opportunists and Cold Climate Specialists dominated the remnant haymeadows, followed by Generalized Myrmicinae and Cryptic Species. Only about 1% of the collection consisted of Dominant Dolichoderinae and Subordinate Camponotini.



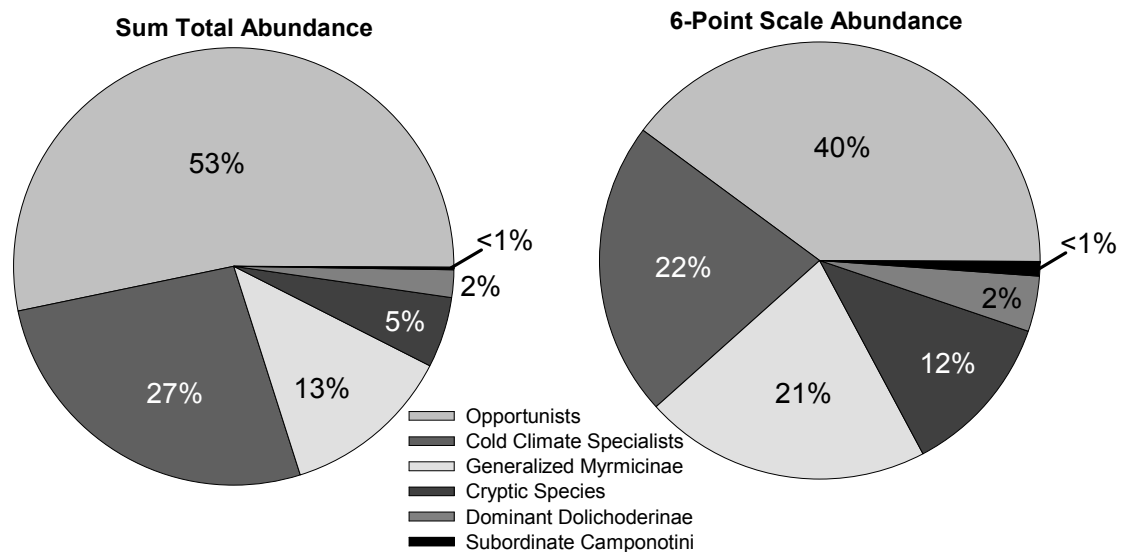


Figure 6. Percentage of the total ant abundance belonging to each functional group for 2010 and 2011 combined. Includes the sum total abundance and abundance using a 6-point scale (Andersen 1997). Opportunists are dominant using both methods, but Generalized Myrmicinae are nearly even with Cold Climate Specialists using the 6-point scale method.

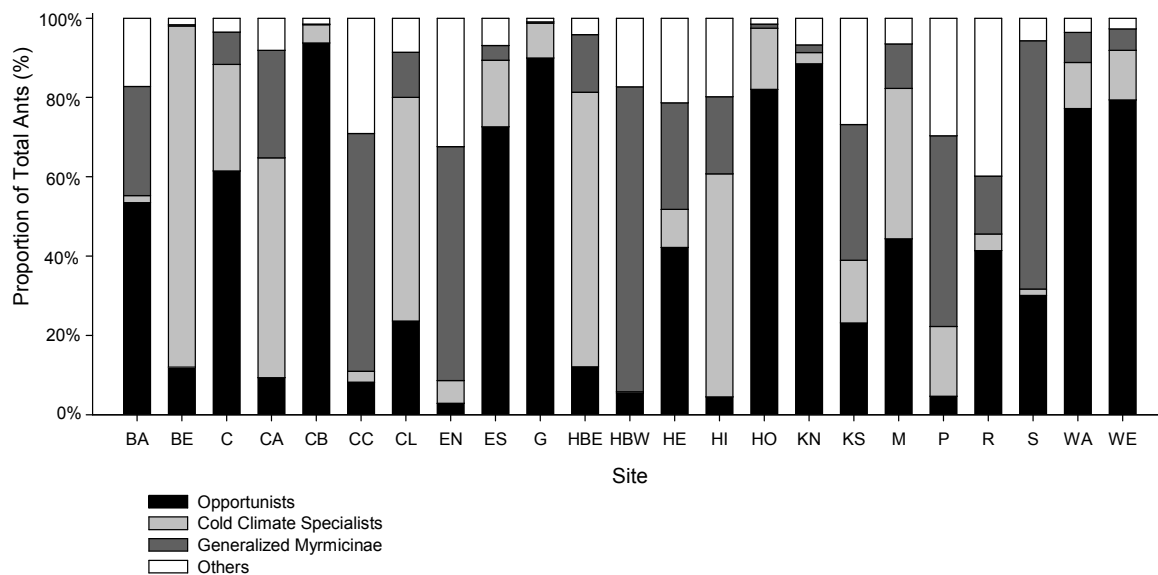


Figure 7. Proportion of total ants comprised of each functional group for all study sites, 2010 and 2011 combined.

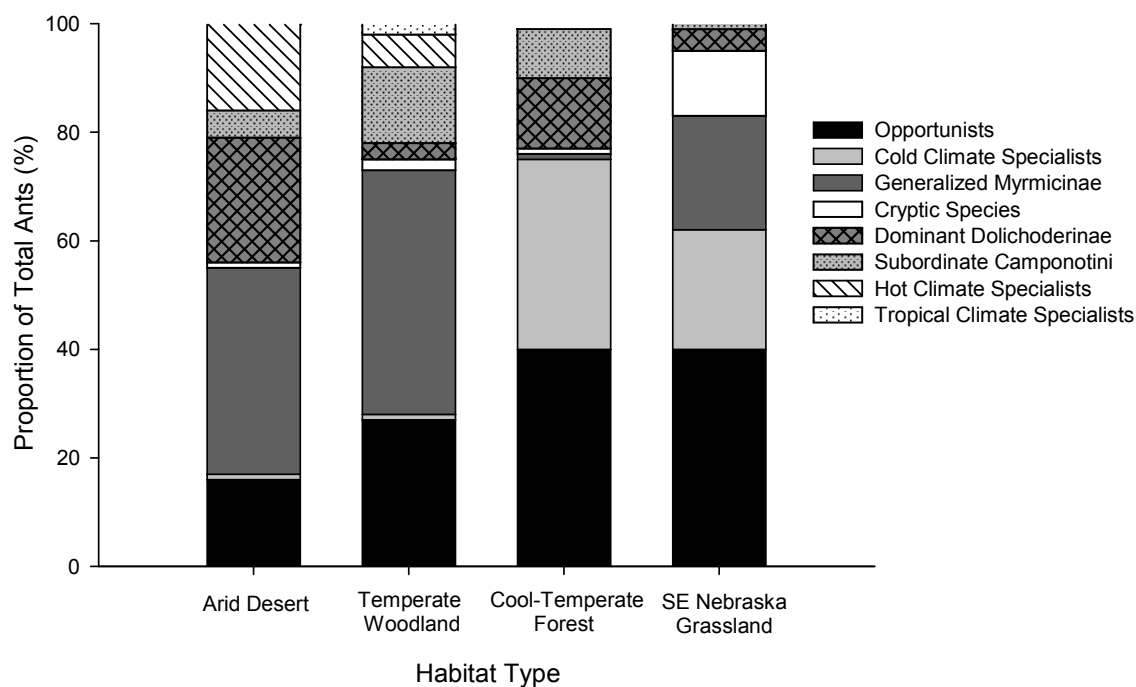


Figure 8. Percentage of ants belonging to each functional group in arid desert, temperate woodland, and cool-temperate forest (Andersen 1997) compared to southeast Nebraska grassland. The 6 point scale method of abundance was used for comparison. The functional group composition in the grassland was most similar to cool-temperate forests in that both are dominated by Opportunists and Cold Climate Specialists.

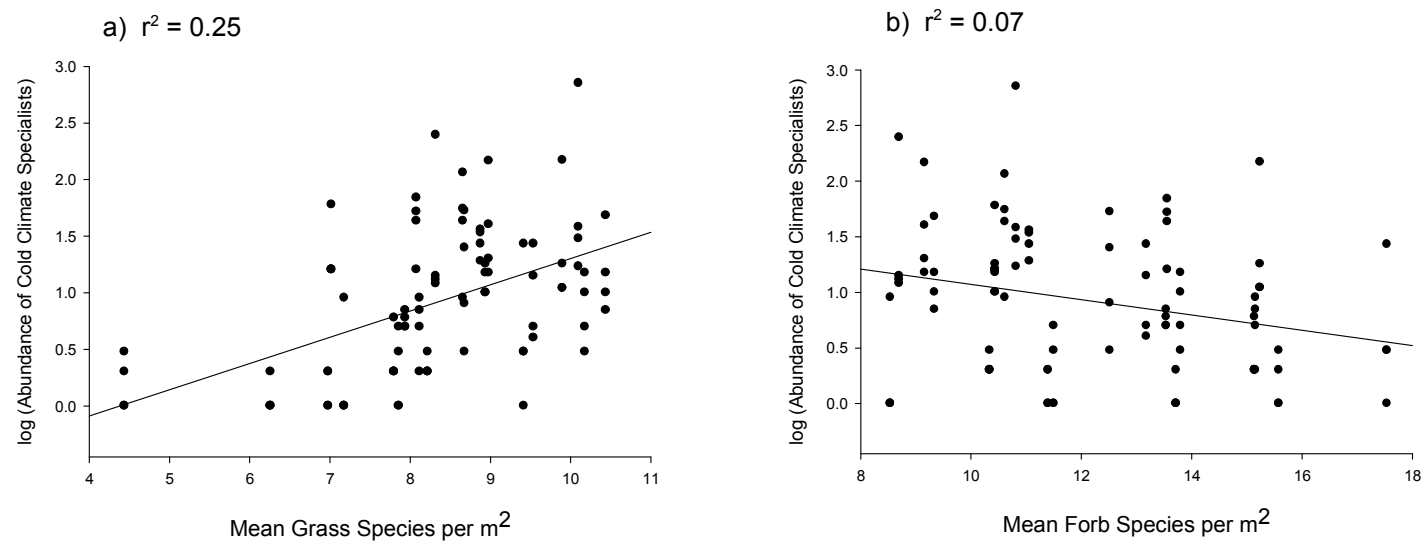


Figure 9. Plot of the log abundance of Cold Climate Specialists vs. (a) the mean grass species richness per m<sup>2</sup> and (b) the mean forb species richness per m<sup>2</sup>. Grasses have a positive correlation while forbs have a negative correlation.

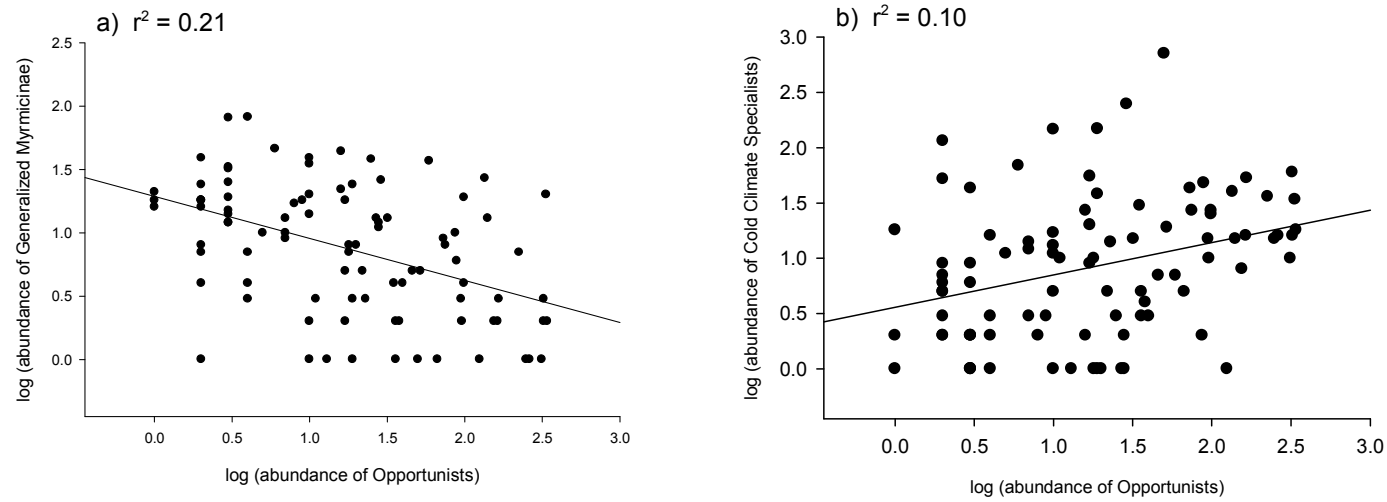


Figure 10. Plot of the log abundance of (a) Generalized Myrmicinae vs. Opportunists and (b) Cold Climate Specialists vs. Opportunists. Opportunists have a negative correlation with the more aggressive Generalized Myrmicinae, but a positive correlation with Cold Climate Specialists.

Table 1. Models used for analyses of Shannon diversity, abundance, species richness, or presence. “Month” was included as a fixed factor and “siteyear” as a random factor in all models (not shown below).

Models	Type
<b>Combination</b> forbs + grasses density+litter haymeadow + pasture + crop + CRPgrass + trees	floral composition vegetation structure landscape composition
<b>Single Variable</b> haying clayloam forbs grasses density litter haymeadow pasture crop CRPgrass trees	management soil texture floral composition floral composition vegetation structure vegetation structure landscape composition landscape composition landscape composition landscape composition landscape composition
<b>Other</b> all factors no factors	global model null model

forbs = mean number of forb species/m<sup>2</sup>

grasses = mean number of grass species/m<sup>2</sup>

density = Robel pole readings of vegetation density

litter = average depth of lying litter

haymeadow = % haymeadow within 250m of center pitfall trap

pasture = % cattle pasture within 250m of center pitfall trap

crop = % cropland within 250m of center pitfall trap

CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center pitfall

Trees = % trees within 250m of center pitfall trap

haying = average annual haying day

clayloam = % of site covered in clay loam soil

Global model = all covariates

Table 2. Number of each ant species collected in June and July of 2010 and 2011 on 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.

Species	2010		2011		Total
	June	July	June	July	
<i>Myrmica americana</i>	706	649	295	615	2265
<i>Lasius neoniger</i>	363	247	150	1487	2247
<i>Tapinoma sessile</i>	173	572	227	897	1851
<i>Crematogaster lineolata</i>	75	124	86	341	626
<i>Solenopsis molesta</i>	121	154	117	190	482
<i>Monomorium minimum</i>	121	116	157	83	477
<i>Formica incerta</i>	32	52	73	144	301
<i>Forelius pruinosus</i>	8	43	73	63	187
<i>Leptothorax pergandei</i>	20	44	38	66	168
<i>Formica pallidefulva</i>	30	21	29	80	160
<i>Formica dolosa (schaufussi)</i>	2	12	24	50	88
<i>Formica argentea</i>	20	19	13	32	84
<i>Nylanderia (Paratrechina) parvula</i>	15	16	14	24	69
<i>Crematogaster cerasi</i>	15	34	2	3	54
<i>Aphaenogaster rudis</i>	2	3	21	18	44
<i>Myrmecina americana</i>	4	0	4	10	18
<i>Tetramorium caespitum</i>	0	8	2	3	13
<i>Camponotus americanus</i>	1	2	3	3	9
<i>Leptothorax ambiguus</i>	2	1	1	2	6
<i>Camponotus castaneus</i>	1	2	0	2	5
<i>Camponotus pennsylvanicus</i>	0	1	3	0	4
<i>Dorymyrmex insanus</i>	0	2	0	2	4
<i>Formica rubicunda</i>	0	2	0	1	3
<i>Ponera pennsylvanica</i>	0	1	0	1	2
<i>Acanthomyops interjectus</i>	1	0	0	0	1
<i>Formica difficilis</i>	0	1	0	0	1
<i>Nylanderia (Paratrechina) faisonensis</i>	1	0	0	0	1
<i>Pheidole pilifera</i>	0	1	0	0	1

Table 3. Ant functional group abundance for every sampling event at each of 23 tallgrass prairie haymeadows in the Southeast Prairies BUL.

Site	Opportunists					Cold Climate Specialists					Generalized Myrmicinae			
	2010		2011			2010		2011			2010		2011	
	June	July	June	July		June	July	June	July		June	July	June	July
BA	27	24	15	86		1	2	1	1		11	37	21	9
BE	9	18	34	49		16	37	29	708		0	0	3	0
C	10	45	31	88		9	6	14	47		2	4	12	5
CA	0	4	9	18		17	10	10	147		20	9	38	23
CB	340	248	95	313		17	14	9	9		1	0	1	0
CC	2	0	1	6		0	0	1	2		24	17	17	8
CL	72	16	2	1		42	54	8	114		8	1	12	23
EN	2	0	1	1		1	1	1	5		14	15	15	38
ES	37	66	22	74		3	4	13	26		1	0	2	7
G	322	323	163	261		59	15	15	15		1	2	1	0
HBE	9	6	6	28		12	13	11	246		13	9	12	25
HBW	9	2	2	3		0	1	0	0		34	80	32	81
HE	3	1	21	58		1	8	4	6		6	7	4	36
HI	1	2	3	5		51	42	15	68		3	11	2	45
HO	35	98	154	165		2	24	7	52		0	3	1	2
KN	12	39	9	124		0	2	4	0		0	3	1	0
KS	3	8	18	15		2	2	0	26		3	17	2	43
M	9	94	16	134		145	14	19	39		19	2	17	26
P	2	1	1	1		5	4	4	6		12	17	6	17
R	19	16	17	27		0	8	0	0		7	4	7	10
S	2	7	2	26		0	1	1	0		18	16	31	12
WA	1	35	17	140		2	4	9	14		0	1	6	12
WE	98	334	51	224		26	33	18	35		18	20	4	6



Site	Cryptic Species					Dominant Dolichoderinae					Subordinate Camponotini			
	2010		2011			2010		2011			2010		2011	
	June	July	June	July		June	July	June	July		June	July	June	July
BA	1	4	3	0		0	1	35	3		0	0	2	0
BE	5	1	5	2		0	0	0	2		0	0	0	0
C	1	2	3	3		0	0	0	1		0	0	0	0
CA	10	3	8	6		0	0	0	0		0	0	0	0
CB	5	6	3	2		0	0	0	0		0	0	0	0
CC	10	14	3	3		0	1	0	1		0	0	0	0
CL	8	21	4	0		0	0	0	0		0	0	0	0
EN	0	0	7	5		0	6	7	20		0	0	0	0
ES	1	7	3	3		0	0	0	5		0	0	0	0
G	10	1	0	0		0	0	0	0		0	0	0	0
HBE	1	3	3	0		0	5	3	2		0	0	0	0
HBW	6	11	2	20		7	1	0	1		0	2	1	0
HE	9	13	15	3		0	0	0	2		0	0	0	0
HI	31	20	7	4		0	0	0	0		0	0	0	0
HO	2	2	1	3		0	0	0	0		0	0	0	0
KN	1	6	4	2		0	0	0	0		0	0	1	0
KS	9	12	7	1		0	3	5	6		0	2	2	4
M	2	14	10	8		0	0	0	0		1	2	0	0
P	5	2	3	3		0	3	5	11		0	0	0	0
R	4	7	12	8		1	21	17	6		0	0	0	0
S	0	1	2	2		0	1	1	0		0	0	0	0
WA	2	2	2	0		0	1	0	2		0	0	0	0
WE	3	2	10	6		0	0	0	1		1	0	0	1

Table 4. Taxa of the Formicidae with their abundance and the functional group to which they belong (Andersen 1997).

