THE EFFECTS OF LOCAL GRASSLAND HABITAT AND SURROUNDING LANDSCAPE COMPOSITION ON THE PREDATORS OF GRASSLAND BIRD NESTS

A Thesis

Presented to the

Department of Biology

and the

Faculty of the Graduate College

University of Nebraska

In Partial Fulfillment

of the Requirements for the Degree

Masters of Science

University of Nebraska at Omaha

by

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May 2005
THESIS ACCEPTANCE

Acceptance for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree Master of Science in Biology, University of Nebraska at Omaha.

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Date 18 April 2005
In agroecosystems birds use fragmented grasslands which are saturated by numerous nest predators. Multiple predator threats should increase nest predation, but predator interactions complicate relationships. I studied nest predators of Dickcissels (Spiza americana), a bird of conservation concern. I asked: (1) Does predator community explain predators documented on video? (2) What predator combinations best explains nesting success? (3) How does the predator community respond to habitat at multiple levels?

The common predators on video were snakes and raccoons (Procyon lotor). Predation by Brown-headed Cowbirds (Molothrus ater), mink (Mustela vison), ground squirrels (Spermophilus spp.), and mice occurred with increased Brown-headed Cowbirds but fewer snakes suggesting a decrease in common predators may create opportunities for less important predators (MANOVA: $F_{5,6}=3.99$, $P=0.06$).

I modeled predator combinations on reproductive success and compared models using Akaike’s Information Criterion to arrive at the best working hypotheses. Single-species models did not explain satisfactory amounts of variation. The “broad” predator
group (mid-sized mammals, small mammals, reptiles, and birds) was selected as a
candidate model for each stage of Dickcissel development indicating the importance of
the entire predator community. Within the candidate models, snakes and ground squirrels
negatively influence nesting success; mid-sized mammals and small mammals vary in
direction of effect suggesting community interactions may influence predation patterns.

The predator community responded to multiple habitat levels (local vegetation,
local patch, landscape) indicating the importance of scale. In 2003, the best working
hypothesis shows the predator community associated with increased development and
decreased grassland causes a decrease in nestling survivorship. In 2004 litter depth
heterogeneity best explains the predator community and decreased survivorship at
incubation.

Although managers have limited control over landscape, my research suggests
increasing the proximity of grasslands to each other and decreasing human structures
will minimize predation by altering the predator community. Habitat manipulation to
increase reproductive success will have more value if monitoring efforts include the
entire predator community’s response to habitat along with predation rates.
ACKNOWLEDGMENTS

Funding for this project came from the University of Nebraska at Omaha Biology Department Graduate Research Funds, University of Nebraska at Omaha Summer Rhoden Biological Fellowship, University of Nebraska at Omaha Phi Delta Gamma Scholarship, University of Nebraska at Omaha Summer Graduate Scholarship, University of Nebraska at Omaha Graduate Thesis Scholarship, The American Museum of Natural History Frank M. Chapman Memorial Fund, The Center for Great Plains Studies Grant-in-aid for Graduate Students, Sigma Xi Grants-in aid of Research, USDA Biotechnology Risk Assessment Research Grants Program, and the U.S. Fish and Wildlife Challenge Grant (Boyer Chute National Wildlife Refuge).

I thank the refuge managers, Bryan Schultz at Boyer Chute National Wildlife Refuge and Larry Klimick DeSoto National Wildlife Refuge, for financial and logistical support. I thank the private land owners for permission to work on their land.

I extend my gratitude to S. Balint, T. Bean, A. Cade, K. Dougherty, T. Eidem, A. Garton, A. Hanson, J. Henningsen, J. Jorgensen, E. McIntyre, E. Mehsling, M. Ortega, N. Poole, R. Pumphrey, K. Simmons, G. Toll, and K. Wells for their work as field assistants. I especially thank those who participated in the lugging more than two tons of sand, the inking of 2,120 ink tubes, and the daily treks carrying 50 pound batteries and video systems. A special thanks to Tim Bean and John Henningsen for helping with GIS and digitizing the study sites.
I would also like to thank my committee members Dr. Larkin Powell and Dr. Thomas Bragg. I appreciate all of their comments and suggestions that improved the quality of my thesis. I realize the effort and time spent, and I extend my gratitude.

I thank the faculty and staff in the Biology Department as well as my fellow graduate students. I thank all the members of my lab Lorelle Berkeley, Shannon Engberg, Joel Jorgensen, Erin McIntyre, Nichollette Rider, and Katy Simmons. Special thanks extended to Lorelle Berkeley for conquering the cockroaches at the cabin as well as her friendship.

I extend a sincere thank you to my advisors, Dr. John P. McCarty and Dr. L. LaReesa Wolfenbarger for all their guidance and support. I am grateful for their effort and time spent in my training as a scientist. I genuinely appreciate all of their advice and help during every stage of the project and admire their dedication as mentors. I respect them both professionally and personally and am thankful for all they have done for me in making my time at University of Nebraska at Omaha a positive one.