Subfamily	Genus	Species	Total Abundance	Functional Group
Dolichoderinae	<i>Forelius</i>	<i>Forelius pruinosus</i> (Roger)	187	Dominant Dolichoderinae
	<i>Dorymyrmex</i>	<i>Dorymyrmex insanus</i> (Buckley)	4	Opportunist
	<i>Tapinoma</i>	<i>Tapinoma sessile</i> (Say)	1851	Opportunist
Formicinae	<i>Camponotus</i>	<i>Camponotus americanus</i> Mayr	9	Subordinate Camponotini
		<i>Camponotus castaneus</i> (Latreille)	5	Subordinate Camponotini
		<i>Camponotus pennsylvanicus</i> (De Geer)	4	Subordinate Camponotini
	<i>Formica</i>	<i>Formica argentea</i> Wheeler	84	Opportunist
		<i>Formica difficilis</i> Emery	1	Cold Climate Specialist
		<i>Formica dolosa (schaufussi)</i> Wheeler	88	Opportunist
		<i>Formica incerta</i> Emery	301	Opportunist
		<i>Formica pallidefulva</i> Latreille	160	Opportunist
		<i>Formica rubicunda</i> Emery	3	Cold Climate Specialist
	<i>Lasius</i>	<i>Lasius neoniger</i> Emery	2247	Cold Climate Specialist
	<i>Acanthomyops</i>	<i>Acanthomyops interjectus</i> (Mayr)	1	Cryptic Species
	<i>Nylanderia (Paratrechina)</i>	<i>Nylanderia faisonensis</i> (Forel)	1	Opportunist
		<i>Nylanderia parvula</i> (Mayr)	69	Opportunist
Myrmicinae	<i>Aphaenogaster</i>	<i>Aphaenogaster rudis</i> (Enzmann)	44	Opportunist
	<i>Crematogaster</i>	<i>Crematogaster cerasi</i> (Fitch)	54	Generalized Myrmicinae
		<i>Crematogaster lineolata</i> (Say)	626	Generalized Myrmicinae
	<i>Leptothorax (Temnothorax)</i>	<i>Leptothorax ambiguus</i> Emery	6	Cold Climate Specialist
		<i>Leptothorax pergandei</i> Emery	168	

Myrmicinae cont'd.				
	<i>Monomorium</i>	<i>Monomorium minimum</i> (Buckley)	477	Generalized Myrmicinae
	<i>Myrmecina</i>	<i>Myrmecina americana</i> Emery	18	Cold Climate Specialist
	<i>Myrmica</i>	<i>Myrmica Americana</i> Weber	2265	Opportunist
	<i>Pheidole</i>	<i>Pheidole pilifera pilifera</i> (Roger)	1	Generalized Myrmicinae
	<i>Solenopsis</i>	<i>Solenopsis molesta molesta</i> (Say)	482	Cryptic Species
	<i>Tetramorium</i>	<i>Tetramorium caespitum</i> (Linnaeus)	13	Opportunist
Ponerinae	<i>Ponera</i>	<i>Ponera pennsylvanica</i> (Buckley)	2	Generalized Myrmicinae

Table 5. Results of model selection for functional groups of ants. Opportunists, Cold Climate Specialists, Generalized Myrmicinae, and Cryptic Species use linear mixed models to predict abundance. Dominant Dolichoderinae and Subordinate Camponotini use a generalized linear mixed model with a binomial distribution to predict presence. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
Opportunists				
Global model	14	137.32	0.00	0.87
<i>forbs<sup>e</sup></i> + <i>grasses<sup>f</sup></i> + <i>month<sup>g</sup></i> + <i>siteyear<sup>h</sup></i>	5	141.80	4.49	0.09
Cold Climate Specialists				
<i>forbs</i> + <i>grasses</i> + <i>month</i> + <i>siteyear</i>	5	138.33	0.00	0.63
<i>grasses</i> + <i>month</i> + <i>siteyear</i>	4	139.75	1.42	0.31
Generalized Myrmicinae				
Global model	14	103.98	0.00	0.97
Cryptic Species				
Null model	2	64.00	0.00	0.23
Dominant Dolichoderinae				
CRPgrass <sup>j</sup> + <i>month</i> + <i>siteyear</i>	4	101.62	0.00	0.72
<i>haymeadow<sup>k</sup></i> + <i>pasture<sup>l</sup></i> + <i>crop<sup>m</sup></i> + CRPgrass + <i>trees<sup>n</sup></i> + <i>month</i> + <i>siteyear</i>	8	105.18	3.56	0.12
Subordinate Camponotini				
Global Model	14	62.36	0.00	0.54
Null model	2	64.66	2.30	0.17

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-h</sup> *forbs* = mean number of forb species/m<sup>2</sup>; *grasses* = mean number of grass species/m<sup>2</sup>; *month* = month sampled (June or July); *siteyear* = the site and year sampled

<sup>j-n</sup> CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center trap; haymeadow = % haymeadow within 250m of center trap; pasture = % cattle pasture within 250m of center trap; trees = % of landscape covered by trees within 250m of center trap

Table 6. Estimates of parameters affecting abundance of ant functional groups. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Opportunists				
Grasses	0.0217	0.0794	-0.1339	0.1773
Forbs	-0.2006	0.0418	-0.2825	-0.1187
Density	0.0812	0.0912	-0.0975	0.2598
Litter	0.0077	0.0302	-0.0516	0.0670
Clay Loam	0.0120	0.0026	0.0069	0.0172
Haying	-0.0010	0.0045	-0.0098	0.0077
Haymeadow	0.0767	0.0377	0.0028	0.1506
Pasture	0.0750	0.0396	-0.0250	0.1526
Crop	0.0701	0.0389	-0.0062	0.1463
CRP Grass	0.0714	0.0410	-0.0089	0.1518
Trees	0.0667	0.0381	-0.0079	0.1412
Month (June)	-0.2450	0.0844	-0.4104	-0.0797
Cold Climate Specialists				
Grasses	0.2242	0.0502	0.1259	0.3225
Forbs	-0.0540	0.0276	-0.1081	0.0001
Month (June)	-0.2569	0.0748	-0.4035	-0.1103
Intercept	-0.3826	0.6359	-1.6288	0.8637
Generalized Myrmicinae				
Grasses	-0.0316	0.0504	-0.1304	0.0672
Forbs	0.1044	0.0221	0.0612	0.1477
Density	0.0046	0.0739	-0.1401	0.1494
Litter	0.0141	0.0264	-0.0375	0.0658
Clay Loam	-0.0054	0.0018	-0.0090	-0.0018
Haying	-0.0075	0.0032	-0.0138	-0.0012
Haymeadow	-0.0599	0.0262	-0.1113	-0.0085
Pasture	-0.0668	0.0275	-0.1207	-0.0129
Crop	-0.0527	0.0271	-0.1057	0.0004
CRP Grass	-0.0533	0.0285	-0.1092	0.0026
Trees	-0.0579	0.0265	-0.1098	-0.0061

Table 6 continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Month (June)	-0.1058	0.0787	-0.2601	0.0485
Intercept	6.0903	2.8165	0.5701	11.6106
Cryptic Species				
Grasses	-0.0210	0.0370	-0.0935	0.0514
Forbs	0.0279	0.0180	-0.0074	0.0631
Density	0.0262	0.0627	-0.0966	0.1491
Litter	0.0227	0.0204	-0.0172	0.0627
Clay Loam	0.0009	0.0013	-0.0034	0.0016
Haying	0.0007	0.0025	-0.0043	0.0057
Haymeadow	0.0268	0.0313	-0.0346	0.0883
Pasture	0.0281	0.0336	-0.0378	0.0941
Crop	0.0316	0.0320	-0.0311	0.0943
CRP Grass	0.0200	0.0286	-0.0360	0.0761
Trees	0.0320	0.0320	-0.0306	0.0947
Month (June)	0.0407	0.0552	-0.0675	0.1488
Intercept	0.3348	1.2587	-2.1322	2.8018
Dominant Dolichoderinae				
CRP Grass	0.0622	0.0887	-0.1116	0.2360
Haymeadow	-0.1203	0.1776	-0.4684	0.2279
Pasture	-0.1029	0.1909	-0.4771	0.2712
Crop	-0.0833	0.1830	-0.4419	0.2753
Trees	-0.1474	0.1807	-0.5015	0.2068
Month (June)	-2.4422	0.6527	-3.7214	-1.1630
Intercept	0.9617	7.8392	-14.4029	16.3263
CRP Grass	0.0622	0.0887	-0.1116	0.2360
Haymeadow	-0.1203	0.1776	-0.4684	0.2279
Pasture	-0.1029	0.1909	-0.4771	0.2712
Crop	-0.0833	0.1830	-0.4419	0.2753
Trees	-0.1474	0.1807	-0.5015	0.2068
Month (June)	-2.4422	0.6527	-3.7214	-1.1630
Intercept	0.9617	7.8392	-14.4029	16.3263

**Chapter 4: DIVERSITY AND ABUNDANCE OF GROUND BEETLES  
(COLEOPTERA: CARABIDAE) IN REMNANT TALLGRASS PRAIRIE  
HAYMEADOWS**

*Abstract:*

I investigated ground beetle composition in twenty-three tallgrass prairie remnants in southeast Nebraska to obtain baseline data on a functionally important insect group and determine what environmental and management factors influence its diversity and abundance. In 2010 and 2011, nineteen species were collected with nearly 95% of individuals belonging to one of two species: *Cyclotrachelus sodalis colossus* or *Pasimachus elongatus*. Neither of these species can fly and both do not climb vegetation, factors that may decrease their exposure to predators and increase their abundance at sites. Using multi-model inference, the overall ground beetle community was assessed to determine what factors might be influencing Shannon diversity, abundance, and species richness. Results of model selection indicate the average number of grass species per m<sup>2</sup> positively influences Shannon diversity of ground beetles. Tallgrass sites with higher grass species richness may therefore be the priority for conservation of ground beetle biodiversity. Model selection was also performed on subsets of ground beetles based on their flying, climbing, burrowing, and running ability. Strong burrowers and moderate runners were more abundant in sites with higher vegetation density and less litter. With a positive correlation, the top model for climbing ground beetles involved the amount of haymeadow within 250 meters.

## INTRODUCTION

Ground beetles (Coleoptera: Carabidae) are one of the most numerous, diverse and ecologically important groups of surface-dwelling insects (Harris and Whitcomb 1974). Though some herbivorous species exist (Thiele 1977), the majority are primarily predatory (Toft and Bilde 2002) consuming a variable diet that includes many agricultural pests such as aphids, lepidopteran caterpillars, slugs, and the eggs and larvae of dipterans and coleopterans (Holland and Luff 2000). In agroecosystems they are among the most diverse and beneficial arthropods (Holland and Luff 2000).

Due to their cost-effective collection methods, sensitivity to environmental factors, and wide habitat requirements, ground beetles have served as bioindicators of habitat alteration and classification (Rainio and Niemela 2003). The presence or lack of specialist species may indicate the disturbance of a particular habitat (Rainio and Niemela 2003). In a comparison of northeastern Iowa habitats, Larsen (2003) found that tallgrass prairie remnants contained not only the highest species richness of ground beetles, but the majority of specialists as well. These results highlight the importance of properly managing and maintaining remnant tallgrass prairies in order to maintain the biodiversity of ecologically important insects that depend on them.

In Nebraska, where the historic extent of the tallgrass prairie has been reduced by 98% (Samson and Knopf 1994), the Southeast Prairies Biologically Unique Landscape (BUL) has been identified as an area for priority conservation (Schneider et al. 2006). The landscape of the Southeast Prairies BUL was once contiguous tallgrass prairie, but is now fragmented into cattle pastures, crops, trees, and haymeadows. The majority of remaining historic biodiversity is contained within those remnants serving as



haymeadows. Understanding what landscape, habitat, and management factors affect the ecology of these prairie fragments is necessary for conserving what remains.

Although ground beetles have been the subject of many studies, the vast majority of these studies have been conducted in Western Europe (Casale 1990, Lövei and Sunderland 1996, Eyre et al. 2003, Jeanneret et al. 2003, Rainio and Niemelä 2003). Of the relatively few North American studies that exist, much of the focus has been on their effectiveness as biocontrol agents in agricultural crops (e.g., Varchola and Dunn 1999). To further the limited knowledge of ground beetles in North American grasslands, this study aims to provide a general account of ground beetle composition in remnant tallgrass prairies, determine how ground beetle physiology might be influencing this composition, and assess what environmental and management factors predict their diversity and abundance.

## **METHODS AND MATERIALS**

### **STUDY SITES**

The study area was the Southeast Prairies BUL, which consists of Pawnee County and portions of Richardson, Johnson, and Gage Counties in southeast Nebraska (Fig. 1). The landscape is dominated by cattle pasture, but the area contains considerable amounts of cropland, trees, and other types of grassland. The study sites were 23 privately-owned, annually-hayed haymeadows (Fig. 2). None of these sites have ever been plowed and consequently retain much of the native tallgrass biodiversity. Although management is similar at all sites, some are hayed early in the summer (mid-July) while others are hayed late (late September).

Study sites were identified by searching the Southeast Prairies BUL for grassland fragments that had never been farmed (i.e., lacked terraces), that possessed key tallgrass species easily identifiable from the road (e.g., compass plant (*Silphium aconitum*) and wild alfalfa (*Psoralea tenuiflora*)), and had high, apparent plant diversity. The edges of the fragments were closely correlated with the edges of annual mowing, often adjacent to treelines, roads, crops, or cattle pastures. Sites varied in size from approximately 1.75 to 26.9 ha.

## STUDY DESIGN

### *Pitfall Trap Sampling*

Pitfall traps are the most common and convenient way to sample for ground-dwelling invertebrates in spite of noted biases (Thomas and Sleeper 1977, Topping and Sunderland 1992). Pitfall traps sample 24 hours a day, collecting both diurnal and nocturnal species, and do not select for rare or against common species (Esau and Peters 1975). This study used a 3 x 3 grid of traps spaced 25 meters apart (Fig. 3). The center of this grid was haphazardly chosen near the center of each fragment; the remaining traps were arranged in transects that coincided with the cardinal directions (Fig. 3). Grid placement was kept primarily to upland areas at all sites, avoiding lowlands where the vegetation may change dramatically.

The pitfall traps consisted of test tubes in conduit pipe sleeves (New 1998). The 6 in. long, 3/4 in. diameter PVC pipes were placed in the ground where they remained throughout the duration of each summer, corked to prevent debris or insects from falling in. Each trap was recorded with GPS and marked with flagging tape on nearby

vegetation. Keeping pipe sleeves in the ground allowed for repeated sampling at the same location. PVC sleeves were inserted at least a week before sampling, allowing time for the disturbed soil around the trap to recover (New 1998).

Sampling was conducted by placing test tubes containing propylene glycol (antifreeze) in the PVC pipe sleeves. Propylene glycol was chosen over ethylene glycol because it captures as efficiently but is less toxic to non-target wildlife (Weeks and McIntyre 1996). Tubes were filled halfway to give leeway in the event of precipitation and displacement of the liquid by insects. Traps were placed in the ground at all sites on the same day to minimize differences in collection due to changes in weather rather than site characteristics. Traps were left in the ground for 72 hours, a time observed in a pilot study to collect insects without getting so many that some traps fill entirely. Sampling occurred in early June and early July of both 2010 and 2011. Because some managers begin cutting sites for hay in mid-July, early July was the latest sampling could safely occur without risk of being mowed over and lost.

### *Sample Processing*

Collected samples were poured through a fine mesh strainer to filter them from the propylene glycol and dirt particles. They were then rinsed with 70% ethyl alcohol to remove all remaining propylene glycol. Ground beetles were separated from leaves, twigs, and other arthropods and placed in a vial of 70% ethyl alcohol labeled with the collection date, site, and sample numbers. All adult ground beetles were eventually pinned with the exception of two morphotypes. These morphotypes each had well over a thousand individuals, thus only a representative sample of 20 each was pinned from

various sites, months, and years. Samples were shipped to Foster Purrington (Ohio State University - Department of Evolution and Ecology) who identified the specimens to species. Of the two representative morphotype samples, each was identified to a single species (*Cyclotrachelus sodalis colossus* and *Pasimachus elongatus*). All other individuals of each morphotype were assumed to be the same corresponding species.

### *Habitat Characteristics*

When compared to other types of habitat in the Southeast Prairies BUL, the haymeadows in this study are strikingly similar to one another; when compared to each other, however, their habitat characteristics vary widely. The floral composition, vegetation structure, litter depth, and type of soil are all factors that may directly or indirectly influence the species composition and abundance of ground beetles at each site. Thus it was critical to gather data on those habitat characteristics which previous studies have implicated in affecting ground beetles.

Data on the floral composition was gathered at 50 sampling locations along transects arranged to cover the breadth of each site. At each location a one square meter quadrat was placed on the ground and all plant species within it were identified. By averaging the 50 samples together, mean estimates of grass and forb species richness (i.e., total number of species) per square meter were obtained. Floral composition data collection began in 2009 and was completed in 2010. Five sites were sampled both years to confirm that plant composition remained relatively consistent from year to year (see Appendix A: Fig. 1).

The structure of vegetation includes the density (above-ground biomass), the vertical structure/heterogeneity, and the amount of lying litter. These factors are important in that they may change shade and moisture levels at the ground's surface. Habitat structural data was gathered using a Robel pole (Robel et al. 1970) at twelve locations in each site. The locations were kept local to the pitfall trap sampling area by spacing them halfway between the traps, and 12.5 m to the east and west of the outer traps (Fig. 3). Vegetation sampling was conducted following each pitfall collection round and completed for all sites within a week to avoid temporal changes in vegetation.

The Robel pole was read from each of the cardinal directions and values averaged to give a relative estimate of vegetation density for each site. During June, litter depth to the nearest half centimeter was also measured at each reading of the Robel pole. To estimate vertical structure, the height of every plant touching the Robel pole was recorded. This data was analyzed using a Shannon diversity index for an estimate of vertical heterogeneity. This estimate was highly correlated ( $r^2=0.62$ ,  $p<0.001$ ) with the vegetation density, however, and subsequently eliminated from the analysis.

Soil texture (i.e., particle size) can influence the ability of ground beetles to burrow, oviposit, and survive the winter (Holland and Luff 2000). The Web Soil Survey (2012) was used to determine the percentage of each site covered by loam, clay loam, silty loam, and silty clay loam. These soil classes are similar and in some cases highly correlated. Because clay loam was present to varying degrees at almost every site, percentage of clay loam was the only soil factor used in this analysis. The term loam refers to soil composed of relatively equal parts clay (small particles), silt (medium particles) and sand (large particles). Clay loam consists of all three particle types but has

a greater proportion of clay than the other two. (See the tables in Appendix A for additional habitat data.)