I would like to thank my family and friends for their support and interest in my career. I thank my father, Bill Klug, for donating the two tons of sand and its transportation and my mother, Susan Klug, for joining me in the field.
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CHAPTER 1
THE EFFECTS OF LOCAL GRASSLAND HABITAT AND SURROUNDING LANDSCAPE COMPOSITION ON THE PREDATORS OF GRASSLAND BIRD NESTS

INTRODUCTION

The tallgrass prairie biome of the Great Plains is listed as a critically endangered ecosystem with less than 2% of the native ecosystem remaining (Noss et al. 1995). In the Great Plains, agriculture and urbanization have replaced native prairie and fragmented the habitat. Declines in Neotropical migrant birds that breed in grasslands have been attributed in part to these land-use changes (Herkert 1995). The fragmentation of remaining grassland habitat can affect avian populations by decreasing suitable breeding habitat (Herkert 1994), minimizing food resources (McIntyre and Thompson 2003), and increasing nest failure by means of human disturbance (Wilcove 1985, Batary and Baldi 2004) and nest predation (Johnson and Temple 1990, Herkert et al. 2003). At the proximate level, nest predation is the leading cause of avian reproductive failure with nest predation accounting for 80% of nest losses, and may be an important limit on bird populations (Martin 1993).

Understanding how predation might limit grassland bird populations is of conservation concern because grassland birds have undergone drastic population declines and are considered the most threatened of any group of birds in North America (Knopf 1994, Rich et al. 2004). According to the U.S. Breeding Bird Survey, Henslow's
Sparrows (*Ammodramus henslowii*), Grasshopper Sparrows (*Ammodramus savannarum*), and Dickcissels (*Spiza americana*) have shown mean estimated population change trends of -8.6%, -3.9%, -1.2% per year respectively from 1966 to 2003 (Sauer et al. 2004) and are representative of the patterns of the grassland bird community as a whole. Many species also face threats on the wintering grounds and during migration, however, even if the decline in Neotropical migrant birds is attributed to another cause, the severity of the decline can be buffered by increasing reproduction on their breeding grounds. The topic of nest predation not only a regional issue but one of widespread interest due to the desire to increase reproductive success of Neotropical migrants.

While predation rates on grassland birds are clearly a topic of concern, how predation might be linked to the ultimate reason for the overall decline of grassland birds is less certain because we neither know all the effects of habitat fragmentation on the ecology of birds nor how these effects might interact. In particular, while it is obvious that the tallgrass prairie biome is heavily impacted by agriculture and that nest predation is an important source of nest failure, it is not known if nest predation rates are greater in the fragmented agroecosystems of today than they were in the days of vast prairies. What we do know is that many generalist nest predators have increased in fragmented agricultural ecosystems making nest predation a special concern in the Great Plains (Dijak and Thompson 2000).

The majority of nest predation studies have investigated the patterns of nest predation in relation to habitat, especially focusing on the presence and importance of an edge effect (Paton 1994, Pasitschniak-Arts et al. 1998, Tewksbury et al. 1998, Winter et
An edge effect occurs when rates of predation are higher where two or more habitat types meet and form a relatively sharp ecotone or edge. Originally the mechanism behind increased predation was explained by increased nesting density of birds along edges resulting in more predators being attracted to those areas (Gates and Gysel 1978). Current studies have recognized that increased predation along ecotone edges may be due to generalist predators using edge habitat as travel corridors or perch sites and not to the density of nests. Most edge effect studies have focused on the nesting success of Neotropical migrant birds residing in eastern deciduous forests and have reported mixed results (Thompson et al. 2002). The general conclusion is that edge effects are not a consistent ecological trend and the importance of edge effects is variable depending on degree of fragmentation, region, size of patch, and the nature of predator assemblages (Lahti 2001). The literature also suggests that to gain a better perspective on the patterns of nest predation, predator guilds in an area must be considered in the context of fragmentation and landscape and not simply as being driven by an edge effect (Heske et al. 2001; Lahti 2001; Pietz and Granfors 2000).

Nest predation research also suggests that identifying important nest predators will help to explain the varying results of nest predation studies but this has seldom been done. Studies that do include information about the predator community only address one or two species and not the entire predator community (Angelstam 1986, Heske et al. 1999, Dijak and Thompson 2000, Renfrew and Ribic 2003). Only a few studies have investigated the direct relationships between the composition of the entire nest predator community and predation risk (Johnson et al. 1989), even though there is a general
consensus among researchers that information about the predator community is needed to understand the mechanisms of nest predation (Pietz and Granfors 2000, Heske et al. 2001, Chalfoun et al. 2002).

My research focuses on Dickcissels (*Spiza americana*), a grassland species of conservation concern to both the state and federal agencies (Knopf 1994, Rich et al. 2004). The core range of the Dickcissel includes both Iowa and Nebraska making it an ideal study location because conservation efforts may be more beneficial where the study species remains relatively abundant (Figure 1). My research expands on current nest predation studies because I investigate predation risk as a factor of the predator community's response to local vegetation structure, local patch variables, and landscape variables. Information about the relationship between predators and habitat and the ultimate influence on predation risk is important because it can be extrapolated to numerous grassland bird species.

**PREDATORS OF GRASSLAND BIRD NESTS**

Even though a great deal of work has been done to improve the reproductive success of the Neotropical migrants, information on the relationship between birds, predators, and habitat is limited. One of the critical research needs identified by the Partner’s in Flight Conservation Plan for Dickcissels and other grassland birds of conservation concern is a better understanding of nest predation, especially in agroecosystems (Partner’s in Flight – U.S. 2005). Nest predation patterns in agroecosystems may be better understood by looking at the predator community’s
response to fragmentation (Heske et al. 2001, Lahti 2001, Chalfoun et al. 2002). Chalfoun et al. (2002) reviewed evidence of predator response to fragmentation which varied according to landscape type, geographic region, predator taxon and spatial scale. Investigating spatial factors that affect the distribution, abundance, and behavior of nest predators, and relating these factors to patterns of nest predation, may be effective in understanding the relationship of habitat fragmentation and landscape on nest predation (Heske et al. 2001).

Several studies on predation have focused on mid-sized mammals such as raccoons (*Procyon lotor*) as important predators of ground-nesting passerines (Thompson et al. 1999, Pietz and Granfors 2000, Ribic and Sample 2001). In addition, small mammals, snakes, and birds have all been documented nest predators on video-camera (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003, Weatherhead and Blouin-Demers 2004). Overwhelming anecdotal and empirical evidence has shown snakes to be important predators of bird nests (Thompson et al. 1999, Renfrew and Ribic 2003, Weatherhead and Blouin-Demers 2004), and even though evidence suggests that snakes may be just as important predators as raccoons, few studies have looked at the behavior or abundance of snakes in relation to nest predation (Weatherhead and Blouin-Demers 2004). Relatively few studies combine investigations of nest predation with information about the entire predator community (Sovada et al. 2000).

With such a wide array of organisms as predators of bird nests, it is unclear how specific predator species respond to overall changes in the predator community. In quantifying the entire predator community, we may better understand how the
interactions between predators influence nest predation risk. One possible interaction is that an increase in alternate prey species may indirectly alleviate the pressure on bird nests by increasing the alternate food resources for important predators (Ackerman 2002). For example, snake predation on bird nests may decrease with increased abundance of small mammals because incidental encounters with small mammals will be greater than incidental encounters with bird nests, and snakes will be more likely to take the small mammals as prey as opposed to the bird nests. Understanding the predator community is an important gap in our understanding because little is known about the correlations between the potential predator community, the predators actually eating the nests, and nesting success.

In agricultural areas such as Nebraska and Iowa, birds are drawn to any available grassland habitat (Best et al. 1995); small fragments of habitat may be population sinks (Donovan et al. 1995) where mortality overwhelms reproductive output. This can be due to predation by wide-ranging generalist predators penetrating the grasslands during foraging combined with the predators restricted to grassland (Sovada et al. 2000, Phillips et al. 2003). Multiple predator threats are likely to decrease the chances of avian reproductive success but also complicate the relationship between predator abundance and nesting success due to intra-guild interactions and species-specific behavioral changes in predator communities of varying compositions. For example, in agricultural areas containing wooded riparian habitat an increase in raccoon abundance would be expected along with a greater rates of nest predation, where decreased predation rates would be expected in areas lacking wooded, riparian habitat but this is not always the
case (Heske et al. 1999). Consistently high predation rates in grasslands of differing vegetation structure and surrounding landscapes may be a function of various predators making nest predation patterns indecipherable by only looking at one predator type. In the absence of wide-ranging, mid-sized mammal predators, species such as snakes, ground squirrels, or birds may take their place and become relatively more important predators. The effect of compensatory predation has been shown in experiments that gauged the effect of removing generalist, mid-sized predators and have found that predation rates remain steady due to other predators taking over as the important predators (Dion et al. 1999) which lends support to the importance of investigating multiple predators. The high diversity of potential predators and their numerous interactions highlight the importance of understanding how changes in the predator community may affect predation risk. By simultaneously looking at the entire potential predator community predation patterns may be better understood.

METHODS OF STUDYING NEST PREDATORS

Most of what we know about nest predators comes from evidence derived from artificial nests and “sign” at real nests to identify predators. Both of these approaches have limitations (Pietz and Granfors 2000, Donalty and Henke 2001, Williams and Wood 2002, Thompson and Burhans 2004). Artificial nests differ from natural nests in positioning, appearance, and odor of the nest as well as in parental and nestling activity (Wilson and Brittingham 1998). Artificial nests are unreliable for predator identification because of the possible exclusion of predators that maintain olfactory search cues
opposed to visual search cues (Martin 1987, Rangen et al. 2000). In addition, artificial nest experiments often use Japanese quail eggs biasing the results due to small-mouthed predator's inability to consume the prey (Haskell 1995).

The other common approach is to examine physical evidence left at failed nests (i.e. "sign"). Characteristics such as the amount of destruction to the nest structure have been used to infer which predator was responsible for nest failure (Best 1978, Vickery et al. 1992, Christman and Dhondt 1997). Inferences drawn from the condition of the nest after egg or nestling loss are based on limited or no evidence, and is an unreliable method due to intra-specific overlap and inter-specific variation in the evidence left at the nest site (Best 1978, Christman and Dhondt 1997, Pietz and Granfors 2000).

A more reliable method of identifying predators is capturing images of predators as they take the eggs or nestlings. Initially, still images were captured when predators triggered the shutter on a camera, but these systems missed many events (Vander Haegen et al. 2002, Liebezeit and George 2003). More recently time-lapse and infrared video systems have become available that allow continual monitoring of nest activity in grasslands (Pietz and Granfors 2000). Video camera monitoring of the nests will not only be more reliable in identification, but can be used to understand the underlying mechanisms of nest predation (Renfrew and Ribic 2003, Peterson et al. 2004).
THE IMPORTANCE OF SCALE IN ECOLOGICAL INVESTIGATIONS OF NEST PREDATORS

The literature has emphasized the importance of assessing multiple scales in studies of nest predation in order to accurately explain ecological mechanisms involved (Weins et al. 1993, Donovan et al. 1997). Individual members of the predator community have been shown to respond to habitat variables at multiple levels (Gehring and Swihart 2003). In simultaneously investigating a wide variety of predator species, each with unique habitat preferences and natural histories, multiple levels are necessary to fully understand the influence of habitat on predator community composition. Habitat variables that influence the predators of grassland bird nests are nest site vegetation structure (micro-habitat variables near the nest), local vegetation structure (vegetation structure of the grassland patch containing the nests), local patch variables (size and shape of the grassland), landscape variables (the landscape composition and position of particular habitats surrounding the grassland), and biogeographic effects (demographics of predators and prey based regional biotic and abiotic factors) (Thompson et al. 2002). The cascade of spatial scales acts upon each other from largest scale to smallest scale. The importance of each scale in understanding the mechanisms of nest predation may be dependant upon another scale.