### *Landscape Characteristics*

Fragmentation has resulted in very abrupt transitions from prairie to other habitats. These other habitats may influence ground beetle composition by affecting the connectivity of the fragments, by subsidizing ground beetles with additional resources, or by harming them with additional predators. Landscape composition around the study sites was determined by digitizing the surrounding landscape in a Geographic Information System (GIS). Each polygon of the digitized landscape was classified as cattle pasture, haymeadow, trees, cropland, or CRP grass. An “other” classification was used for areas that did not fit these major categories. Individual ground beetles have been observed to travel with directed movement as much as 87 m in a day (Baars 1979). A 250 m radius buffer was used in GIS around the center pitfall trap for each site; the proportion of each landscape type within the buffer was calculated. Although size and interior to perimeter ratio are relevant landscape factors, they were not considered in this study because of their close correlation with the percentage of haymeadow ( $r^2=0.76$  and  $0.78$  respectively). (See Appendix A for landscape data tables.)

### *Management*

Although over-seeding of sites and planting of treelines occur occasionally, the predominant management tool is haying. The study sites are cut for hay annually, but the time of haying varies between mid-July and late September. This difference in haying

time can affect vegetation composition and structure over time. If plants are mowed before they have the chance to produce viable seed it will limit their reproduction, potentially eliminating populations from sites hayed early. Vegetation structure may be altered when perennials are mowed annually at the peak of their aboveground production, weakening them over time and decreasing height and biomass.

The time a given site is hayed each year varies based mostly on weather, but remains relatively consistent with each manager (i.e., within two to three weeks). Owners who want to maximize the quality of the hay generally cut early while owners who want to maximize production cut late (Kent Pfeiffer, personal communication). Sites were monitored and haying dates recorded. To quantify haying time, a value was assigned to each day starting in mid-July (i.e., July 15=1, July 16=2, etc.) and the average value was taken between 2010 and 2011 for each site (see Appendix A: Table 5). Larger values correspond with later average haying time.

## STATISTICAL ANALYSIS

### *Physiological Functional Groups*

The ground beetle species in a given ecosystem vary in their functions and requirements. Categorizing ground beetles into relevant functional groups aids in predicting their response to various environmental factors. Larochelle and Lariviere (2003) present the most complete ecological descriptions of individual North American species. Using these descriptions, species were categorized by physiological functions that may influence their diversity or abundance within individual fragments and in the greater ecosystem. Categories were based on flying, climbing, burrowing, and running

ability. They include: beetles capable or incapable of flight; occasional, regular, frequent, or non-climbers of vegetation; strong or regular burrowers; and slow, moderate, or fast runners.

### *Diversity and Abundance*

Diversity was assessed using two methods: the Shannon diversity index and species richness. The Shannon diversity index (diversity) is a commonly used method to characterize species diversity in a community. It accounts for both the number of species and their corresponding abundances to give a measure that reflects evenness. Because some ecosystems may contain certain species that naturally have low or high populations, lower diversity may not necessarily indicate a less natural state for that community. To obtain the most complete picture, it is important to consider species richness and abundance in addition to Shannon diversity. In the case of this study, species richness (richness) is the total number of ground beetle species collected at a site during a sampling event. Abundance values were obtained at each site by summing the total number of ground beetles collected in all nine pitfall traps.

### *Multi-Model Inference*

When ecological studies contain several likely predictors acting in multiple combinations it is useful to employ information-theoretical model selection. This approach weighs evidence among multiple competing hypotheses. This study was limited to a suite of 16 *a priori* models with covariates corresponding to the landscape, habitat, and management data collected for each fragment. The candidate models include a



landscape model, a plant composition model, a habitat structure model, a soil model, and a management model. Additionally, a null model (no effects) and a global model (all variables) were included along with models that measure each explanatory variable independently (Table 1). Using Program R (R Development Core Team 2012), Akaike's Information Criterion adjusted for small sample size (AICc) was calculated to rank the candidate models. From the AICc values, Akaike weights ( $w_i$ ) were calculated to determine the most parsimonious models (i.e., the best fits for the empirical data) (Anderson et al. 2000). The confidence set includes any model with an Akaike weight within 10% of the highest ranked model; this is comparable to the minimum cutoff point suggested by Royall (1997).

To normalize the data, the abundance data was log-transformed for use as the response variable. For abundance and diversity, the models were analyzed as linear mixed models; for species richness, the models were analyzed as generalized linear mixed models with a Poisson distribution. Logistic regression was used for presence/absence data (i.e., generalized linear mixed model with a binomial response distribution). Site and year sampled were combined into a single "site-year" variable and included as a random factor in all models; all other variables were fixed. Because the month sampled had a large impact on the response variables, it was included in every model to negate its effect and allow the environmental and management factors to drive the model selection.

## RESULTS

A total of 3,957 adult ground beetles were collected during the study representing 7 tribes, 12 genera, and 19 species (Tables 2 and 3). This included 1,977 individuals and 16 species in 2010 and 1,980 individuals and 15 species in 2011. The collection was dominated by two highly abundant species: *Cyclotrachelus sodalis colossus* with 1,964 individuals (49.6% of collection); and *Pasimachus elongatus* with 1,788 individuals (45.2% of collection). The total number of ground beetles collected at a single site ranged from 38 (HBW) to 391 (CB) (Fig. 4). The fewest species collected at a site in a given year was 2 (BE and HBE, 2010) and the most was 8 (CB, 2011). The number of ground beetles collected at a given site was relatively consistent between 2010 and 2011 (Fig. 5). These results may not be all-inclusive because of the temporal restriction of sampling due to sites being mowed for hay. Some species may be excluded that are present or even abundant in these sites, but are not active at this time. For instance, autumn breeding species may exist in the soil as larvae or pupae during the June and July sampling periods, but may be active as adults during August and September when no sampling occurred.

### *Functional Groups*

Concerning physiological functions, most species could fly, but the majority of captured individuals could not (Fig. 6). Fifteen of the 19 species were capable and probable fliers; one species (*Cratacanthus dubius*) was dimorphic (i.e., contains individuals capable and incapable of flight). Only one individual from *C. dubius* was captured in this study and it did not possess fused elytra; therefore it was therefore

counted among the capable fliers. Although the majority of species were capable of flight, they comprised a mere 4.3% (171 individuals) of the total ground beetles captured. Only three species (*Pasimachus elongatus*, *Cyclotrachelus sodalis colossus*, and *Chlaenius platyderus*) were incapable of flight, but consisted of 95.7% of the total abundance (3,784 individuals).

Of the 10 species capable of climbing, 3 were frequent climbers, 5 occasional climbers, and 2 regular climbers. Although 9 species were not considered climbers, they comprised 98.3% (3,902 individuals) of the total collection.

Strong burrowers versus regular burrowers are comparatively more even in their proportion of species and individuals. Nine species consisting of 44.3% (1,948 individuals) were strong burrowers and 10 species consisting of 55.7% (2,445 individuals) were not.

Beetles were categorized based on running ability as fast, moderate, or slow. Three species were fast, 12 moderate, and 4 slow. Concerning their abundance, the 3 fast species comprised 1.1% (44 individuals); the 12 moderate species comprised 52.8% (2,088 individuals), and the 4 slow species comprised 46.1% (1,826 individuals).

## MULTI-MODEL INFERENCE

### *Diversity and Abundance*

Of the 16 candidate models considered, two models were selected as the confidence set. With an Akaike weight of 64%, the most supported model predicting Shannon diversity contains the factor of mean grass species per m<sup>2</sup> (Table 4). With 23% of the weight, the second model, which includes the average number of forb and grass

species per m<sup>2</sup>, has the first model nested within it. The grass variable may therefore be driving selection of the second model as well as the top model; however, the large AICc penalty associated with having an additional parameter in the second model makes it unclear if this is the case. In both cases, the mean number of grass species per m<sup>2</sup> at a site has a positive correlation with Shannon diversity.

The model selection results for the abundance of ground beetles are much more ambiguous (Table 4). Twelve models are in the confidence set, led by the model containing mean forb species richness per m<sup>2</sup> (negative correlation). The second model, which involves litter depth, also shows a negative correlation. The next 10 models possess weights ranging between 3% and 8% and involve more habitat, landscape, and management factors (Table 4). Model-averaged estimates of the parameters in the confidence set indicate that forbs are having a negative effect at the 95% confidence level (Table 5).

For species richness of ground beetles, two models were selected. The model containing the percentage of landscape within 250 meters covered by CRP and other low diversity grassland was the strongest predictor, with a negative correlation (Table 4). The second model was the null model.

#### *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus*

Because they were numerically dominant, *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus* were analyzed individually to investigate what factors might be affecting their abundance. Model selection results for *C. sodalis colossus* indicate that, with 38% of the weight, the model showing a positive correlation with vegetation density

is the strongest (Table 6). The global model and the vegetation structural model are the next two models, both of which have the first model nested within them. The final model in the confidence set involves the landscape model containing only trees, with a negative correlation.

*P. elongatus* abundance is best predicted ( $w_i=58\%$ ) by the model containing all landscape composition factors (Table 6). The second model contains only the percentage of haymeadow within 250 m, a positive correlation. The final model in the confidence set contains only the percentage of the landscape covered by trees within 250 m, a negative correlation. Model-averaged estimates of these landscape parameters show the amount of cropland and pasture with 250 m<sup>2</sup> both have a positive effect on *P. elongatus* abundance (Table 7).

### *Fliers*

Model selection was conducted for predicting abundance of the various functional groups. Concerning ground beetles that can fly, the top model, possessing 41% of the Akaike weight, involves the percentage of the landscape within 250 m covered by CRP and other low diversity grassland (Table 8). It has a negative correlation with abundance (Table 9), indicating that with increasing low diversity grassland nearby there are fewer flying ground beetles. The second model, with 10% of the weight, was the null model. *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus* comprised almost all of the non-flying ground beetles. The abundance of these two species was analyzed separately in the previous section.

### *Climbers*

With 73% of the weight, the abundance of climbing ground beetles was best predicted by the percentage of haymeadow within 250 m (positive association) (Table 10 and 11). The second model, with 23% of the weight, is the landscape composition model. Because the first model is nested within the second, it is likely the factor of haymeadow that is driving selection of the second model. As with non-flying ground beetles, most of the non-climbing ground beetles were *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus*, which have been analyzed separately.

### *Strong Burrowers*

The factor influencing strong-burrowing ground beetles was the landscape model involving percentage of haymeadow within 250 m (Table 12). The following two models contain negative associations with mean number of forb species and percentage of trees within 250 m (Table 13).

For ground beetles not considered to be strong burrowers, only two models were selected, both of which involve habitat structure (Table 12). Density of vegetation has a positive correlation while litter depth has a negative correlation.

### *Runners*

The top model for fast-running ground beetles involves the factor of haying (Table 14). Sites hayed later in the year had fewer fast beetles. Ground beetles that were moderate runners are predicted only by two models containing the habitat structure variables vegetation density (positive) and litter depth (negative). Ground beetles classified as slow runners have 5 models in the confidence set. They involve the factors

of landscape composition, floral composition, and soil texture. The strongest predictor was the percentage of haymeadow within 250 m; this has a positive correlation with the number of slow-running ground beetles (Table 15).

## DISCUSSION

Consisting of 94.8% of all captured ground beetles, two species clearly dominate the collection: *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus*. Previous grassland studies of ground beetles indicate that a few species may often comprise the majority of the collection (Dunn 2007), but this extreme appears to be unusual. These two species may possess characteristics that contribute to their success in tallgrass fragments. Of the physiological characteristics considered, these species have two in common: they are incapable of flight and are not climbers. Though with a much smaller abundance, the fourth most common species, *Chlaenius platyderus*, also possesses these same two characteristics. Several other species are not climbers, but these are the only three non-fliers.

It is possible that these species are not more abundant, but instead are more active on the ground and therefore more likely to be captured. Considering they cannot fly and do not climb vegetation, this could logically be part of the explanation. However, such an extreme contrast between the numbers of these two species versus all others supports the conclusion that they are much more abundant. Although other species possess the ability to fly or climb vegetation, most still reside predominantly on the ground's surface; one would therefore expect a greater collection if they had comparable abundances to the top two species.

If *C. sodalis colossus* and *P. elongatus* are in fact far more abundant, a major contributing factor may be their shared inability to fly. When individuals fly they expose themselves to a host of predators, such as birds and bats, potentially reducing their abundance at a site. To a lesser degree, the same may be true of individuals climbing vegetation. *C. sodalis colossus* and *P. elongatus*, both of which are incapable of flight and do not climb, may be better protected from these predators and therefore have higher populations. In this sense, the lack of flight ability may confer an advantage; this would explain why *P. elongatus* has evolved elytra that are completely fused together.

Most individuals captured may be incapable of flight, however, the vast majority of the species (16 of 19) can and likely do fly. Although flying exposes beetles to predators, it can also increase the speed and distance of dispersal. Species may be able to fly to a tallgrass fragment from a variety of habitats, allowing for more of these species in a given fragment. This ability may have also contributed to their persistence over time in a fragmented landscape. Species incapable of flight may dominate the fragments they are in, but may have more trouble dispersing between fragments. This may explain why non-fliers are abundant at sites while fliers are very species rich.

Results of information-theoretical model selection for *C. sodalis colossus* indicate that its abundance is positively influenced by increasing vegetation density. Vegetation may provide increased cover from predators, and is consistent with prior studies of predacious ground beetles (Harvey et al. 2008).

*P. elongatus* results show abundance to be influenced mostly by the landscape composition. Previous research has indicated *P. elongatus* as a potential bioindicator species (Dunn 2007). The abundance of *P. elongatus* has been used successfully to



discriminate between CRP and cattle pasture, with greater abundances in CRP (Dunn 2007). In this study, cattle pasture, cropland, and haymeadow all have positive relationships with *P. elongatus* abundance. Cropland and pasture may be subsidizing ground beetles in the haymeadows with additional prey.

#### *Diversity, Abundance, Species Richness*

The overall Shannon diversity of ground beetles appears to be influenced by plant diversity, in particular the mean number of grass species per m<sup>2</sup>. Previous studies have demonstrated that ground beetle assemblages are affected by plant species richness (Jeanneret et al. 2003). Higher plant species richness offers more diverse habitat structure and more niches for prey that may influence ground beetle diversity. Although the ground beetles in this study function primarily as generalist predators, some of their prey may be more essential than others (Toft and Bilde 2002). Thus, if increases in plant species richness bring more diverse prey, then increases in ground beetle diversity may follow. Plant diversity may also have more direct effects on those omnivorous species consuming seeds and other plant materials in addition to insects.

Although it is not surprising to find that plant diversity characteristics influence ground beetles, the relationship specifically with grasses is intriguing. Previous studies have demonstrated that grass cover significantly influences ground beetle species composition, but grass species diversity is new. Forbs comprise the majority of the prairie's plant diversity while grasses comprise the majority of the biomass. However, the mean number of grass species, which varied at sites from 4.4 to 10.4 species per m<sup>2</sup>, had the greatest influence on ground beetle diversity. Forbs ranged from 8.7 to 17.5 species

per m<sup>2</sup>, but had much less influence. Because of the greater biomass of grasses at these sites, changes in grass species composition may have a more exaggerated effect than changes in forb composition.

Clear differences exist in ground beetle abundance between sites, but none of the considered factors appear to be exceptionally good predictors. Twelve models were in the confidence set with Akaike weights ranging from 3% to 23%. It is possible that many of the factors considered have comparable effects, which leads to the selection of so many models. It is also possible that some other unconsidered factors are strongly influencing abundance such as ground beetle prey or predator abundance.

Species richness of ground beetles appears to primarily be influenced by the amount of low diversity grassland such as CRP in the nearby landscape. Whereas trees, crops, or cattle pasture may have species that spill over, potentially increasing the species diversity of the fragment, the similar habitat of CRP may contain the same species as the haymeadow, or even fewer species because of the lower diversity. Therefore, with more surrounding CRP, there may be fewer species to spill over into the fragment. The top model has only 31% of the weight, while the null model has 11%, and therefore should be interpreted cautiously.

### *Physiological Functional Groups*

The analyses of functional groups indicate that weak-burrowing ground beetles are affected most by habitat structure. They prefer sites with dense vegetation and low amounts of litter, a preference previously observed for predatory ground beetles (Harvey et al. 2008). Whereas strong burrowers may be able to quickly hide beneath the soil, these

other ground beetles may rely on the dense vegetation to hide them from predators. Moderate running ground beetles also prefer high vegetation density and low litter. Less litter leaves the ground surface open for ease of movement and hunting. *C. sodalis colossus*, which comprises a large proportion of weak burrowers and moderate runners, is likely influencing these results more than other species.

Climbing ground beetles benefit from the amount of haymeadow in the nearby landscape. They may prefer haymeadows because of their structural and compositional diversity. There are many more species of plants to climb from which to obtain a greater variety of prey than in neighboring pasture or CRP habitats. Thus with more haymeadow there may be more resources for greater numbers of climbing beetles.

### *Conclusion*

Conserving the ecological community of the tallgrass prairie is primarily dependent on preservation of remaining fragments. Although most conservation-oriented studies focus on plants or vertebrates, there is increasingly more emphasis on incorporating invertebrates and their crucial functions into conservation decisions (Kremen et al. 1993, Oliver and Beattie 1993). To make informed decisions, conservationists need more knowledge about what species are present and how landscape, habitat, and management factors affect their abundance and diversity.

Ground beetles have long been recognized as beneficial insects because of their ecological function as predators. The tallgrass prairie of the Southeast Prairies BUL appears to be dominated numerically by two ground beetle species, *P. elongatus* and *C. sodalis colussus*. Two shared characteristics of these species may contribute to their

success: their inability to fly and climb. Residing on the ground beneath the vegetation may keep them hidden from potential predators. Numerically, the vast majority of ground beetles were incapable of flight; however, most of the species in this study could fly. The increased dispersal ability due to flying may contribute to their species richness in a fragmented landscape.

Plant species richness, particularly the average number of grass species per m<sup>2</sup> at a site, is the best predictor of overall ground beetle diversity. Although the exact cause for correlation remains unclear, this information can be useful in informing conservation decisions. For instance, maximizing grass species in a restoration seed mix may yield the most diverse ground beetle community.

Future studies should investigate the community composition of other types of habitat in the Southeast Prairies BUL. Cattle pasture and CRP, for instance, are different both in their vegetation structure and floral composition. Learning how the abundance of species shifts in these other habitats and whether some species are unique to the tallgrass fragments will be useful in further assessing the importance of these haymeadows in the landscape.