For example, local vegetation structure may be more important than the nest site micro-habitat because local vegetation structure will directly dictate those predators that penetrate the grassland during foraging or reside in the grassland. The importance of nest site habitat on predation risk is dependent on the predator types taking the nests in the
grassland, where the types of predators present are dependent on local vegetation structure. If the vegetative structure is not suitable habitat for a predator species, the likelihood of that predator species being a threat decreases because it will be less abundant. The full array of predators vary in their response to local vegetation structure, therefore, the effects of nest site habitat on predation risk may be indistinguishable when only looking at the nest site because the predator community differs among sites. In grasslands saturated with predators no nest sites will be safe from predation.

In addition to vegetation structure, local patch variables may also influence the predators entering the grassland during foraging or residing in the grassland. Grasslands with a higher edge to interior ratio may receive more visits from wide-ranging predators based on a greater amount of grassland edge that may be along travel corridors thereby increasing incidental predation at nests near the edge. Also, area sensitivity of some grassland obligate predators may decrease their presence in smaller grasslands where generalist predators may not enter larger grasslands due to a small rate of return for effort spent foraging.

Landscape composition and diversity may better explain mechanisms of nest predation than the local vegetation structure or local patch variables. For example raccoons, opossums (*Didelphis virginiana*), and garter snakes (*Thamnophis* spp.) are generalist predators well adapted to fragmentation and associated with wooded areas within agricultural development. The number of Brown-headed Cowbirds (*Molothrus ater*) is also known to increase in fragmented agricultural areas. The presence of certain predators may greatly depend on the adjacent habitat types and the juxtaposition of the
habitats. Landscapes with greater proportions of agriculture, woodlots, and human development are able to support greater numbers of generalist species that can invade grassland during foraging or disperse to nearby grasslands to reside.

The biogeographic scale is the definitive factor in characterizing populations of possible predators because the potential predator community is limited to those species whose geographic range overlaps with the region of interest. Among the species possible in a region, abundance and demographics of species also vary geographically (Thompson et al. 2002).

In this study, I am focusing on the landscape composition and diversity within a 1600 m buffer, local patch variables, and local vegetation structure in relation to reproductive success in grassland birds as a function of predator abundance and behavior. My approach is outlined in Figure 2, where I propose a framework where processes occurring at these spatial scales can impact the community of potential predators, which in turn are linked to predation on nests.

While many studies demonstrate the influence of habitat on birds and their predators, the diversity of predators and their variety of responses to habitat suggests that the relationship between nest predation and habitat may become blurred without proper knowledge of the predator community. This is further emphasized by the fact that there are no nest predation specialists in the Great Plains; rather nest predation is a result of numerous generalist predators with alternative prey sources. Therefore, nest predators are abundant in the environment because of the habitat variables influencing their main sources of prey and not just the availability of bird nests. The ecological relationship
between grassland birds, their predators, and habitat is not a simple one and is influenced by 1) avian settlement in response to habitat, 2) predator community composition in response to habitat, and 3) the interactions between birds and predators resulting in nest predation.

**Effect of Local Vegetation Structure on Birds, Their Predators, and Nest Predation**

As defined by this study, the local vegetation structure is the vegetation of the grassland site (1-50 ha). Local habitat variables have been shown to influence birds (Rotenberry and Weins 1980, Helzer and Jelinski 1999, Dechant et al. 1999 (revised 2002)), their predators (Jones et al. 1983, Morris 1998, Lariviere and Messier 2000, Setser and Cavitt 2003), and nest predation rates (Zimmerman 1982, Patterson and Best 1996, Tewksbury et al. 1998, Friesen et al. 1999, Hughes et al. 1999, Dion et al. 2000, Sovada et al. 2000). The vegetation structure of the grassland has an influence over predation risk through the presence and behavior of both birds and their predators.

Local vegetation structure can influence avian settlement. Predation risk is, in part, a function of the abundance and presence of the birds themselves and how they are influenced by local vegetation structure when selecting grasslands for nesting. One aspect of nesting success is the ability of birds to select appropriate grasslands for nesting. Grassland birds typical of the tallgrass prairie reach highest abundances in areas with high grass coverage (Rotenberry and Weins 1980). Dickcissels increase in abundance in response to dense grass, moderate forbs, moderate litter cover, high vertical
density, and homogeneity in horizontal density (Rotenberry and Weins 1980, Dechant et al. 1999 (revised 2002)).