### LITERATURE CITED

- Casale, A. 1990. Carabid communities of aquatic and semi-aquatic environments in North-western Italy: Their role as ecological indicators. Pages 349-352 *in* N.E. Stork, editor. The role of ground beetles in ecological and environmental studies. Intercept Limited, Andover.
- Dunn, S.M. 2007. A comparison of Carabid beetle taxocenes between rangeland and conservation reserve program fields in western Kansas. Unpublished M.S. thesis, Fort Hays State University, Kansas.
- Esau, K.S. and D.C. Peters. 1975. Carabidae collected in pitfall traps in Iowa cornfields, fencerow, and prairies. *Environmental Entomology* **4**:509-513.
- Eyre, M.D., M.L. Luff, J.R. Staley and M.G. Telfer. 2003. The relationship between British ground beetles (Coleoptera, Carabidae) and land cover. *Journal of biogeography* **30**:719-730.
- Harris, D.L. and W.H. Whitcomb. 1974. Effects of fire on populations of certain species of ground beetles (Coleoptera: Carabidae). *The Florida Entomologist* **57**:97-103.
- Harvey, J.A., W.H. van der Putten, H. Turin, R. Wagenaar and T.M. Bezemer. 2008. Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds. *Agriculture, Ecosystems and Environment* **127**:100-106.
- Holland, J.M. and M.L. Luff. 2000. The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrated Pest Management Reviews* **5**:109-129.

- Jeanneret, Ph., B. Schüpbach, and H. Lukab. 2003. Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. *Agriculture, Ecosystems and Environment* **98**:311-320.
- Kremen, C., R.K. Colwell, T.S. Erwin, D.D. Murphy, R.F. Noss and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**:796-808.
- Larochelle, A. and M.-C. Lariviere. 2003. A Natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft Publishers, Bulgaria.
- Larsen, K.J., T.T. Work and F.F. Purrington. 2003. Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia* **47**:288-299.
- Lövei, L.G. and K.D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**: 231-256.
- New, T.R. 1998. Invertebrate surveys for conservation. Oxford University Press, Oxford.
- Oliver, I., and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* **7**:562-568.
- Rainio, J. and J. Niemela. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* **12**:487-506.
- Samson, F.B., and F.L. Knopf. 1994. Prairie conservation in North America. *BioScience* **44**:418-421.
- Samson, F.B., Knopf, F.L. and Ostlie, W.R. 1998. Grasslands. Status and trends of the nation's biological resources. Pages 437-472 in M.J. Mac, P.A. Opler, C.E. Puckett Haecker and P.D. Doran, editors. United States Department of the Interior, United States Geological Survey, Reston.

- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* **32**:6-15.
- The Nature Conservancy. < <http://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/nebraska/howwework/senebmap.pdf>> Accessed 2012 March.
- Thiele, H.U. 1977. Carabid Beetles in their environments: a study on habitat selection by adaptations in physiology and behaviour. Springer-Verlag, New York.
- Toft, S. and T. Bilde. 2002. Carabid diets and food values. Pages 81-110 *in* J.M. Holland, editor. The agroecology of carabid beetles. Intercept Limited, Hampshire, UK.
- Varchola, J.M. and J.P. Dunn. 1999. Changes in ground beetle (Coleoptera: Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation. *Agriculture, Ecosystems and Environment* **73**:41-49.

## TABLES AND FIGURES



Figure 1. Map showing the Biologically Unique Landscapes of southeast Nebraska (The Nature Conservancy 2012), including the Southeast Prairies BUL which includes most of Pawnee as well as portions of Johnson, Richardson, and Gage counties.



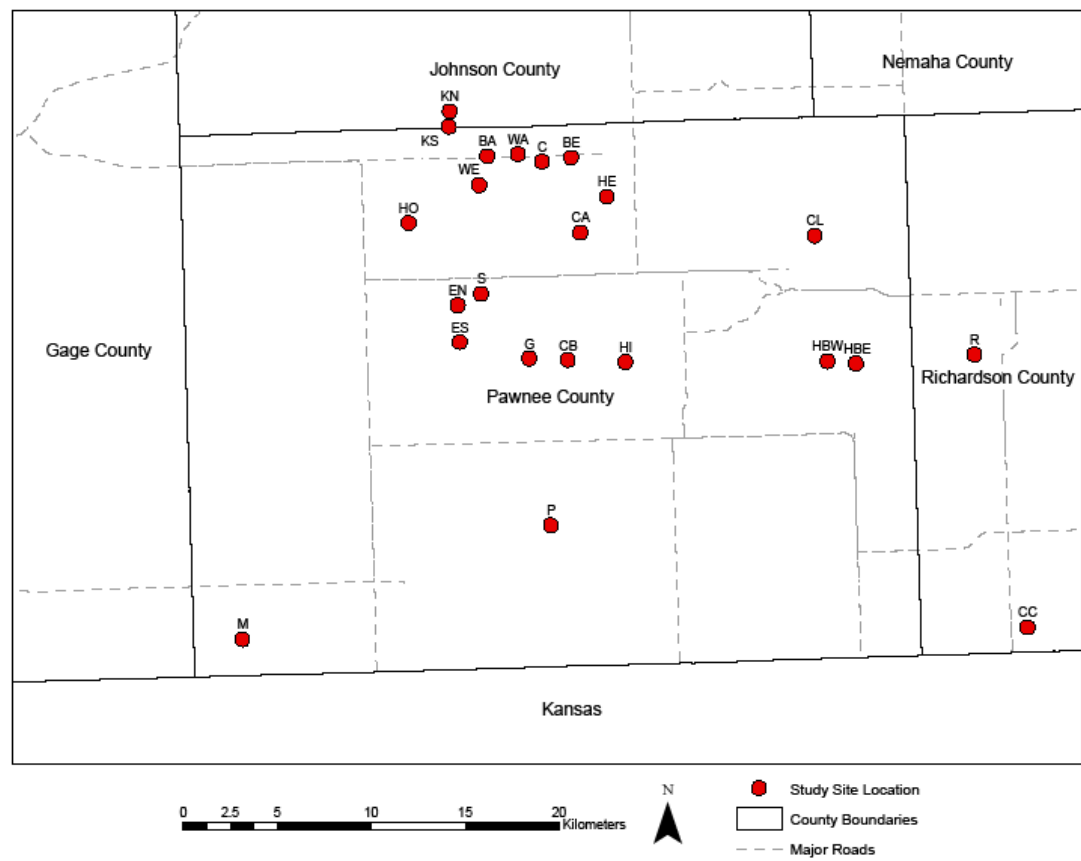


Figure 2. Location of the 23 study sites within the counties of the Southeast Prairies Biologically Unique Landscape.

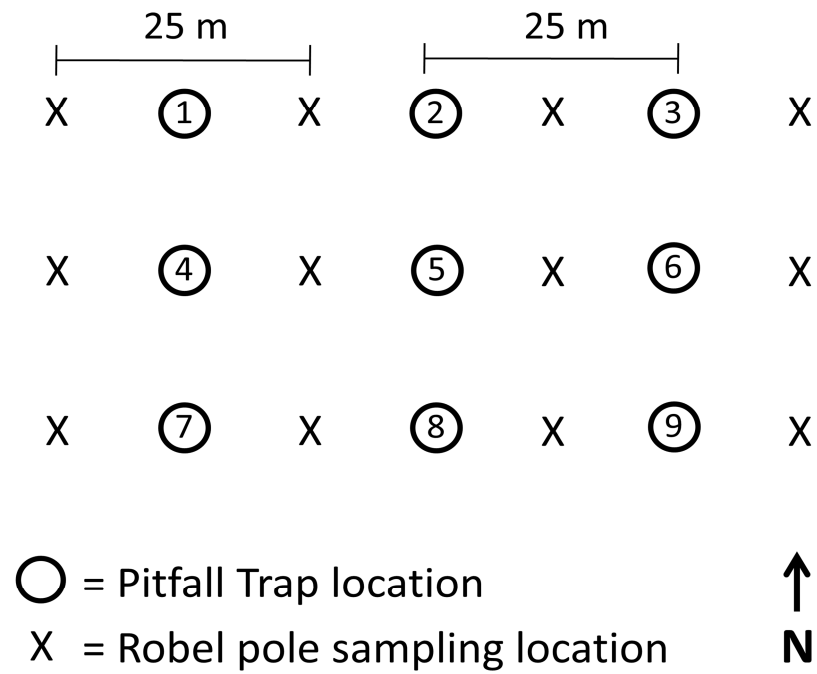


Figure 3. Sampling design used in study sites. Nine pitfall traps were arranged in a 3 x 3 grid spaced 25 m apart. Twelve Robel pole locations were arranged in a 4 x 4 grid spaced evenly between and outside the pitfall traps.

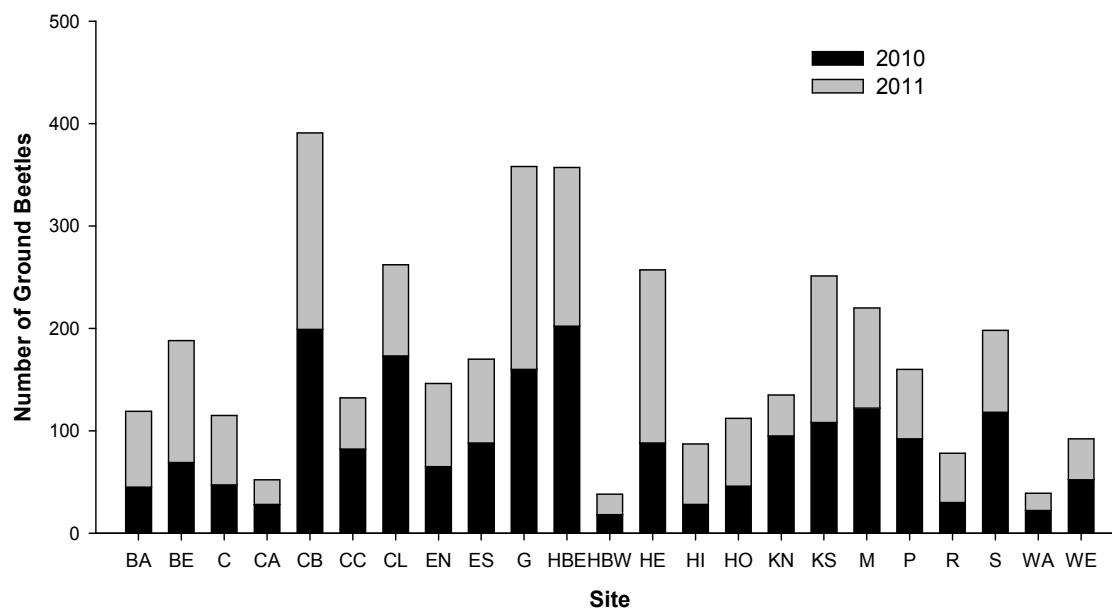


Figure 4. Total number of ground beetles captured at each site for 2010 and 2011. Sites HBW and WA had the fewest with 38 and 39 respectively. Site CB had the most with 391. Most sites were relatively similar in collection numbers over the two years.

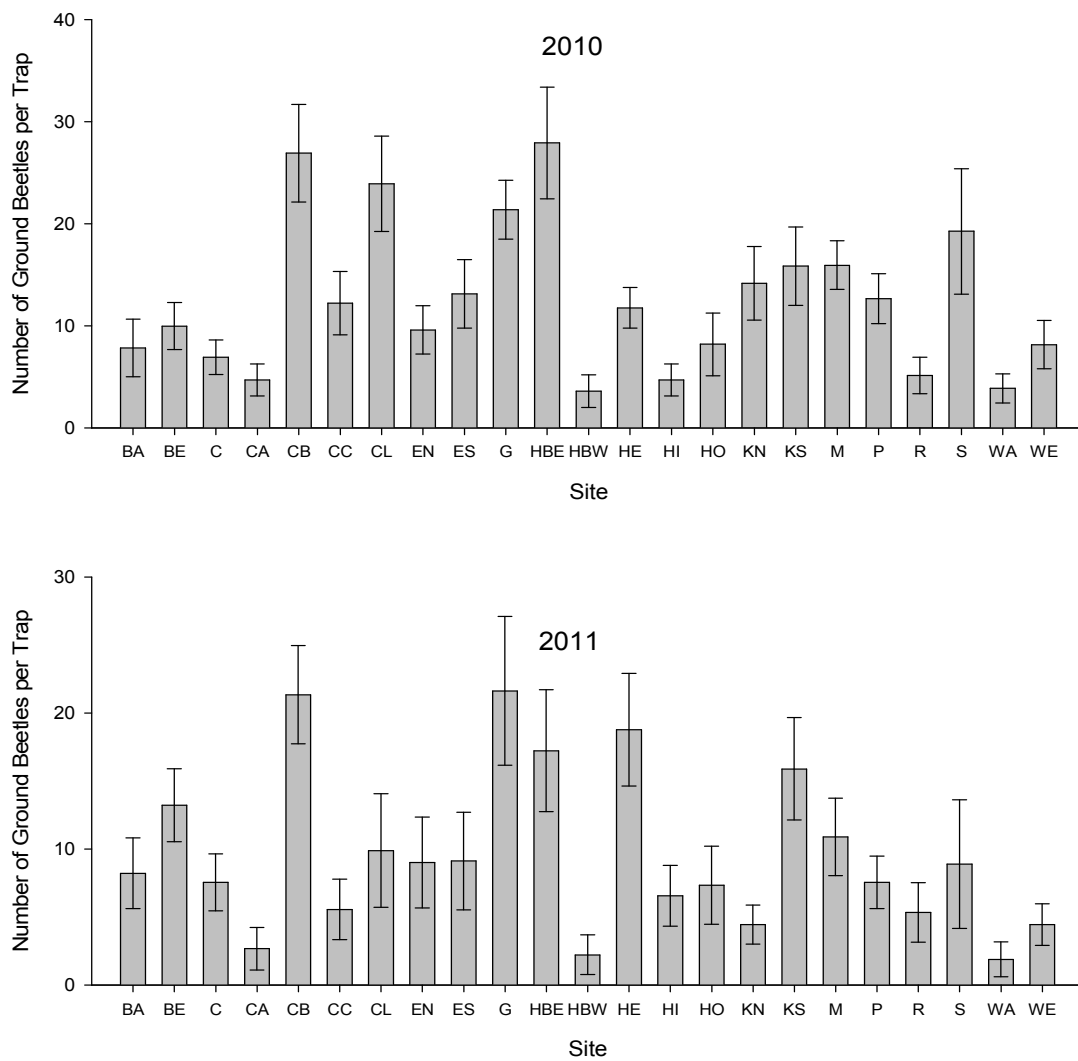


Figure 5. The average number of ground beetles captured at each site with error bars representing the 95% confidence interval.

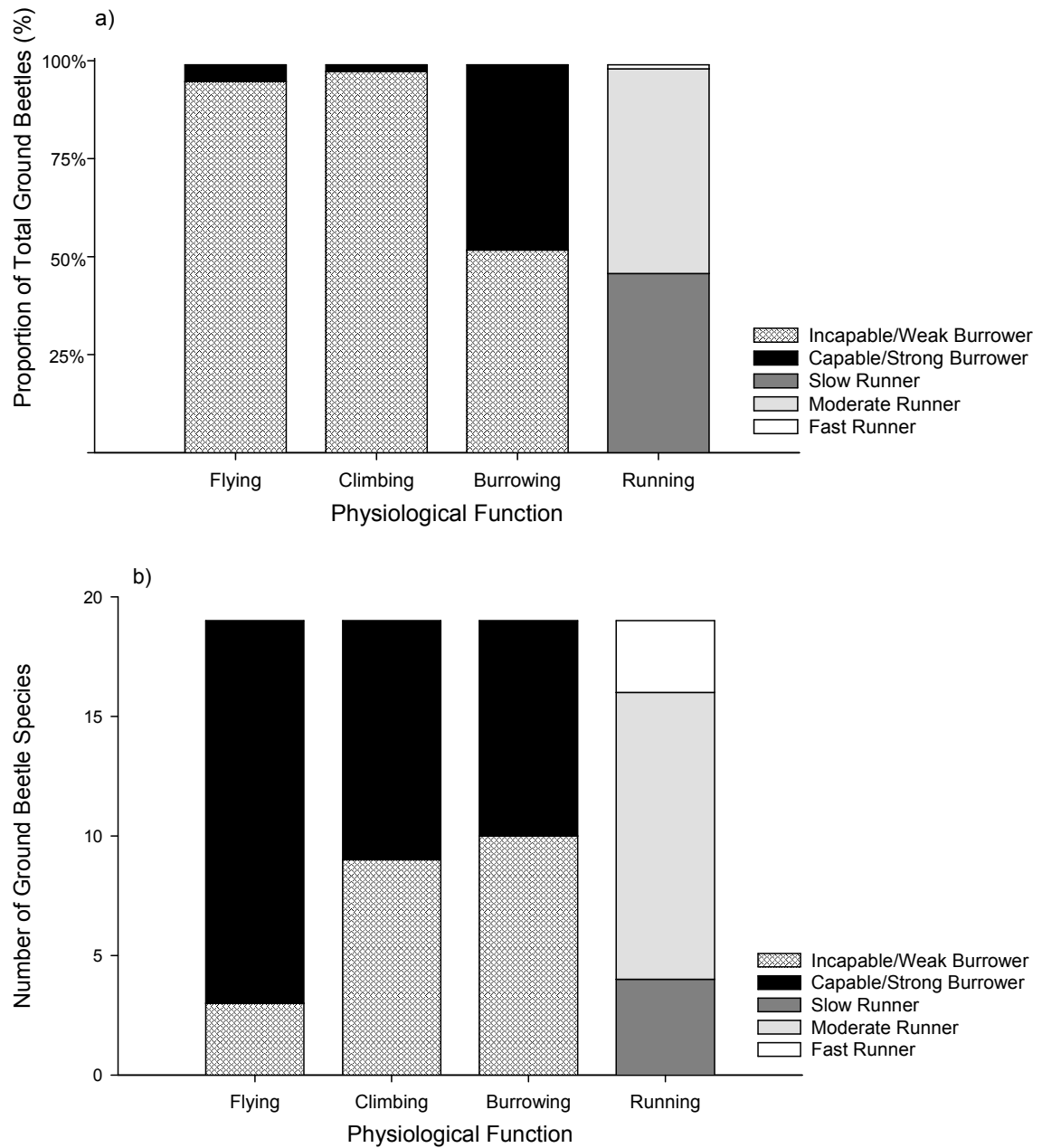


Figure 6. Proportion of (a) individual ground beetles and (b) species belonging to each functional group. Although those incapable of flying and climbing dominate numerically, they are comprised of relatively few species.