Local vegetation structure can also influence predator community composition. The presence and abundance of potential predators is, in part, a response to vegetation. Striped skunks (*Mephitis mephitis*) have been shown to use habitats with potential for litter cover (Lariviere and Messier 2000). Snakes such as the yellow-bellied racer (*Coluber constrictor*) and the red-sided garter snake (*Thamnophis sirtalis*) prefer habitats with tall vegetation and abundant litter (Setser and Cavitt 2003). Thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) prefer habitat with short grass where Franklin’s ground squirrels (*Spermophilus franklinii*) prefer habitat with tall grass (Jones et al. 1983). Brown-headed Cowbirds prefer habitat structure characterized by grazing and choose short grass to tall grass when both are grazed but are still prevalent in non-grazed tallgrass prairies (Morris 1998).

Local vegetation structure may explain patterns of nest predation through the abundance of and interactions between birds and predators present in the grassland. One aspect of nesting success is the ability of birds to avoid predation and may be directly related to the environment in which they chose to nest. Many studies have found correlations between local vegetation structure and nesting success. Hughes et al. (1999) found Dickcissel reproductive success to increase with increased litter cover and decrease with grass canopy cover. Dickcissels and grassland birds in general show an increase in nesting success in vegetation with high forb density and heterogeneous structure (Zimmerman 1982, Patterson and Best 1996, Dion et al. 2000).
**Effect of Local Patch Variables on Birds, Their Predators, and Nest Predation**

As defined by this study, the local patch variables are the size and shape of the grassland site (1-50 ha). Viewing nest predation using local patch variables may reveal patterns that are not distinguishable by examining local vegetation structure. Numerous studies have been conducted to ascertain the importance of patch variables on birds, their predators, and predation rates (Paton 1994) but have varied in their ability to relate nest predation to patch variables depending on region, degree of fragmentation, and predator assemblages. The patch variables of the grassland site have an influence over predation risk through the presence and behavior of both birds and their predators.

Local patch variables can influence avian settlement. Predation risk is, in part, a function of the abundance and presence of the birds themselves and how they are influenced by local patch variables when selecting grasslands for nesting. Helzer and Jelinski (1999) have shown that Dickcissels and grassland birds in general respond with increased presence and richness to grassland with larger areas and smaller edge to interior ratios.

Local patch variables may explain patterns of nest predation through the abundance of and interactions between birds and predators present in the grassland. A review by Paton (1994) found that eight of eight studies examined exhibited an increase in nesting success with increasing patch size but not all studies show this effect. Other studies have found conflicting results and show that habitat patch size does not influences avian reproductive success (Friesen et al. 1999) or that predation rates are higher in larger habitat patches (Tewksbury et al. 1998). In analyzing the relationship between patch size
and duck nesting success, Sovada (2000) found an increase in predation in smaller patches which may be accounted for by smaller grasslands receiving more visits by a diversity of predators. Wilcove (1985) found that long, narrow forest fragments had higher predation rates than those of a circular shape of the same area highlighting the importance of edge to interior ratios.

**Effects of Landscape Composition and Diversity on Birds, Their Predators, and Nest Predation**

As defined by this study, the landscape variables are the diversity and percent composition of habitat types surrounding the grassland site within 400, 800, and 1600 m buffers. Viewing nest predation using landscape composition and diversity may reveal patterns that are not distinguishable by examining local patch variables and local vegetation structure. Numerous studies have been conducted to ascertain the importance of landscape in avian settlement (Soderstrom and Part 2000, Coppedge et al. 2001, Ribic and Sample 2001, Bakker et al. 2002, Fletcher and Koford 2002), predator abundances (Fritzell 1978, Morris 1998, Heske et al. 1999, Keller and Heske 2000, Gehring and Swihart 2003), and nest predation (Johnson and Temple 1990, Andren 1992, Burger et al. 1994, Donovan et al. 1997, Bergin et al. 2000, Winter et al. 2000, Roos 2002) with varying results depending on region, degree of fragmentation, and predator assemblages. Multiple landscape indices have been used in landscape studies such as landscape composition (diversity and proportion of habitat types) (Turner 1989, Dunning et al.
1992), landscape connectivity (distance between similar habitats) (Taylor et al. 1993), and landscape richness (number habitat types) (Bergin et al. 2000).

Landscape composition and diversity can influence avian settlement. Predation risk is, in part, a function of the abundance and presence of the birds themselves and how they are influenced by landscape when selecting grasslands for nesting. Many studies have shown bird abundance to be related to landscape variables at multiple levels within the landscape (Soderstrom and Part 2000, Coppedge et al. 2001, Ribic and Sample 2001, Bakker et al. 2002, Fletcher and Koford 2002).

Landscape composition and diversity can also influence predator community composition. The presence and abundance of potential predators is partially a response to landscape features, and each predator type responds uniquely to overall changes in landscape. Raccoons are shown to preferentially use building sites, wooded areas, and wetlands both day and night during the avian breeding season (Fritzell 1978). Striped skunks (Mephitis mephitis) have been shown to use forests and increase in presence with greater proportion of crop fields, and human development; opossums avoid agricultural fields but use corridors; coyotes (Canis latrans) avoid forests, select corridors, and use agricultural fields; and red foxes (Vulpes vulpes) avoid agricultural fields and use forests and corridors (Gehring and Swihart 2003). Although mid-sized generalist predators differ in their habitat preferences, these species reach their highest population densities in fragmented agricultural landscapes and are a threat to grassland birds (Heske et al. 1999).

According to Blouin-Demers (2001) snakes use habitat selection as a tool in thermoregulation; and black rat snakes (Elaphe obsoleta) are often found in forest edges
after feeding regardless of where the meal was taken. Blue racers (*Coluber constrictor*) and fox snakes (*Elaphe vulpina*) have been shown to prefer old fields and prairie restorations and avoid agricultural fields and forests (Keller and Heske 2000). Brown-headed Cowbird parasitism patterns are often the most evident at the landscape scale and increased parasitism is a result of increased habitat structure (woodlots) characterized by fragmentation and available feeding sites (agricultural sites) (Morrison and Hahn 2002).

Habitat variables surrounding the grassland influence nest predation risk through the suite of potential predators. The landscape mosaic surrounding the grassland has an influence over predation risk through the presence and behavior of birds and their predators (Andren 1992, Donovan et al. 1997, Bergin et al. 2000, Roos 2002). Roos (2002) found that nest predation risk was higher in grasslands contained in agricultural landscapes than those contained in forested landscapes in Sweden. Overwhelming evidence shows that prairie fragments surrounded by wooded habitats are associated with greater nest predation demonstrating that predation risk varies with surrounding landscape and region (Johnson and Temple 1990, Burger et al. 1994, Bergin et al. 2000, Winter et al. 2000). However, without a better understanding of the predator community, we cannot identify causal relationships.

**STUDY AREA**

My research is conducted in eastern Nebraska and western Iowa in the Dissected Till Plains physiographic region where the landscape is intensive agriculture interspersed with small parcels of restored or marginal grasslands (Fitzgerald and Pashley 2000). I
worked at a total of 36 grassland sites with only select sites being used in both 2003 and 2004 (a total of 23 sites in 2003 and 30 sites in 2004) (Figure 3). The sites were located across an 815 km² area.

Both public and private grasslands were used, and the variety of management activities used created differences in the local vegetation structure. Grassland sites differed in their isolation, shape, and size with areas ranging from 1 to 50 ha. I worked at 16 farm sites, consisting of one Conservation Reserve Program (CRP) parcel, two switchgrass (Panicum virgatum) stands, and 13 sites consisting of agricultural terraces within crop fields planted to cool season brome (Bromus spp.). I collected data from nine grassland sites (7-110 ha) at the Desoto National Wildlife Refuge (3,166 ha) and six grassland sites (7-45 ha) at the Boyer Chute National Wildlife Refuge (1,295 ha). I had three grassland sites (4-28 ha) at the Allwine Prairie Preserve (65 ha), a 30-year old restored prairie managed by the University of Nebraska at Omaha and one grassland site at the Cuming City Cemetery Nature Preserve (4 ha), a remnant native prairie managed by Dana College. All areas containing the grassland sites including the refuges and preserves are a mosaic of habitat types characterized by agriculture consisting mainly of corn and soybeans. Habitats surrounding the grassland sites of interest included human development, woodlots, forests, wetlands, water, grasslands, and marginal grasslands (terraces, waterways, ditches) but minimal hayfields and pasture.
PROJECT DESIGN

I designed my research to evaluate mechanisms for predation patterns by looking at the potential predator community’s influence on predation rates in addition to the association between the potential predator community and the most common predators on video (Figure 2). To further understand the potential predator community, I evaluated the predators’ response to habitat at multiple levels including local vegetation structure, local patch variables, and landscape composition and diversity. From this understanding of the predator community, I look at predation rates in direct relation to habitat. If the habitat variables found to explain the predator communities are also shown to directly impact nesting success, management recommendations for habitat alterations can be given to induce semi-natural predator control and reduce predation risk.

This approach is unique in that I include (1) information on the entire potential predator community, (2) identification of predators actually documented on video, and (3) the quantification of habitat including local vegetation structure, local patch variables, and landscape composition and diversity in relation to predation rates on natural nests. My goal is to understand interactions among the habitat variables and the predator community to understand what produces variation in predation rates (Figure 2).

I ask six questions in this study: (1) Does the predator community explain the predators documented on video? (2) What grouping of the predator community (guild to species) best explains nest predation? (3) How do the individual predator types as members of the entire predator community influence the probability of survival for Dickcissel nests? (4) What habitat variables including landscape composition and
diversity, local patch variables, and local vegetation structure influence the presence and abundance of predators and how does this influence the probability of survival for bird nests? (5) What spatial scales are the most important in best explaining predator community composition and individual predator presence? (6) What management recommendations can be offered from this work to reverse the decline in grassland birds?

OVERVIEW

Each of the following chapters addresses a specific objective of my work’s primary goals. Chapter 2 discusses the influence of the predator community on nest predation risk in grassland birds. It also examines the relationship between the potential predator community and the predators recorded on video eating Dickcissel nests. Chapter 3 evaluates causal mechanisms for predation patterns by looking at the predator community’s response to habitat including the local vegetation structure, local patch variables, and landscape composition and diversity. Chapter 4 addresses the site-based and regional management implications for grassland birds. The influence of my research for site-based conservation at DeSoto National Wildlife Refuge and Boyer Chute National Wildlife Refuge will be explored along with the conservation implications for conservation of grassland birds in the Great Plains. I also use Chapter 4 to detail the future directions that nest predation research can be taken.
REFERENCES


Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory

predators and nest fates reliable? An experiment with Wood Thrushes
(Hylocichla mustelina) using miniature video cameras. The Auk 119:1126-1132.

Wilson, G. R., and M. C. Brittingham. 1998. How well do artificial nests estimate success
of real nests? The Condor 100:357-364.

levels in tallgrass prairie. The Condor 102:256-266.