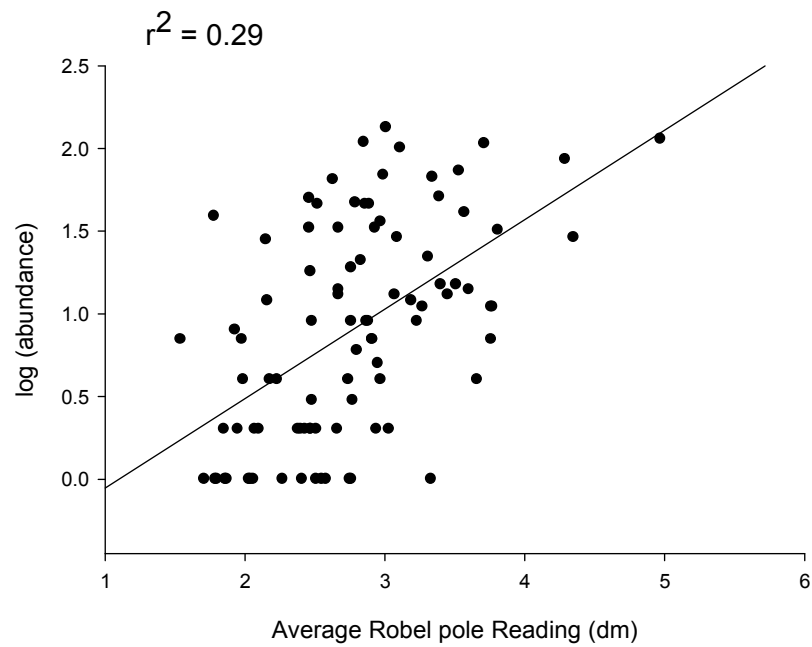


Figure 7. Linear regression of the log of the abundance of *Cyclotrachelus sodalis colossus* vs. the density of the vegetation as measured with a Robel pole.

Table 1. Models used for analyses of Shannon diversity, abundance, species richness, or presence. “Month” was included as a fixed factor and “siteyear” as a random factor in all models (not shown below).

Models	Type
<b>Combination</b> forbs + grasses density+litter haymeadow + pasture + crop + CRPgrass + trees	floral composition vegetation structure landscape composition
<b>Single Variable</b> haying clayloam forbs grasses density litter haymeadow pasture crop CRPgrass trees	management soil texture floral composition floral composition vegetation structure vegetation structure landscape composition landscape composition landscape composition landscape composition landscape composition
<b>Other</b> all factors no factors	global model null model

forbs = mean number of forb species/m<sup>2</sup>

grasses = mean number of grass species/m<sup>2</sup>

density = Robel pole readings of vegetation density

litter = average depth of lying litter

haymeadow = % haymeadow within 250m of center pitfall trap

pasture = % cattle pasture within 250m of center pitfall trap

crop = % cropland within 250m of center pitfall trap

CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center pitfall

Trees = % trees within 250m of center pitfall trap

haying = average annual haying day

clayloam = % of site covered in clay loam soil

Global model = all covariates

Table 2. Total number of each ground beetle species collected in June and July of 2010 and 2011 on 23 tallgrass prairie haymeadows in the Southeast Prairies Biologically Unique Landscape.

Species	2010		2011		Total
	June	July	June	July	
<i>Cyclotrachelus sodalis colossus</i>	348	626	34	920	1964
<i>Pasimachus elongatus</i>	354	482	508	415	1788
<i>Chlaenius tomentosus</i>	14	20	15	8	50
<i>Chlaenius platyderus</i>	3	10	10	9	33
<i>Anisodactylus rusticus</i>	6	12	5	3	26
<i>Pterostichus permundus</i>	8	7	4	7	23
<i>Scarites subterraneus</i>	5	3	2	10	18
<i>Scarites vicinus</i>	8	11	3	2	17
<i>Anisodactylus ovularis</i>	2	3	5	6	15
<i>Anisodactylus dulcicollis</i>	1	1	2	1	5
<i>Harpalus caliginosus</i>	0	1	0	2	4
<i>Harpalus faunus</i>	0	1	1	2	4
<i>Harpalus pennsylvanicus</i>	0	0	0	4	4
<i>Cratacanthus dubius</i>	0	0	0	1	1
<i>Galerita janus</i>	0	0	1	0	1
<i>Harpalus compar</i>	0	1	0	0	1
<i>Helluomorphoides praeustus bicolor</i>	1	0	0	0	1
<i>Panagaeus fasciatus</i>	0	1	0	0	1
<i>Poecilus lucublandus</i>	0	1	0	0	1



Table 3. Taxa of Carabidae with total number collected and physiological abilities. Flying ability is either capable (x) or incapable (-); climbing ability is occasional, regular, frequent, or non-climber (-); burrowing ability is strong or not strong (-); running ability is slow, moderate or fast.

Tribe	Species	No. Collected	Flying	Climbing	Burrowing	Running
Chlaeniini	<i>Chlaenius platyderus</i> Chaudoir	33	-	-	-	moderate
	<i>Chlaenius tomentosus</i> Say	50	x	-	strong	moderate
Galeritini	<i>Galerita janus</i> Fabricius	1	x	frequent	-	fast
Harpalini	<i>Anisodactylus dulcicollis</i> LaFerté-Sénéctère	5	x	-	strong	slow
	<i>Anisodactylus ovularis</i> Casey	15	x	-	-	fast
	<i>Anisodactylus rusticus</i> Say	26	x	regular	-	fast
	<i>Cratacanthus dubius</i> Beauvois	1	x	regular	strong	moderate
	<i>Harpalus caliginosus</i> Fabricius	4	x	frequent	strong	moderate
	<i>Harpalus compar</i> LeConte	1	x	occasional	-	moderate
	<i>Harpalus faunus</i> Say	4	x	occasional	-	moderate
	<i>Harpalus pennsylvanicus</i> DeGeer	4	x	frequent	strong	moderate
Helluonini	<i>Helluomorphoides praeustus bicolor</i> Harris	1	x	-	-	moderate
Panagaenini	<i>Panagaeus fasciatus</i> Say	1	x	occasional	-	moderate

Table 3. continued.

Pterostchini	<i>Cyclotrachelus sodalis colossus</i> LeConte	1,964	-	-	-	moderate
	<i>Poecilus lucublandus</i> Say	1	x	occasional	strong	moderate
	<i>Pterostichus permundus</i> Say	23	x	occasional	-	moderate
Scaritini	<i>Pasimachus elongatus</i> LeConte	1,788	-	-	strong	slow
	<i>Scarites subterraneus</i> Fabricius	18	x	-	strong	slow
	<i>Scarites vicinus</i> Chaudoir	17	x	-	strong	slow

Table 4. Results of information theoretical model selection for ground beetles. The response variables of Shannon diversity and abundance use linear mixed models while species richness uses a generalized linear mixed model with a Poisson distribution. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
<b>Shannon Diversity</b>				
grasses <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	31.53	0.00	0.64
forbs <sup>h</sup> + grasses + month + siteyear	5	33.60	2.07	0.23
<b>Abundance</b>				
<i>forbs</i> + month + siteyear	4	51.03	0.00	0.23
<i>litter</i> <sup>i</sup> + month + siteyear	4	52.23	1.20	0.13
haymeadow <sup>j</sup> + month + siteyear	4	53.08	2.05	0.08
<i>forbs</i> + <i>grasses</i> + month + siteyear	5	53.23	2.19	0.08
density <sup>k</sup> + litter + month + siteyear	5	53.46	2.43	0.07
crop <sup>l</sup> + month + siteyear	4	53.54	2.51	0.07
<i>pasture</i> <sup>m</sup> + month + siteyear	4	53.60	2.57	0.06
<i>trees</i> <sup>n</sup> + month + siteyear	4	54.02	2.99	0.05
<i>clayloam</i> <sup>o</sup> + month + siteyear	4	54.74	3.71	0.04
<i>CRPgrass</i> <sup>p</sup> + month + siteyear	4	54.75	3.72	0.04
hay <sup>q</sup> + month + siteyear	4	54.82	3.79	0.04
<i>grasses</i> + month + siteyear	4	55.03	4.00	0.03
<b>Species Richness</b>				
<i>CRPgrass</i> + month + siteyear	4	42.66	0.00	0.31
Null model	2	44.76	2.11	0.11

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-h</sup> grasses = mean number of grass species/m<sup>2</sup>; month = month sampled (June or July); siteyear = the site and year sampled; forbs = mean number of forb species/m<sup>2</sup>

<sup>i-q</sup> litter = average depth of lying litter; haymeadow = % haymeadow within 250m of center trap; density = Robel readings of vegetation density; crop = % cropland within 250m of center trap; pasture = % cattle pasture within 250m of center trap; trees = % of landscape covered by trees within 250m of center trap; clayloam = % of site covered in clay loam soil; CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center trap; hay = average annual haying day

Table 5. Estimates of parameters affecting ground beetle Shannon Diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Diversity				
Grasses	0.0760	0.0210	0.0349	0.1172
Forbs	0.0052	0.0118	-0.0179	0.0283
Month (June)	-0.1499	0.0561	-0.2599	-0.0400
Intercept	0.1025	0.2006	-0.2907	0.4958
Abundance				
Grasses	-0.0059	0.0313	-0.0672	0.0555
Forbs	-0.0351	0.0171	-0.0687	-0.0015
Density	0.0679	0.0665	-0.0625	0.1983
Litter	-0.0336	0.0202	-0.0732	0.0060
Clay Loam	-0.0007	0.0012	-0.0030	0.0017
Haying	0.0011	0.0025	-0.0038	0.0060
Haymeadow	0.0032	0.0023	-0.0013	0.0077
Pasture	-0.0028	0.0023	-0.0074	0.0018
Crop	0.0031	0.0025	-0.0018	0.0079
CRP Grass	-0.0014	0.0027	-0.0067	0.0039
Trees	-0.0025	0.0025	-0.0073	0.0023
Month (June)	-0.2849	0.0505	-0.3838	-0.1860
Intercept	1.7907	0.0286	1.2299	2.3516
Species Richness				
Grasses	0.0411	0.0425	-0.0423	0.1245
Forbs	-0.0152	0.0234	-0.0611	0.0307
Density	0.0568	0.1248	-0.1877	0.3013
Litter	-0.0101	0.0272	-0.0633	0.0432
Clay Loam	0.0017	0.0016	-0.0014	0.0048
Haying	-0.0015	0.0033	-0.0080	0.0049
Haymeadow	0.0035	0.0030	-0.0023	0.0094
Pasture	0.0017	0.0031	-0.0043	0.0077

Table 5 continued.

<b>Parameter</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>95% Confidence Interval</b>	
			<b>Low</b>	<b>High</b>
Crop	0.0004	0.0033	-0.0069	0.0061
CRP Grass	-0.0077	0.0039	-0.0154	0.0000
Trees	0.0005	0.0032	-0.0059	0.0068
Month (June)	-0.1717	0.1150	-0.3972	0.0538
Intercept	1.2928	0.2222	0.8574	1.7283

Table 6. Results of information theoretical model selection for the abundance of *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus*. Linear mixed models were evaluated using program R. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

Model	K <sup>a</sup>	AICc <sup>b</sup>	ΔAICc <sup>c</sup>	wi <sup>d</sup>
<i>Cyclotrachelus sodalis colossus</i>				
density <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	145.19	0.00	0.38
Global model	14	145.95	0.76	0.26
density + <i>litter</i> <sup>h</sup> + month + siteyear	5	146.20	1.01	0.23
<i>trees</i> <sup>i</sup> + month + siteyear	4	147.99	2.80	0.09
<i>Pasimachus elongatus</i>				
haymeadow <sup>j</sup> + pasture <sup>k</sup> + crop <sup>l</sup> + CRPgrass <sup>m</sup> + trees				
+ month + siteyear	8	54.98	0.00	0.58
haymeadow + month + siteyear	4	57.65	2.67	0.15
<i>trees</i> + month + siteyear	4	59.33	4.35	0.07

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-i</sup> density = Robel readings of vegetation density; month = month sampled (June or July); siteyear = the site and year sampled; litter = average depth of lying litter; trees = % of landscape covered by trees within 250m of center trap

<sup>j-m</sup> haymeadow = % haymeadow within 250m of center trap; pasture = % cattle pasture within 250m of center trap; crop = % cropland within 250m of center trap; CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center trap

Table 7. Estimates of parameters affecting abundance of *Cyclotrachelus sodalis colossus* and *Pasimachus elongatus*. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
<i>Cyclotrachelus sodalis colossus</i>				
Grasses	0.0400	0.0615	-0.0806	0.1606
Forbs	-0.0193	0.0265	-0.0712	0.0326
Density	0.3612	0.1044	0.1566	0.5659
Litter	-0.0489	0.0332	-0.1140	0.0161
Clay Loam	0.0013	0.0021	-0.0029	0.0055
Haying	-0.0076	0.0035	-0.0146	0.0007
Haymeadow	-0.0202	0.0307	-0.0803	0.0400
Pasture	0.0078	0.0072	-0.0062	0.0218
Crop	0.0158	0.0074	0.0013	0.0303
CRP Grass	-0.0305	0.0338	-0.0967	0.0358
Trees	0.0013	0.0100	-0.0183	0.0209
Month (June)	-0.4638	0.1344	-0.7272	-0.2003
Intercept	0.0223	0.8993	-1.7403	1.7849
<i>Pasimachus elongatus</i>				
Haymeadow	0.0049	0.0070	-0.0089	0.0187
Pasture	0.0145	0.0051	0.0046	0.0244
Crop	0.0177	0.0056	0.0068	0.0286
CRP Grass	-0.0242	0.0230	-0.0692	0.0208
Trees	0.0106	0.0076	-0.0044	0.0256
Month (June)	-0.0798	0.0488	-0.1754	0.0158
Intercept	0.0455	0.7654	-1.4546	1.5456

Table 8. Results of information theoretical model selection for the abundance of ground beetles grouped by flying ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wt<sup>d</sup></b>
Fliers				
<i>CRPgrass<sup>e</sup></i> + month <sup>f</sup> + siteyear <sup>g</sup>	4	-827.43	0.00	0.41
Null model	2	-824.64	2.79	0.10

<sup>a-d</sup> *K* = number of model parameters; *AICc* = Akaike's Information Criterion adjusted for small sample size;  $\Delta AICc$  = relative *AICc*; *wi* = Akaike weight

<sup>e-g</sup> *CRPgrass* = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center trap; *month* = month sampled (June or July); *siteyear* = the site and year sampled



Table 9. Estimates of parameters affecting abundance of flying ground beetles. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

<b>Parameter</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>95% Confidence Interval</b>	
			<b>Low</b>	<b>High</b>
Fliers				
Haying	-0.0027	0.0017	-0.0060	0.0006
Haymeadow	0.0029	0.0016	-0.0002	0.0061
Pasture	0.0029	0.0016	-0.0002	0.0059
CRP Grass	-0.0045	0.0018	-0.0080	-0.0011
Month (June)	-0.051	0.0501	-0.1492	0.0472
Intercept	0.4074	0.0807	0.2493	0.5655

Table 10. Results of information theoretical model selection for the abundance of ground beetles grouped by climbing ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
Climbers				
haymeadow <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	-40.52	0.00	0.73
haymeadow + <i>pasture</i> <sup>h</sup> + crop <sup>i</sup> + <i>CRPgrass</i> <sup>j</sup> + trees <sup>k</sup> + month + siteyear	2	-38.24	2.28	0.23

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-k</sup> haymeadow = % haymeadow within 250m of center trap; month = month sampled (June or July); siteyear = the site and year sampled; pasture = % cattle pasture within 250m of center trap; crop = % cropland within 250m of center trap; CRPgrass = % Conservation Reserve Program and other unclassified, low diversity grasslands within 250m of center trap; trees = % of landscape covered by trees within 250m of center trap

Table 11. Estimates of parameters affecting abundance of climbing ground beetles. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Climbers				
Crop	0.0027	0.0099	-0.0168	0.0222
Haymeadow	0.0048	0.0047	-0.0045	0.0141
Pasture	0.0003	0.0103	-0.0206	0.0199
CRP Grass	-0.0011	0.0105	-0.0216	0.0194
Month (June)	-0.0808	0.0354	-0.1502	-0.0114
Intercept	0.0103	0.4647	-0.9006	0.9211

Table 12. Results of information theoretical model selection for the abundance of ground beetles grouped by burrowing ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in italics.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
<b>Strong Burrowers</b>				
haymeadow <sup>e</sup> + month <sup>f</sup> + siteyear <sup>g</sup>	4	52.60	0.00	0.30
<i>forbs</i> <sup>h</sup> + month + siteyear	4	53.65	1.05	0.18
<i>trees</i> <sup>i</sup> + month + siteyear	4	54.23	1.62	0.13
Null model	2	55.29	2.68	0.08
<b>Regular Burrowers</b>				
density <sup>j</sup> + <i>litter</i> <sup>k</sup> + month + siteyear	5	144.75	0.00	0.78
density + month + siteyear	4	148.39	3.63	0.13

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-i</sup> haymeadow = % haymeadow within 250m of center trap; month = month sampled (June or July); siteyear = the site and year sampled; forbs = mean number of forb species/m<sup>2</sup>; trees = % of landscape covered by trees within 250m of center trap

<sup>j-k</sup> density = Robel readings of vegetation density; litter = average depth of lying litter

Table 13. Estimates of parameters affecting abundance of climbing ground beetles. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Strong Burrowers				
Haymeadow	0.0054	0.0022	0.0011	0.0097
CRP Grass	-0.0029	0.0027	-0.0081	0.0024
Trees	-0.0049	0.0024	-0.0096	-0.0002
Clay Loam	-0.0015	0.0012	-0.0038	-0.0009
Density	-0.0862	0.0683	-0.22	0.0477
Grasses	0.019	0.0306	-0.0409	0.0789
Forbs	-0.0371	0.0171	-0.0706	-0.0036
Month (June)	-0.0618	0.0516	-0.163	0.0394
Intercept	1.33	0.3076	0.7272	1.9328
Regular Burrowers				
Density	0.2753	0.0964	0.0863	0.4642
Litter	-0.0628	0.0251	-0.1119	-0.0137
Month (June)	-0.2474	0.1212	-0.4849	-0.0099
Intercept	0.6913	0.3452	0.0147	1.3678

Table 14. Results of information theoretical model selection for the abundance of ground beetles grouped by running ability. Log of abundance was used in place of absolute abundance numbers to normalize the data. Results display any models with weights above the null model and at least 10% of the highest ranked model. Factors with negative effects are displayed in *italics*.

<b>Model</b>	<b>K<sup>a</sup></b>	<b>AICc<sup>b</sup></b>	<b>ΔAICc<sup>c</sup></b>	<b>wi<sup>d</sup></b>
<b>Fast Runners</b>				
<i>haying<sup>e</sup></i> + month <sup>f</sup> + siteyear <sup>g</sup>	4	-44.33	0.00	0.26
<i>forbs<sup>h</sup></i> + month + siteyear	4	-43.07	1.25	0.14
Null model	2	-42.90	1.42	0.13
<b>Moderate Runners</b>				
density <sup>i</sup> + <i>litter<sup>j</sup></i> + month + siteyear	5	122.31	0.00	0.42
<i>litter</i> + month + siteyear	4	148.39	3.63	0.13
<b>Slow Runners</b>				
haymeadow <sup>k</sup> + month + siteyear	4	62.94	0.00	0.32
<i>forbs</i> + month + siteyear	4	63.72	0.77	0.22
<i>trees<sup>l</sup></i> + month + siteyear	4	64.90	1.96	0.12
<i>forbs</i> + grasses + month + siteyear	5	65.71	2.77	0.08
clayloam <sup>m</sup> + month + siteyear	4	66.86	3.91	0.05

<sup>a-d</sup> K = number of model parameters; AICc = Akaike's Information Criterion adjusted for small sample size; ΔAICc = relative AICc; wi = Akaike weight

<sup>e-h</sup> *haying* = average annual haying day; *month* = month sampled (June or July); *siteyear* = the site and year sampled; *forbs* = mean number of forb species/m<sup>2</sup>

<sup>i-j</sup> *density* = Robel readings of vegetation density; *litter* = average depth of lying litter

<sup>k-m</sup> *haymeadow* = % haymeadow within 250m of center trap; *trees* = % of landscape covered by trees within 250m of center trap; *grasses* = mean number of grass species/m<sup>2</sup>; *crop* = % cropland within 250m of center trap; *pasture* = % cattle pasture within 250m of center trap; *clayloam* = % of site covered in clay loam soil

Table 15. Estimates of parameters affecting ground beetle Shannon Diversity, abundance, and species richness. Estimates were calculated using program R. Results displayed include the average between all models in the confidence set (i.e, weight is at least 10% of the highest ranked model).

Table 5 continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Low	High
Fast Runners				
Haymeadow	0.0021	0.0010	0.0001	0.0041
Clay Loam	-0.0010	-0.0005	-0.0021	0.0001
Forbs	-0.0171	0.0078	-0.0324	-0.0017
Grasses	-0.0143	0.0139	-0.0416	0.0130
Haying	-0.0026	0.0011	-0.0047	-0.0005
Month (June)	-0.0158	0.0374	-0.0890	0.0574
Intercept	0.2162	0.1399	-0.0579	0.4904
Moderate Runners				
Density	0.2103	0.0921	0.0298	0.3909
Litter	-0.0464	0.0251	-0.0955	0.0028
Month (June)	-0.4764	0.1011	-0.6746	-0.2783
Intercept	0.8078	0.3271	0.1666	1.4490
Slow Runners				
Haymeadow	0.0058	0.0023	0.0013	0.0103
Forbs	-0.0411	0.0178	-0.0760	-0.0062
Trees	-0.0051	0.0025	-0.0100	-0.0002
Grasses	0.0165	0.0319	-0.0460	0.0790
Clay Loam	-0.0018	0.0014	-0.0043	0.0007
Month (June)	-0.0895	0.0525	-0.1925	0.0134
Intercept	1.3397	0.3682	0.6181	2.0614

## **Chapter 5: SYNTHETIC SUMMARY**

The extreme reduction of Great Plains' grasslands has resulted in the loss of many important services such as soil formation, nutrient cycling, and water regulation (Safriel and Adeel 2005). In Nebraska, tallgrass prairie has declined by an estimated 98% (Samson and Knopf 1994). What remains in southeast Nebraska are remnants scattered throughout a landscape fragmented by crops, trees, cattle pastures, and other types of grassland. The only source pools for much of the region's historic biodiversity, preservation of such remnants should be a priority for conservation (Ricketts 1999). In order to make effective conservation decisions, it is imperative we learn more about the functioning of these remnants in the context of a fragmented landscape.

Although plants and vertebrates often receive more consideration, some experts suggest including arthropods as an essential component of conservation decisions (Kremen et al. 1993, Oliver and Beattie 1993). Two of the most abundant and functionally important groups of arthropods in the tallgrass prairie are ants and ground beetles. Both are generalist predators, consuming a wide variety of agricultural pests, yet no one has formally investigated them in the Southeast Prairies Biologically Unique Landscape (BUL).

In addition to finding what species are present, this study attempts to understand what factors predict their abundance and diversity within tallgrass fragments. Various landscape, habitat, and management characteristics have previously been demonstrated to affect ants and ground beetles. Knowing how important particular factors are in relation to others can help prioritize the focus for conservation decisions. The relationships of



these factors are inherently complex in how they interact with different species and with other environmental factors. An increasingly common method of dealing with these ecological complexities is multi-model inference. This approach weighs evidence among multiple competing hypotheses to determine what models are most supported relative to others. The results in this thesis lay the groundwork for more in-depth future studies and should be incorporated into ongoing decisions that promote conservation of the entire ecosystem while continuing to meet the agricultural objectives of the private landowners.

In chapters 2 and 3, ants were analyzed according to their habitat preference and functional group, respectively. Twenty-eight species were collected consisting of 9,171 individuals. Concerning habitat preference, the vast majority were grassland-obligates, followed by a considerable number of habitat-generalists. The percentage of haymeadow within 250 m appears to positively influence the abundance of grassland-obligate ants and negatively influence habitat-generalist abundance. The Shannon diversity and species richness of grassland ants is best predicted by the average number of grass species per m<sup>2</sup>. Species richness was also affected by the average annual haying date, with sites hayed later possessing fewer species.

Concerning functional group composition, the majority were Opportunists, followed by Cold Climate Specialists, and Generalized Myrmicinae. Compared to prior studies, this pattern most closely resembles the Douglas fir forests in the higher elevations of Arizona. Though very different habitats, the similar functional group composition of ants in grassland and fir forest is likely a result of the cooler climates. Though a lower elevation, the higher latitude of southeast Nebraska produces a relatively

cool climate that limits aggressive functional groups such as Dominant Dolichoderinae, allowing Opportunists and Cold Climate Specialists to dominate. Most model-selection results concerning the abundance of functional groups were relatively ambiguous, with global or null models having the most weight. Functional group abundance may therefore not be predicted effectively by the fragment characteristics considered in this study.

In Chapter 4, the investigation of ground beetles produced 3,957 individuals consisting of 19 species. Approximately 95% of the collection was comprised of just two species, *Cyclotrachelus sodalis colossus* or *Pasimachus elongatus*. The dominance of these two species may be due in part to their shared inability to fly, which may keep them hidden from predators beneath the vegetation. Ground beetle Shannon diversity, as with ants, was positively associated with average number of grass species per m<sup>2</sup>.

Management of an ecosystem is complex, with any given action targeting a group of organisms invariably having unexpected consequences for other groups. Such management should be done in an adaptive framework that can be altered as more knowledge is acquired and goals are refined. The outcomes of this study should be incorporated into an adaptive management plan as some of the initial concepts for tallgrass prairie conservation in the Southeast Prairies BUL. For instance, although the exact relationship between grass diversity and ant and ground beetle diversity remains unclear, a positive correlation was demonstrated between them in this study.

Conservation focused on maximizing biodiversity of these insects may give priority to sites with more grass species per m<sup>2</sup>. This information may also be incorporated by maximizing grass species in restoration mixes, or attempting to increase grass species at

sites. Future studies may want to further investigate the differing effects of annuals versus perennials, natives versus non-natives, or cool-season versus warm-season grasses. The introduction or promotion of some grass species, particularly non-natives, may have unintended negative consequences and therefore should be done cautiously if at all.

Understanding what affects grassland-obligate ants is important for tallgrass prairie conservation because of their direct reliance on grasslands. If seeking to maximize the abundance of grassland-obligate ants, priority should be given to sites with more haymeadow in the nearby landscape. This may often mean large sites, which have been recognized as important for the abundance or species richness of many other organisms, including grassland birds (Helzer 1999). However, for the abundance of grassland ants, small patches of haymeadow may be equally beneficial when more haymeadow is in the nearby landscape. Separation of haymeadows by treelines or roads is a common occurrence that may not inhibit ants from crossing over and using the resources in these additional areas.

The sole management factor, haying time, was demonstrated to be important to the species richness of grassland ants. The standing litter left throughout the fall and winter of sites hayed early may be necessary for some species. Future studies should investigate how haying time affects species on a short-term basis (the year they are hayed or the following growing season) and a long-term basis (sites annually hayed early or late for decades). On a short-term basis, when a site is cut may affect the structure of the vegetation and the amount of litter the following year. The number and type of insects occupying or reproducing in the late summer or fall may be affected, which in turn may

influence the community composition the following year. On a long-term basis, when a site is cut may alter the entire plant community, altogether changing the insect community composition. Additional study is needed for the plants, mammals, birds, and reptiles of the Southeast Prairies BUL which may also be affected by haying time.

Although the number of grass species per m<sup>2</sup> is positively associated with both grassland ant and ground beetle diversity, other factors do not have the same relationship with both groups. For instance, grassland-obligate ant abundance has a strong correlation with the percentage of haymeadow within 250 m, but ground beetle abundance is not strongly predicted by any of the factors. Even sub-groups within the same order can vary considerably; for instance, habitat-generalist ants have the opposite relationship with haymeadow as grassland-obligate ants. These examples demonstrate the difficulty of managing an ecosystem for multiple groups of organisms that may be affected differently by the same factors.

Combining taxa, such as the overall abundance or species richness of ants and ground beetles together, may yield very different results than their analysis individually. Such results may be useful in a certain context, such as investigating the impact of the generalist predator community, but it may limit our understanding of the individual ecological components. Conservationists and managers must decide what groups of organisms are most important to their goals. With a focus on tallgrass prairie conservation, ants may be more important in terms of their greater biomass and wider range of ecological functions. With biodiversity conservation in mind, the subset of grassland-obligate ants, possibly dependent on tallgrass fragments, may take precedence over

habitat-generalists that can live in a variety of habitats. If the goal is to reduce a particular crop pest, such as armyworm, ground beetle abundance may take priority due to their demonstrated biocontrol ability in agroecosystems (Clark et al. 1994).

Aside from the habitat, landscape, and management factors considered in this study, ants and ground beetles may also be influenced by the composition of other insect groups. Although no significant correlation appears to exist between ants and ground beetles, other insect prey or predators may contribute to their abundance and diversity. Future studies may investigate a broader community of insects that considers herbivores or parasitoids in addition to predators and looks for relationships between these groups. It is possible the influence of insect groups on one another through trophic cascades may be more important than the environmental or management factors considered in this study. It will also be useful to find if the diversity of ants or ground beetles is indicative of the diversity of the broader insect community.

By inventorying and investigating two key groups of insects, this study lays the groundwork for conservation efforts in the Southeast Prairies BUL. Although relevant patterns were observed, populations of insect species can vary dramatically year-to-year and additional research is needed to build on the results of this short-term study. Current insights should therefore be applied in an adaptive management framework that acknowledges the uncertainty of the tallgrass prairie ecosystem and allows for change with the acquisition of new information.

### LITERATURE CITED

- Clark, M.S., J.M. Luna, N.D. Stone and R.R. Youngman. 1994. Generalist predator consumption of armyworm (Lepidoptera: Noctuidae) and effect of predator removal on damage in no-till corn. *Environmental Entomology* **23**:617-622.
- Helzer, C.J., and D.E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* **9**:1448-1458.
- Kremen, C., R.K. Colwell, T.S. Erwin, D.D. Murphy, R.F. Noss and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**:796-808.
- Oliver, I., and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* **7**:562-568.
- Ricketts, T.H., D.M. Olson, C.J. Loucks, W. Eichbaum, D. Della-Sala, K. Kavenagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abell, and S. Walters. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, D.C.
- Safriel, U. and Z. Adeel. 2005. Dryland systems. Pages 623-662 *in* R. Hassan, R. Scholes, and N. Ash, editors. *Ecosystems and human well-being: current state and trends. The millennium ecosystem assessment, Vol. 1.* Island Press, Washington, D.C.
- Samson, F.B., and F.L. Knopf. 1994. Prairie conservation in North America. *BioScience* **44**:418-421.

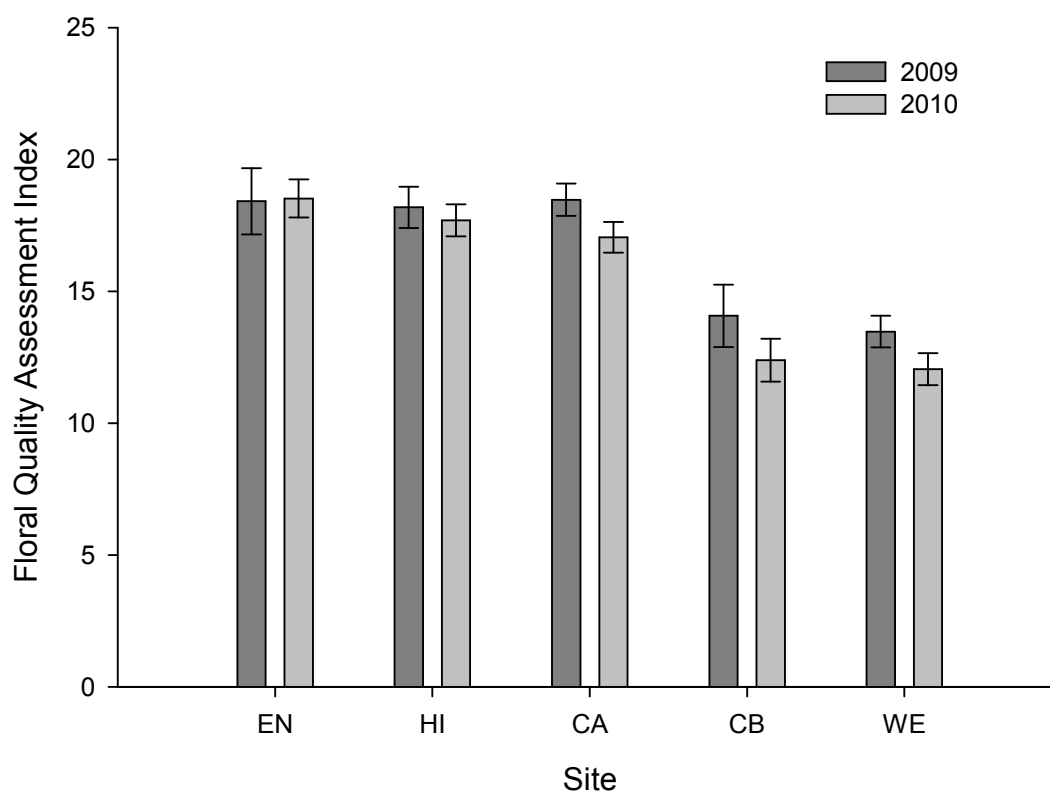
**Appendix A: SUPPLEMENTAL TABLES FOR LANDSCAPE, HABITAT, AND MANAGEMENT DATA**

Figure 1. Comparison of sites between 2009 and 2010 using the Floral Quality Assessment Index. At the 95% confidence interval, FQI values were consistent between the two years.

Table 1. Landscape data for study sites in the Southeast Prairies Biologically Unique Landscape. Includes the latitude and longitude of the center pitfall trap, the size of sites, and the percentage of land within a 250 m radius of the center trap covered by each of six classes (haymeadow, cattle pasture, CRP grassland, trees, cropland, and other).

Site	Latitude (N)	Longitude (W)	Size (ha)	Haymeadow (%)	Pasture (%)	CRP (%)	Trees (%)	Crop (%)	Other (%)
BA	40°14'52"	96°16'17"	7.69	40.45	2.19	9.51	11.90	32.26	3.70
BE	40°14'45"	96°13'8"	11.06	48.53	42.04	0.00	7.72	0.00	1.70
C	40°14'40"	96°14'14"	5.98	28.14	55.18	0.00	9.71	0.00	6.97
CA	40°12'34"	96°12'53"	15.02	67.74	9.21	0.00	6.37	15.37	1.32
CB	40°8'55"	96°13'31"	14.98	62.76	21.37	5.42	8.13	2.32	0.00
CC	40°0'44"	95°56'39"	16.24	50.51	15.08	1.43	25.72	7.26	0.00
CL	40°4'8"	96°14'19"	10.90	54.42	0.00	20.28	2.14	18.63	4.54
EN	40°10'34"	96°17'34"	6.67	33.33	0.00	12.83	10.71	38.45	4.69
ES	40°9'31"	96°17'31"	14.39	63.00	19.48	0.00	7.46	5.56	4.49
G	40°8'59"	96°14'56"	26.90	83.03	11.52	0.00	5.45	0.00	0.00
HBE	40°8'33"	96°2'44"	7.98	35.33	0.00	40.70	8.25	7.54	8.18
HBW	40°8'38"	96°3'46"	7.78	35.97	2.34	43.75	4.35	11.79	1.81
HE	40°13'36"	96°11'51"	5.54	28.19	31.36	28.73	8.06	0.00	3.66
HI	40°8'48"	96°11'21"	8.54	29.04	17.15	5.09	48.72	0.00	0.00
HO	40°13'1"	96°19'19"	12.44	50.78	27.25	5.43	14.33	0.00	2.20
KN	40°16'13"	96°17'38"	1.75	13.64	0.00	4.04	75.46	3.10	3.75
KS	40°15'46"	96°17'41"	4.21	21.39	28.28	9.73	1.82	33.70	5.08
M	40°1'6"	96°25'60"	4.90	28.31	0.00	1.62	7.61	62.46	0.00
P	40°12'17"	96°4'7"	23.10	81.86	15.39	0.00	2.35	0.00	0.40
R	40°8'41"	95°58'17"	5.83	29.67	0.00	58.25	0.62	8.23	3.22
S	40°10'54"	96°16'40"	5.30	26.97	0.00	1.49	27.20	44.35	0.00
WA	40°14'55"	96°15'7"	5.15	24.90	64.46	0.00	6.09	0.00	4.55
WE	40°14'3"	96°16'38"	4.65	45.75	0.00	14.78	36.90	0.00	2.57



Table 2. Vegetation structural data from 2010 and 2011 for study sites in the Southeast Prairies Biologically Unique Landscape. Includes date of sampling, average litter depth (cm), average vegetation density (Robel measurement to nearest  $\frac{1}{4}$  decimeter), and vertical heterogeneity of the vegetation (Shannon diversity index of every plant touching the Robel pole every  $\frac{1}{4}$  decimeter). For data collection details see chapter 2.

2010							
Site	June				July		
	Date	Litter Depth	Vegetation Density	Vertical Heterogeneity	Date	Vegetation Density	Vertical Heterogeneity
BA	6/10/10	4.06	2.76	2.74	7/12/10	3.77	3.00
BE	6/10/10	2.65	1.54	2.57	7/14/10	2.16	2.70
C	6/8/10	2.28	1.93	2.63	7/7/10	2.87	2.83
CA	6/8/10	4.43	2.07	2.61	7/8/10	2.95	2.76
CB	6/11/10	3.27	3.60	2.87	7/13/10	4.97	2.97
CC	6/15/10	2.28	2.91	2.56	7/15/10	3.33	2.99
CL	6/15/10	3.56	2.99	2.53	7/9/10	1.78	2.37
EN	6/8/10	0.26	3.31	2.91	7/14/10	4.35	3.11
ES	6/8/10	0.61	1.99	2.59	7/14/10	3.09	2.86
G	6/8/10	3.26	2.91	2.91	7/13/10	4.29	2.97
HBE	6/14/10	4.71	3.39	2.74	7/9/10	3.53	2.87
HBW	6/14/10	4.06	3.76	2.89	7/9/10	3.76	3.11
HE	6/15/10	3.90	2.67	2.60	7/8/10	2.52	2.70
HI	6/11/10	1.25	2.77	2.65	7/15/10	3.40	2.63
HO	6/9/10	4.59	2.51	2.66	7/7/10	3.23	2.88
KN	6/9/10	1.52	2.03	2.71	7/13/10	2.75	2.74
KS	6/10/10	0.68	2.46	2.61	7/13/10	2.93	2.85
M	6/10/10	5.08	2.88	2.60	7/15/10	3.81	3.05
P	6/15/10	0.94	1.98	2.59	7/15/10	3.19	2.49
R	6/15/10	3.18	2.94	2.72	7/14/10	3.03	2.89
S	6/11/10	3.43	2.67	2.63	7/13/10	3.34	2.83
WA	6/10/10	4.22	1.95	2.51	7/8/10	2.55	2.71
WE	6/9/10	3.81	2.48	2.48	7/8/10	3.07	2.83

Table 2. continued.