Zimmerman, J. L. 1982. Nesting success of Dickcissels (Spiza americana) in preferred
and less preferred habitats. The Auk 99:292-298.
Figure 1. Summer distribution of Dickcissels illustrated by the U.S. Breeding Bird Survey (BBS) (from Sauer et al. 2004). Darker colors indicate higher densities of Dickcissels on BBS survey routes.
Figure 2. This diagram illustrates the variables that influence nest predation: (a) shows the influence of the potential predator community on the documented nest predators taking the nests and the influence on predation rates, discussed in Chapter 2; (b) shows the landscape composition and diversity, local patch (grassland size and shape), and local vegetation structure variables that influence the presence and abundance of the potential predators, discussed in Chapter 3.
Figure 3. Study sites for this research were located in eastern Nebraska and western Iowa and ranged over an 815 km² area. These included 16 farm sites (red dots) and sites at two natural areas managed by universities- Allwine Prairie Preserve (3 sites) and Cuming City Cemetery (1 site). Sites were also located at two large National Wildlife Refuges (NWR)- Boyer Chute NWR (six sites) and DeSoto NWR (nine sites).
CHAPTER 2

THE INFLUENCE OF PREDATOR COMMUNITY ON NEST PREDATION IN DICKCISSELS*

Abstract: In agricultural areas, grassland birds are drawn to any available grassland habitat. Often, these remaining fragments are saturated with potential predators. Multiple predator threats are likely to decrease the chances of avian reproductive success but the relationship maybe complicated by interactions among predators. I monitored the community of potential predators at 36 sites using standard census methods, and compared the predator community to the predators at dickcissel (Spiza americana) nests determined by time-lapse video. I documented nine snakes, six raccoons (Procyon lotor), four ground squirrels (Spermophilus spp.), two Murine rodents (Peromyscus sp.), two brown-headed cowbirds (Molothrus ater), and one mink (Mustela vison) as predators of dickcissel nests in this area. I found the predators on video are associated with the potential predators in corresponding surveys with the potential predator community explaining the presence or absence of subsidiary predators (mink, mice, brown-headed cowbirds, and ground squirrels) on video (MANOVA: $F = 3.99$, df = 5 and 6, $P = 0.06$). Subsidiary predation events occurred at sites with more brown-headed cowbirds and fewer snakes suggesting a decrease in the most common predator (snakes) may create an opportunity for predation events by predators of lesser importance. I examined seven groupings of the predator community in relation to

*To be submitted to Journal of Wildlife Management. Authors: Klug, P.E.; Wolfenbarger, L.L; McCarty, J.P
survivorship of dickcissel nests using Akaike's Information Criterion. Considering a set of candidate models for which there is support (Akaike's weights $> 0.1$), the broad predator community (mid-sized mammals, small mammals, reptiles, birds) was consistently selected as a candidate model to explain the predator community's effect on nest predation in both years. Two exceptions occurred; for the incubation and nestling stages in 2004, selected models included only raccoons and documented snakes and not the broad predator community. The candidate models show that snake abundance had a negative influence on nesting success and snakes were also the most common predators on video. The candidate models show that ground squirrel abundance negatively influenced nesting success and ground squirrels are the second most common predator on video in 2003. The effect of mid-sized mammal and small mammal abundance varied in direction indicating that community interactions among members of the mid-sized mammal groups or small mammals may influence nest predation risk. Information about the entire predator community will maximize the success of management efforts intending to increase the reproductive success of grassland birds breeding in agricultural mosaics. My results emphasize that management strategies should consider the entire predator community because of the high diversity of predators and interactions among predators. Attempting to increase nesting success by directly managing specific species may not be effective due to compensatory predators that are present to take the place of the removed predator. Studies that simultaneously look at the predator community's response to habitat in conjunction with nest predation rates may better explain the value of habitat manipulation for predator control and increasing avian reproductive success.
Grassland birds are of management concern because they have undergone population declines greater than any group of birds in North America (Knopf 1994, Rich et al. 2004). The ultimate cause of these declines is likely a function of habitat fragmentation and land-use changes in the Great Plains of North America (Herkert 1994). Fragmentation of remaining habitat can affect avian populations by decreasing suitable breeding habitat (Herkert 1994), minimizing food resources (McIntyre and Thompson 2003), and increasing nest failure by means of human disturbance (Wilcove 1985, Batary and Baldi 2004) and nest predation (Johnson and Temple 1990, Herkert et al. 2003). At a proximate level, nest predation is the leading cause of avian reproductive failure, with nest predation accounting for 80% of nest losses, and may be a limit on bird populations (Martin 1993).

Nest predation is an important issue if wildlife professionals wish to reverse the declining populations of Neotropical migrants. Although the reproductive success of Neotropical migrants has received extensive attention, information on the relationship between birds and the entire predator community is limited. Researchers have recognized the importance of identifying the predator community to better understand the mechanisms of predation, but despite the general consensus on this point, there is a lack of studies that follow the entire predator community in conjunction with measuring nest...
predation rates. Understanding the predator community is important because little is
known about the correlations among members of the predator community, the
documented predators eating the nests, and nesting success of the birds affected.