**2011**

Site	June				July		
	Date	Litter Depth	Vegetation Density	Vertical Heterogeneity	Date	Vegetation Density	Vertical Heterogeneity
BA	6/7/11	3.14	2.40	2.49	7/6/11	3.57	2.81
BE	6/8/11	6.00	1.87	2.55	7/6/11	2.46	2.70
C	6/8/11	8.52	2.27	2.55	7/6/11	2.83	2.73
CA	6/8/11	8.00	2.41	2.44	7/7/11	2.80	2.82
CB	6/7/11	3.19	2.47	2.54	7/7/11	3.11	2.68
CC	6/9/11	3.26	2.47	2.50	7/12/11	3.66	2.92
CL	6/9/11	5.84	2.47	2.63	7/7/11	2.89	2.76
EN	6/6/11	0.63	2.74	2.42	7/8/11	3.27	2.80
ES	6/6/11	1.47	2.18	2.33	7/5/11	2.97	2.77
G	6/7/11	1.60	2.38	2.66	7/7/11	3.01	2.87
HBE	6/9/11	4.47	2.10	2.53	7/7/11	2.63	2.61
HBW	6/9/11	6.67	2.66	2.81	7/7/11	3.45	2.80
HE	6/9/11	5.68	2.23	2.63	7/7/11	2.85	2.68
HI	6/9/11	5.31	2.04	2.60	7/11/11	2.67	2.84
HO	6/8/11	0.19	1.85	2.42	7/6/11	2.76	2.62
KN	6/7/11	3.79	1.71	2.28	7/6/11	2.51	2.69
KS	6/7/11	4.23	2.76	2.71	7/6/11	3.71	2.88
M	6/9/11	4.70	2.43	2.41	7/8/11	2.86	2.52
P	6/9/11	5.52	1.79	2.46	7/11/11	2.15	2.51
R	6/9/11	2.82	1.86	2.34	7/12/11	2.97	2.75
S	6/7/11	6.69	2.06	2.27	7/8/11	2.79	2.70
WA	6/8/11	6.31	1.80	2.44	7/6/11	2.48	2.75
WE	6/8/11	8.19	2.58	2.59	7/6/11	3.51	3.02

Table 3. Plant diversity of study sites in the Southeast Prairies Biologically Unique Landscape. Includes year sampled, average number of plant species, grass species, and forb species per m<sup>2</sup>. See chapter 2 for a description of data collection.

Site	Year	Plant Spp./m <sup>2</sup>	Forb Spp./m <sup>2</sup>	Grass Spp./m <sup>2</sup>
BA	2009	21.76	10.34	8.22
BE	2009	23.84	10.82	10.10
C	2009	21.98	9.34	10.44
CA	2010	26.9	15.24	9.90
CB	2010	21.30	10.44	8.94
CC	2010	24.50	15.58	4.44
CL	2009	22.34	10.62	8.66
EN	2010	25.34	15.14	7.80
ES	2009	25.78	13.18	9.54
G	2010	20.04	10.44	7.02
HBE	2009	19.60	8.70	8.32
HBW	2010	22.06	13.72	6.26
HE	2010	26.52	15.16	8.12
HI	2010	24.86	13.56	8.08
HO	2010	22.96	12.52	8.68
KN	2009	21.98	11.50	7.86
KS	2010	29.24	17.54	9.42
M	2009	21.28	9.16	8.98
P	2010	23.12	13.54	7.94
R	2009	18.08	8.540	7.18
S	2009	20.78	11.40	6.98
WA	2009	27.18	13.80	10.18
WE	2010	21.62	11.06	8.88

Table 4. Percentage of each study site in the Southeast Prairies Biologically Unique Landscape comprised of five soil classes (loam, clay loam, silty loam, silty clay loam, and other).

<b>Site</b>	<b>Loam</b>	<b>Clay Loam</b>	<b>Silty Loam</b>	<b>Silty Clay Loam</b>	<b>Other</b>
BA	26.1	66.8	7.1	0.0	0
BE	56.5	43.5	0	0	0
C	22.5	74.6	2.9	0	0
CA	57.3	42.7	0	0	0
CB	30.8	48.9	20.3	0	0
CC	0	0	0	96.3	3.7
CL	54.1	0	0	42.0	3.8
EN	0	87.8	12.2	0	0
ES	64.2	22.3	0	0.9	12.5
G	40.5	47.9	11.5	0	0
HBE	34.4	0	0	62.3	3.4
HBW	0	23.1	0	76.9	0
HE	0	99.1	0	0	0.8
HI	43.3	56	0	0	0.7
HO	0	97.9	1	0	1.7
KN	0	100	0	0	0
KS	0	100	0	0	0
M	0	0	0	100	0
P	55.6	22.9	0	0	21.4
R	0	2.9	15	82.1	0
S	68.9	17.9	0	0	13.2
WA	42.5	54.3	3.1	0	0
WE	0	76.3	2.2	21.4	0

Table 5. Haying dates of study sites in the Southeast Prairies Biologically Unique Landscape and corresponding “haying” values. Values are based on date hayed with July 15 = 1, July 16 = 2, etc. In 2010, sites CB, EN, ES, and R were hayed at an unknown date after September 21; therefore the 2011 value was used as the average value.

Site	2010		2011		Average Value
	Date Hayed	Value	Date Hayed	Value	
BA	8/4	21	7/14	0	11
BE	8/11	28	8/2	19	24
C	7/26	12	7/17	3	8
CA	7/26	12	7/20	16	14
CB	-	-	7/31	17	17
CC	8/25	42	9/5	53	48
CL	8/21	38	7/27	13	26
EN	-	-	9/17	65	65
ES	-	-	9/17	65	65
G	8/8	25	7/31	17	21
HBE	8/29	46	9/7	55	51
HBW	7/30	16	8/4	21	19
HE	8/4	21	8/1	18	20
HI	8/10	27	8/23	40	34
HO	7/26	12	7/26	12	12
KN	8/30	47	8/24	41	44
KS	8/9	26	7/26	12	19
M	8/18	35	7/28	14	25
P	8/21	38	8/3	20	29
R	-	-	9/17	65	65
S	8/4	21	7/21	17	19
WA	8/11	28	8/1	18	23
WE	7/29	15	8/31	48	32

## Appendix B: SUPPLEMENTAL TABLES FOR ANT PITFALL TRAPPING RESULTS

Table 1 continued. June 4-7, 2010 - Ants.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymymex insanus</i>	<i>Forelius pruinosus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
CA9	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-
CB1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	12	-	-	-	-	-	-	-
CB2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	25	-	-	-	-	-	-	-
CB3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	-	-	-	-	3	1	-
CB4	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	65	-	-	-	-	-	-	-
CB5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	37	-	1	-	-	-	-	-
CB6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	60	-	-	-	-	1	-	-
CB7	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	-	-	87	-	-	-	-	-	1	-
CB8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-
CB9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	15	-	-	-	-	1	-	-
CC1	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
CC2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-
CC3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-
CC4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	1	-	-
CC6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-
CC7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
CC8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	1	-	-
CC9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CL1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
CL3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL4	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-
CL5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	3	-	-
CL6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
CL7	-	-	-	-	-	-	-	-	-	-	-	-	16	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
CL9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN3	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN4	-	-	-	-	-	4	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
EN5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN6	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN7	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
EN8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
ES1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	1	-	-
ES2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
ES3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	-	-	-	-	-	-	-	-









Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymymex insanus</i>	<i>Forelius pruinosis</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lastius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
WA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
WE1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
WE2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-
WE3	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	3	-	-	-	-	-	-	-	-	-	-	-	14
WE4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
WE5	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	1	-	-	2	3	-
WE6	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	36	-
WE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-
WE8	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
WE9	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	26	-	-

Table 2. June 29-July 2, 2010 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinosus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
BA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	7	-
BA2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
BA3	-	-	-	-	-	2	-	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1	-
BA4	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA5	-	-	-	-	-	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-
BA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-
BA8	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
BA9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
BE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	1	-	-	-	-	-	-	-	-	-	-
BE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	1	-	-	-	-	-	-	-
BE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	4	-	-	-	-	-	-	-
BE4	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	5	-	1	-	-	-	-	-	-	-	-	-	-
BE5	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	3	-	-	-	-	2	-	-	-	-	-	-	-
BE6	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-
BE7	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	2	-	-	3	-	-	-	-	-	-	-
BE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-
BE9	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-
C1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
C2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	20	-
C3	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	1	8	-
C4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
C5	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
C6	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	1	-	-	-	-	-	9	-
C7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-
C8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
CA2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-
CA3	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	5	-	-	1	-	-	-	-	-	-	-	-	-
CA4	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
CA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
CA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA8	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CA9	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
CB1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	13	-	-	-	-	-	-	-
CB2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	1	-	-

Table 2. continued. June 29-July 2, 2010 - Ants.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
CB3	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	28	-	-	-	-	-	-	-	-
CB4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	36	-	-	-	-	-	-	-	-
CB5	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	48	-	-	-	-	-	-	-	-
CB6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-
CB7	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	65	-	-	-	-	3	-	-	-
CB8	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	26	-	1	-	-	-	-	-	-
CB9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	7	-	-	-	-	2	-	-	-
CC1	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-
CC3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
CC4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
CC5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CC6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-	-	-	-	3	-	-	-
CC7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
CC8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CC9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	1	-	-	-
CL2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	1	-
CL3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	1	-	1	-
CL4	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-
CL5	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-
CL6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	4	-	-	-
CL7	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	5	3	-	-	-	-	2	-	-	3	-	-	-
CL8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	1	1	-	-	-	1	-	-	4	-	-	-
CL9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	-	-	-	-	-	-	-	-	-	-	-
EN1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN3	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN4	-	-	-	-	-	-	8	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
EN5	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN7	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN9	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ES1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	21	-	-	-	-	-	-	-	-
ES2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	1	-	1	-
ES3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	2	-	1	-
ES4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	-	-	-
ES5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-	-	-	1	-	-	-
ES6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	4	-









Table 2. continued. June 29-July 2, 2010 - Ants.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
WE1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	2	-	-
WE2	-	-	-	-	-	-	4	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
WE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	1	-	54	-
WE4	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE5	-	-	-	-	-	-	7	-	-	-	-	-	1	-	-	9	-	-	-	-	2	-	-	-	-	-	-	-
WE6	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	71	-
WE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	23	-
WE8	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	1	-	-	-	-	-	-	-	-	12	-
WE9	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	7	-	-	-	-	-	-	1	-	-	-	127	-

Table 3. June 3-6, 2011 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinosus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambigua</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
BA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	1	3	-
BA2	-	-	-	-	-	-	-	-	35	-	-	-	-	2	-	-	-	-	6	-	-	-	-	-	-	-	-	-
BA3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
BA4	-	-	1	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
BA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-
BA6	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	2	-
BA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	2	-
BA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
BA9	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-
BE1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	8	-	3	-	-	-	-	-	-	-	-	-	-
BE2	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
BE3	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	7	-	-	-	-	2	-	-	-	-	1	-	-
BE4	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	1	-	1	2	3	-	-	-	-	-	-	-	-
BE5	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-
BE6	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
BE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	1	-	2	-	-	-	-	-	-	-	-
BE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2	-	-
BE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
C1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	7	-	-	-	-	-	-	-	-	-	-
C2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
C3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	25	-
C4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	1	-	-
C5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	2	1	-	-	-	-	-	-	-	1	-
C6	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-
C7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C8	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	3	-	-	1	-	-	-	-	-	-	-	-	-
C9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
CA1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
CA2	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
CA4	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1	2	-	-	-	-	-	-	4	-	-
CA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	2	-	-	-	-	2	-	-
CA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-
CA7	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	3	-	-	-	-	-	-	-	-	-
CA8	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
CA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	1	-	-
CB1	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	7	-	-	-	-	-	-	-	-
CB2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-	-	1	-



Table 3. continued. June 3-6, 2011 - Ants.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinosis</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
ES7	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	1	-	-
ES8	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	4	-	-	-	4	-	-	-	-	-	1	-	-
ES9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-
G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	23	-	-	-	-	-	-	-	-
G2	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-	1	-	6	-	-	-	-	-	1	-	-
G3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	6	-	-	-	-	-	-	-	-
G4	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	10	-	-	-	-	-	-	-	-
G5	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-
G6	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	24	-	-	-	-	-	-	-	-
G7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	44	-	-	-	-	-	-	-	-
G8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	28	-	-	-	-	-	-	-	-
G9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	7	-	-	-	-	-	-	-	-
HBE1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBE2	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
HBE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
HBE4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
HBE5	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBE6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	7	-	-	-	-	-	-	-	-	-
HBE7	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
HBE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	1	-	-	1	-	-	-
HBE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-	1	-	-	-	-	-	-
HBW1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW4	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	-	-	-	-	-	-	-	-	-
HBW6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
HBW7	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
HBW8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-
HBW9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	1	-	-	-
HE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
HE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-
HE3	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-
HE4	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	4	-	-	-
HE5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
HE6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
HE7	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
HE8	-	1	-	-	-	-	1	-	-	-	-	-	3	-	-	-	-	1	2	-	-	-	-	-	6	-	-	-
HE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
HI1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	1	-	-	-

Table 3. continued. June 3-6, 2011 - Ants.

[illegible]

Table 3. continued. June 3-6, 2011 - Ants.

[illegible]

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinosus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothroax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
WE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE2	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	6	-
WE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	20	-
WE4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
WE5	-	1	-	-	-	-	-	-	-	-	-	-	1	1	-	14	-	-	-	1	-	-	-	-	-	2	17	-
WE6	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
WE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	3	2	-

Table 4. June 28-July 1, 2011 pitfall trap sampling results for ants. Includes the number of each species captured in every trap at every site.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymyrmex insanus</i>	<i>Forelius pruinosus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothorax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
BA1	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	5	-	-	-	-	-	-	-	15	-
BA2	-	-	-	-	-	-	-	-	3	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	11	-
BA3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-
BA4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	4	-
BA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	9	-
BA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	4	-
BA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	21	-
BA8	-	3	-	-	-	-	-	2	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA9	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	-	-	-	-	-	-	-	-	-
BE1	-	-	-	-	-	-	-	-	1	-	-	-	4	-	-	8	-	1	-	-	1	-	-	-	-	-	-	-
BE2	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	70	-	-	-	-	-	-	-	-	-	1	-	-
BE3	-	-	-	-	-	-	-	-	-	-	-	1	1	3	-	280	-	-	-	-	-	-	-	-	-	-	-	-
BE4	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-
BE5	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	13	-	-	-	-	-	-	-	-	-	-	-	-
BE6	-	-	-	-	-	-	-	-	-	-	-	6	-	-	21	-	-	-	3	-	-	-	-	-	-	-	-	-
BE7	-	-	-	-	-	-	-	-	1	-	-	-	6	-	3	-	1	-	4	-	-	-	-	-	-	-	-	-
BE8	-	-	-	-	-	-	-	-	-	-	-	2	-	-	40	-	2	-	-	1	-	-	-	-	-	1	-	-
BE9	-	-	-	-	-	-	-	-	-	-	-	5	-	-	262	-	-	-	-	-	-	-	-	-	-	-	-	-
C1	-	-	-	-	-	-	1	-	-	-	-	2	6	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-
C2	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
C3	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	1	-	1	-	-	-	-	-	-	11	-
C4	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
C5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	1	-	-	-	-	-	-	-	-	1	-
C6	-	-	-	-	-	-	-	-	-	-	-	1	-	-	3	-	-	-	-	2	-	-	-	-	-	-	31	-
C7	-	-	-	-	-	-	-	-	-	-	-	1	2	-	22	-	-	-	-	-	-	-	-	-	-	-	-	-
C8	-	-	-	-	-	-	-	-	-	-	-	4	-	-	5	-	-	-	-	-	-	-	-	-	-	1	5	-
C9	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	1	-	-	-	-	-	2	7	-
CA1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	1	-	-
CA2	-	-	-	-	-	-	-	-	-	-	-	5	-	-	8	-	-	1	-	-	-	-	-	-	-	1	-	-
CA3	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	1	3	-	-	-	-	-	-	-	1	-	-
CA4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	95	-	-	-	-	-	-	-	-	-	1	-	-
CA5	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	5	-	-	-	-	-	2	-	-
CA6	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
CA7	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	22	-	1	1	-	-	-	-	-	-	-	-	-
CA8	-	-	-	-	-	-	-	-	-	-	-	2	1	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-
CA9	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CB1	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	27	-	-	-	-	-	1	-
CB2	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	-	-	-	41	-	-	-	-	-	-	-



Table 4. continued. June 28-July 1, 2011 - Ants.

Site Trap	<i>Acanthomyops interjectus</i>	<i>Aphaenogaster rudis</i>	<i>Camponotus americanus</i>	<i>Camponotus castaneus</i>	<i>Camponotus pennsylvanicus</i>	<i>Crematogaster cerasi</i>	<i>Crematogaster lineolata</i>	<i>Dorymymex insanus</i>	<i>Forelius pruinosus</i>	<i>Formica argentea</i>	<i>Formica difficilis</i>	<i>Formica dolosa</i>	<i>Formica incerta</i>	<i>Formica pallidefulva</i>	<i>Formica rubicunda</i>	<i>Lasius neoniger</i>	<i>Leptothorax ambiguus</i>	<i>Leptothroax pergandei</i>	<i>Monomorium minimum</i>	<i>Myrmecina americana</i>	<i>Myrmica americana</i>	<i>Nylanderia faisonensis</i>	<i>Nylanderia parvula</i>	<i>Pheidole pilifera</i>	<i>Ponera pennsylvanica</i>	<i>Solenopsis molesta</i>	<i>Tapinoma sessile</i>	<i>Tetramorium caespitum</i>
CB3	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	1	-	-	-	29	-	-	-	-	-	1	-	-
CB4	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-	52	-	-	-	-	-	1	3	-
CB5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	38	-	-	-	-	-	-	-	-
CB6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	7	-	-	-	-	-	-	-	-
CB7	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	1	-	-	-	28	-	-	-	-	-	-	-	-
CB8	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	1	-	18	-	-	-	-	-	-	-	-
CB9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	1	-	-	-	-	-	-
CC1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC2	-	-	-	-	-	-	1	-	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
CC3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-
CC4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CC5	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
CC6	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CC8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
CC9	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-
CL1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	2	-	-
CL2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	1	-	-
CL4	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	3	-	2	-	-	-	-	-	-	-	-	-	-
CL5	-	-	-	-	-	-	13	-	-	-	-	-	-	-	-	96	-	-	-	-	-	-	-	-	-	2	-	-
CL6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	1	-	-
CL7	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN1	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
EN3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
EN4	-	-	-	-	-	-	15	-	10	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
EN5	-	-	-	-	-	-	2	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
EN6	-	-	-	-	-	-	12	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
EN7	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN8	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
EN9	-	-	-	-	-	-	3	-	3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-
ES1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	13	-	-	-	-	-	-	-	-
ES2	-	2	-	-	-	-	3	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
ES3	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	5	-	1	-	-	-	-	-	-
ES4	-	-	-	-	-	-	-	-	2	-	-	-	2	1	-	7	-	-	-	-	1	-	-	-	-	-	-	19
ES5	-	-	-	-	-	-	4	-	-	-	-	-	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
ES6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	3	-	-	-	-	-	-	-	-



















Table 1. continued. June 4-7, 2010 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heliumorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
KN5	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-
KN6	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-
KN7	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
KN8	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-
KN9	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-
KS1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KS2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
KS3	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
KS4	-	-	-	-	-	-	2	-	-	-	-	-	-	-	4	-	-	-	-
KS5	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
KS6	-	-	-	-	1	-	8	-	-	-	-	-	-	-	2	-	1	-	-
KS7	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
KS8	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KS9	-	-	-	-	-	-	4	-	-	-	-	-	-	-	1	-	-	-	-
M1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
M2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	5	-	-	-	-
M3	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	-	-	-
M4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
M5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
M6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	6	-	-	-	-
M7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-
M8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	9	-	-	-	-
M9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	6	-	-	-	-
P1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-
P2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
P3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-
P4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
P5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
P6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	7	-	-	-	-
P7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
P9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
R1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
R2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
R3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
R4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

Table 1. continued. June 4-7, 2010 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
R5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
R7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
R9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S1	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-
S2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
S3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
S4	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
S5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
S6	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
S7	-	-	-	-	2	-	3	-	-	-	-	-	-	-	2	-	-	-	-
S8	-	-	1	-	1	-	10	-	-	-	-	-	-	-	2	-	-	-	-
S9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
WA4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA7	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
WA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WE3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
WE4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
WE5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
WE6	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-
WE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

[illegible]

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Helluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
CA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CB1	-	-	-	-	-	-	21	-	-	-	-	-	-	-	2	-	-	-	-
CB2	-	-	-	-	-	-	9	-	1	-	-	-	-	-	4	-	-	-	-
CB3	1	-	-	-	-	-	9	-	-	-	-	-	-	-	1	-	-	-	-
CB4	-	-	2	-	-	-	12	-	-	-	-	-	-	-	5	-	-	-	-
CB5	-	-	-	1	-	-	18	-	-	-	-	-	-	-	4	-	-	-	-
CB6	-	-	-	-	-	-	25	-	-	-	-	-	-	-	2	-	-	-	-
CB7	-	-	1	2	-	-	10	-	-	-	-	-	-	-	1	-	1	-	-
CB8	-	-	-	-	-	-	6	-	-	-	-	-	-	-	5	-	-	-	-
CB9	-	-	-	-	-	-	3	-	-	-	-	-	-	-	3	-	-	-	-
CC1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-
CC2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
CC3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CC4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
CC5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
CC6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
CC8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
CC9	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	-	-	-	-
CL1	-	1	-	-	2	-	6	-	-	-	-	-	-	-	5	-	-	-	-
CL2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-
CL3	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-
CL4	-	-	-	-	-	-	4	-	-	-	-	-	-	-	4	-	-	-	-
CL5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	8	-	-	-	-
CL6	-	-	1	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-
CL7	-	-	-	-	-	-	5	-	-	-	-	-	-	-	1	-	-	-	-
CL8	-	-	-	-	-	-	4	-	-	-	-	-	-	-	6	-	-	-	-
CL9	-	1	-	-	-	-	13	-	-	-	-	-	-	-	3	-	-	-	-
EN1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
EN2	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
EN3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	1	-
EN4	-	-	-	-	-	-	7	-	-	-	-	-	-	-	2	-	-	-	-
EN5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
EN6	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
EN7	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
EN8	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-



Table 2. continued. June 29-July 2, 2010 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pennsylvanicus</i>	<i>Heluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
HE1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
HE2	-	-	-	-	1	-	6	-	-	-	-	-	-	-	2	-	-	-	-
HE3	-	-	-	-	-	-	4	-	-	-	-	-	-	-	2	-	-	-	-
HE4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	3	-	-	-	-
HE5	-	-	-	-	1	-	4	-	-	-	-	-	-	-	1	-	-	-	-
HE6	-	-	-	-	-	-	5	-	-	-	-	-	-	-	5	-	-	-	-
HE7	-	-	-	-	-	-	6	-	-	-	-	-	-	-	3	-	-	-	-
HE8	-	-	-	-	-	-	4	-	-	-	-	-	-	-	3	-	-	-	-
HE9	-	-	-	-	-	-	10	-	-	-	-	-	-	-	2	-	-	-	-
HI1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HI2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
HI3	-	-	-	-	1	-	2	-	-	-	-	-	-	-	1	-	-	-	-
HI4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HI5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HI6	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
HI7	-	-	-	-	-	-	4	-	-	-	-	-	-	-	2	-	-	-	-
HI8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HI9	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
HO1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	2	-	-	-	-
HO2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
HO3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HO4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	2	-	-	-	-
HO5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HO6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HO7	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
HO8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
HO9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	8	-	-	-	-
KN1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KN2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-
KN3	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KN4	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	-	-	-
KN5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KN6	-	-	-	-	-	-	6	-	-	-	-	-	-	-	1	-	-	-	-
KN7	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
KN8	-	-	-	-	-	-	7	-	-	-	-	-	-	-	2	-	-	-	-
KN9	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KS1	-	-	-	-	-	-	7	-	-	-	-	-	-	-	4	-	-	-	-

Table 2. continued. June 29-July 2, 2010 - Ground Beetles.

	Ground Beetles																		
Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Helluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
KS2	-	-	-	-	-	-	8	-	-	-	-	-	-	-	8	-	-	-	-
KS3	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
KS4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	4	-	-	-	-
KS5	-	-	-	-	-	-	4	-	-	-	-	-	-	-	2	-	-	-	-
KS6	-	-	-	-	-	-	2	-	-	-	-	-	-	-	8	-	-	-	-
KS7	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KS8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
KS9	-	-	-	-	-	-	3	-	-	-	-	-	-	-	3	-	-	-	-
M1	-	-	-	-	-	-	9	-	-	-	-	-	-	-	3	-	-	-	-
M2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
M3	-	-	-	-	-	-	4	-	-	-	-	-	-	-	1	-	-	-	-
M4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
M5	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-
M6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	7	-	-	-	-
M7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-
M8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	6	-	-	-	-
M9	-	-	1	-	-	-	4	-	-	-	-	-	-	-	5	-	-	-	-
P1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	9	-	-	-	-
P2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	5	-	-	-	-
P3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-
P4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-
P5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	4	-	-	-	-
P6	-	-	-	-	-	-	4	-	-	-	-	-	-	-	3	-	-	-	-
P7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
P8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
P9	-	-	1	-	-	-	2	-	-	-	-	-	-	-	4	-	-	-	-
R1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
R2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
R3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-
R7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
R8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
R9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S1	-	-	-	-	-	-	16	-	-	-	-	-	-	-	-	-	-	-	-
S2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-



Table 2. continued. June 29-July 2, 2010 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
S3	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
S4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
S5	-	-	-	1	-	-	7	-	-	-	-	-	-	-	5	-	-	-	-
S6	-	-	-	-	-	-	25	-	-	-	-	-	-	-	-	1	-	-	-
S7	-	-	-	-	-	-	5	-	-	-	-	-	-	-	1	-	-	-	-
S8	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
S9	-	-	-	-	1	-	4	-	-	-	-	-	-	-	-	-	-	-	-
WA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WA3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1
WA4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1
WA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA7	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WA9	-	-	-	-	1	-	-	-	-	-	-	-	-	-	4	-	-	-	1
WE1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	2	-	-	-	-
WE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
WE4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WE6	-	-	-	-	-	-	5	-	-	-	-	-	-	-	2	-	-	-	-
WE7	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-
WE8	-	-	-	-	1	-	1	-	-	-	-	-	-	-	3	-	-	-	-
WE9	-	-	1	-	-	-	4	-	-	-	-	-	-	-	4	-	-	-	-

Table 3. June 3-6, 2011 pitfall trap sampling results for ground beetles. Includes the number of each species captured in every trap at every site.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Helluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
BA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
BA2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
BA3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
BA4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
BA5	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	1	-
BA7	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
BE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
BE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
BE3	-	-	-	-	1	-	-	-	-	-	-	-	-	-	4	-	-	-	-
BE4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
BE5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
BE6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
BE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
BE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
BE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
C1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
C2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
C4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
C6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
C8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
CA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
CA4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CA7	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

Table 3. continued. June 3-6, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
CA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CB1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
CB2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	7	-	-	-	1
CB3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	4	-	-	-	-
CB4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	1	-	-
CB5	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
CB6	-	-	-	-	-	-	3	-	-	-	-	-	-	-	2	-	-	-	-
CB7	-	-	-	-	-	-	2	-	-	-	-	-	-	-	3	-	-	-	-
CB8	-	-	-	1	-	-	2	-	-	-	-	-	-	-	2	-	-	-	-
CB9	-	-	-	3	-	-	4	-	-	-	-	-	-	-	5	-	-	-	-
CC1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CC2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-
CC3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
CC4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	6	-	-	-	-
CC5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-
CC6	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-
CC7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC8	-	-	-	-	1	-	-	1	-	-	-	-	-	-	4	-	-	-	-
CC9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
CL1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
CL2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-
CL3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
CL4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
CL7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
CL8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-
CL9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
EN1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
EN2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
EN3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
EN4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-
EN5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
EN6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	8	-	-	-	-
EN7	-	-	-	1	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
EN8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
EN9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	8	-	-	-	-

Table 3. continued. June 3-6, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
ES1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
ES2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-
ES3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	-
ES4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-
ES5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
ES6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
ES7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
ES8	-	-	-	-	1	-	-	-	-	-	-	-	-	-	5	-	-	-	-
ES9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
G1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
G2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-
G3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
G4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
G5	-	-	2	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
G6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
G8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	9	-	-	-	-
G9	-	1	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-
HBE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
HBE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-
HBE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-
HBE4	-	-	-	-	1	-	-	-	-	-	-	-	-	-	5	-	-	-	-
HBE5	-	-	-	-	1	-	1	-	-	-	-	-	-	-	4	-	-	-	-
HBE6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-
HBE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-
HBE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
HBE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-
HBW1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
HBW6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
HBW9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

Table 3. continued. June 3-6, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heluomorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
HE2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	11	-	-	-	-
HE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HE4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
HE5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
HE6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
HE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HE8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
HE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HI1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HI2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HI3	-	-	-	-	1	-	-	-	-	-	-	-	-	-	4	-	-	-	-
HI4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
HI5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HI6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
HI7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
HI8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
HI9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HO1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
HO2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HO3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HO4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
HO5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
HO6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HO7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
HO8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
HO9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
KN3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
KN6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
KS1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
KS2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

[illegible]

Table 3. continued. June 3-6, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heliumorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
S4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
S5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
S8	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-
S9	-	-	1	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
WA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WA2	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WA3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA4	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WA8	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
WE1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WE7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
WE9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-





Table 4. continued. June 28-July 1, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pennsylvanicus</i>	<i>Heliumorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
CA9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
CB1	-	-	-	-	-	-	8	-	-	-	-	-	-	-	7	-	-	1	-
CB2	-	-	-	-	-	-	6	-	1	-	-	-	-	-	4	-	-	1	-
CB3	-	-	-	-	-	-	8	-	-	-	-	-	-	-	1	-	-	-	-
CB4	-	-	-	-	-	-	5	-	-	-	-	-	-	-	6	-	-	-	-
CB5	-	-	-	-	-	-	14	-	-	-	-	-	-	-	4	-	-	-	-
CB6	-	-	-	-	-	-	19	-	-	-	-	-	-	-	4	-	-	-	-
CB7	-	-	-	2	-	-	11	-	-	-	-	-	-	-	4	-	-	-	-
CB8	-	-	-	-	-	-	14	-	-	-	-	-	-	-	3	-	-	-	-
CB9	-	-	-	1	-	-	15	-	-	-	-	-	-	-	1	-	-	2	-
CC1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
CC2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
CC3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CC4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CC6	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
CC7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CC8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CC9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL1	-	-	-	-	-	-	5	-	-	-	-	-	-	-	8	-	1	-	-
CL2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	3	-	-	-	-
CL3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL4	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
CL5	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
CL6	-	-	-	-	-	-	5	-	-	-	-	-	-	-	3	-	-	-	-
CL7	-	-	-	-	-	-	14	-	-	-	-	-	-	-	2	-	1	-	-
CL8	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
CL9	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
EN1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
EN2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
EN3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
EN4	-	-	-	-	-	-	5	-	-	-	-	-	-	-	2	-	-	-	-
EN5	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
EN6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
EN7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EN8	-	-	-	-	-	-	1	-	-	-	-	1	-	-	2	-	-	-	-
EN9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-

Table 4. continued. June 28-July 1, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pennsylvanicus</i>	<i>Heliumorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
ES1	-	-	-	-	-	-	6	-	-	-	-	-	-	-	2	-	-	-	-
ES2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
ES3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
ES4	-	-	-	-	-	-	10	-	-	-	-	-	-	-	4	-	-	-	-
ES5	-	-	-	-	-	-	9	-	-	-	-	1	-	-	2	-	-	-	-
ES6	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
ES7	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ES8	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
ES9	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
G1	-	-	-	-	-	-	22	-	-	-	-	-	-	-	1	-	-	-	-
G2	-	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	-	-
G3	-	-	-	-	-	-	10	-	-	-	-	-	-	-	2	-	-	1	-
G4	-	-	-	-	-	-	15	-	-	-	-	-	-	-	3	-	-	-	-
G5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G6	-	-	-	-	-	-	22	-	-	-	-	-	-	-	2	-	1	-	-
G7	-	-	-	-	-	-	11	-	-	-	-	-	-	-	5	-	-	-	-
G8	-	-	-	-	-	-	14	-	-	-	-	-	-	-	4	-	-	-	-
G9	-	-	-	-	-	-	16	-	-	-	-	-	-	-	2	-	-	-	-
HBE1	-	-	-	-	-	-	4	-	-	-	-	-	-	-	7	-	-	-	-
HBE2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
HBE3	-	-	-	-	-	-	15	-	-	-	-	-	-	-	3	-	-	-	-
HBE4	-	-	-	-	-	-	16	-	-	-	-	-	-	-	3	-	-	-	-
HBE5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	4	-	-	-	-
HBE6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	4	-	-	-	-
HBE7	-	-	-	-	-	-	16	-	-	-	-	-	-	-	3	-	-	-	-
HBE8	-	-	-	-	-	-	6	-	-	-	-	-	-	-	2	-	-	-	-
HBE9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
HBW1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
HBW3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
HBW4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
HBW6	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
HBW7	-	-	-	-	-	-	6	-	-	-	-	-	-	-	1	-	-	-	-
HBW8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HBW9	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
HE1	-	-	-	-	-	-	24	-	-	-	-	-	-	-	2	-	-	-	-

Table 4. continued. June 28-July 1, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heliumorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
HE2	-	-	-	-	-	-	13	-	-	-	-	-	-	-	5	-	-	-	-
HE3	-	-	-	-	-	-	12	-	-	-	-	-	-	-	5	-	-	-	-
HE4	-	-	-	-	1	-	7	-	-	-	-	-	-	-	3	-	-	-	-
HE5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	-	-	-	-
HE6	-	-	-	-	-	-	18	-	-	-	-	-	-	-	2	-	-	-	-
HE7	-	-	-	-	-	-	11	-	-	-	-	-	-	-	3	-	-	-	-
HE8	-	-	-	-	-	-	8	-	-	-	-	-	-	-	2	-	-	-	-
HE9	-	-	-	-	-	-	15	-	-	-	-	-	-	-	2	-	-	-	-
HI1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	9	-	-	-	-
HI2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	4	-	-	-	-
HI3	-	-	-	-	2	-	3	-	-	-	-	-	-	-	1	-	-	-	-
HI4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HI5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HI6	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
HI7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
HI8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	5	-	-	-	-
HI9	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
HO1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	4	-	-	-	-
HO2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	5	-	-	-	-
HO3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-	-
HO4	-	-	-	-	-	-	2	-	-	-	-	-	-	-	7	-	-	-	-
HO5	-	-	-	-	-	-	4	-	-	-	-	-	-	-	3	-	-	-	-
HO6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
HO7	-	-	-	-	-	-	4	-	-	-	-	-	-	-	3	-	-	-	-
HO8	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
HO9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KN1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
KN2	-	-	-	-	1	-	5	-	-	-	-	-	-	-	-	-	-	-	-
KN3	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
KN4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-
KN5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-
KN6	-	-	-	-	-	1	1	-	-	-	-	-	-	-	3	-	-	1	-
KN7	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	1
KN8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
KN9	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
KS1	-	-	-	-	-	-	16	-	-	-	-	-	-	-	4	-	-	-	-
KS2	-	-	-	-	-	-	14	-	-	-	-	-	-	-	2	-	-	-	-



Table 4. continued. June 28-July 1, 2011 - Ground Beetles.

Site Trap	<i>Anisodactylus dulcicollis</i>	<i>Anisodactylus ovularis</i>	<i>Anisodactylus rusticus</i>	<i>Chlaenius platyderus</i>	<i>Chlaenius tomentosus</i>	<i>Cratacanthus dubius</i>	<i>Cyclotrachelus sodalis colossus</i>	<i>Galerita janus</i>	<i>Harpalus caliginosus</i>	<i>Harpalus compar</i>	<i>Harpalus faunus</i>	<i>Harpalus pensylvanicus</i>	<i>Heliumorphoides praeustus bicolor</i>	<i>Panagaeus fasciatus</i>	<i>Pasimachus elongatus</i>	<i>Poecilus lucublandus</i>	<i>Pterostichus permundus</i>	<i>Scarites subterraneus</i>	<i>Scarites vicinus</i>
S4	-	1	-	-	-	-	13	-	-	-	-	-	-	-	3	-	-	-	-
S5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
S6	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
S7	-	-	-	-	-	-	7	-	-	-	-	-	-	-	2	-	-	-	-
S8	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
S9	-	1	-	-	-	-	5	-	-	-	-	-	-	-	5	-	-	-	-
WA1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA2	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-
WA3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
WA5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WA6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WA8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
WA9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
WE2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-
WE3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE4	-	-	-	-	-	-	1	-	-	-	-	1	-	-	3	-	-	1	-
WE5	-	-	-	-	-	-	3	-	-	-	-	-	-	-	1	-	-	-	-
WE6	-	-	-	-	-	-	4	-	-	-	-	-	-	-	1	-	-	-	-
WE7	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
WE8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WE9	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-