In agricultural areas grassland habitat may be saturated with potential predators
due to wide-ranging generalist predators penetrating the grasslands during foraging,
combined with the predators restricted to the grassland habitats (Sovada et al. 2000,
Phillips et al. 2003). Multiple predator threats are likely to decrease avian reproductive
success. Multiple predators also complicate the relationship between predator abundance
and predation risk due to intra-guild interactions and species-specific behavioral changes
in predator communities of varying compositions. Small mammals, mid-sized mammals,
snakes, and birds have been documented previously as nest predators in the grasslands of
North America (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic
2003, Weatherhead and Blouin-Demers 2004). Each of these predator types responds
uniquely to overall changes in the predator community and interactions between potential
predators. For example, an increase in prey species may indirectly alleviate the pressure
on bird nests by increasing the alternate food resources for important predators
(Ackerman 2002). Also the absence of a predator type may change the behavior of the
overall community. For example, consistent predation rates in patches of differing mid-
sized mammal abundances may be a function other compensatory predators making nest
predation patterns indecipherable by looking at mid-sized mammals alone (Heske et al.
1999). The high diversity of potential predators and their numerous interactions highlight
the importance of understanding how changes in the predator community may affect predation risk.

The majority of previous studies of nest predation have focused on a particular taxonomic group or species (Chalfoun et al. 2002). Species studied include mid-sized mammals, such as raccoons, canines, and striped skunks (*Mephitis mephitis*) (Dion et al. 1999, Heske et al. 1999, Dijak and Thompson 2000, Lariviere and Messier 2001, Schmidt 2003), bird predators such as brown-headed cowbirds and corvids (Johnson and Temple 1990, Andren 1992), and small mammals (Ackerman 2002, Bradley and Marzluff 2003). Anecdotal and empirical evidence has also shown snakes to be important predators of bird nests (Thompson et al. 1999, Renfrew and Ribic 2003, Weatherhead and Blouin-Demers 2004), but no studies have looked at the behavior or abundance of snakes in relation to nest predation. Nest predation studies have varied in whether predation patterns were explained by predator abundance, suggesting the need to include the entire predator assemblage of an area to explain predation patterns (Donovan et al. 1997, Lahti 2001).

Most of what we know about nest predators comes from evidence derived from artificial nests and "sign" (i.e., what remains and the state of the nest when a researcher returns to monitor a nest) at empty nests to identify predators. Both of these approaches have limitations (Haskell 1995, Pietz and Granfors 2000, Donalty and Henke 2001, Williams and Wood 2002, Thompson and Burhans 2004). A more reliable method of identifying predators is capturing images of predators as they take the eggs or nestlings from real nests. Time-lapse and infrared video systems now allow continual monitoring
of nest activity in grasslands (Pietz and Granfors 2000). Video camera monitoring of the nests will not only be more reliable in predator identification, but also can be used to understand the underlying mechanisms of nest predation (Renfrew and Ribic 2003, Peterson et al. 2004).

In this study I ask three questions: (1) does the composition of predator communities explain the predators documented locally on video? (2) What potential predator communities best explain the probability of survival for dickcissel nests? (3) What grouping of the predator community (guild to species) will best explain nest predation? To address these, I compare information on the potential predator community to information on nest predators documented at nests and to nest predation rates (Figure 1).

STUDY AREA

I collected data at 36 distinct study sites (23 in 2003 and 30 in 2004) located in eastern Nebraska and western Iowa. The sites ranged over an 815-km² area. This area lies in the Dissected Till Plains physiographic region where the landscape is intensive agriculture interspersed with small isolated parcels of restored or marginal grasslands (Fitzgerald and Pashley 2000). Sites were located both on private farmland and at wildlife refuges. The private grasslands in the Nebraska and Iowa that I used are managed by minimal grazing and limited burning, though in some cases woody plants are removed manually or with herbicides. I had 16 farm sites, consisting of a Conservation Reserve Program (CRP) parcel, 2 switchgrass (*Panicum virgatum*) stands, and 13 sites of
agricultural terraces within crop fields planted to cool season brome (*Bromus* spp.). The refuge grasslands in the area are managed with prescribed burning and no grazing. I had 9 sites at the Desoto National Wildlife Refuge and 6 sites at the Boyer Chute National Wildlife Refuge. I had 3 sites at the Allwine Prairie Preserve (managed by the University of Nebraska at Omaha) and a site at the Cuming City Cemetery Nature Preserve, a remnant native prairie (managed by Dana College).

**METHODS**

Dickcissel nests were found and monitored to establish reproductive success at each grassland site. Video monitoring was used at real nests to document predators consuming or removing dickcissel offspring. Information on the potential predator community was used to construct a model that best explains nest predation. The information on the potential predator community was also used to explain the documented predators found on video at the corresponding sites. I followed the university approved animal welfare protocol for all procedures involving vertebrates (IACUC # 03-038-05).

**Nest Monitoring**

Dickcissels construct cup nests anywhere from the ground to one meter above the ground. Nests were located using behavior observations and rope dragging techniques and were checked for contents and parental activity every third day to monitor reproductive success. The daily survival rates were calculated for each nest using a
Mayfield correction (Mayfield 1975). The mean probability of survival was calculated for each stage of development (incubation, nestling) at each site. A mean probability of overall survival was calculated at each site by multiplying the survivorship rate of incubation and nestling stages with hatch success. Number fledged was obtained by monitoring nest areas around the expected fledge date for parental feeding and alarm calls. For analyses, I used the mean probability of survival at incubation, the mean probability of survival of nestlings, the mean probability of overall survival, and the mean probability of number fledged for each site.

**Video Monitoring**

To document nest predators, I used video systems to record activity at the nest. The video systems included an infrared bullet camera, hooked to a time-lapse video recorder by 8.5 m of cable that was buried under the litter (Figure 2). The camera was connected to a wooden dowel staked into the ground or supported by a tripod. The camera was set 15 to 20 cm above the nest. This distance allowed activity to be recorded at the nest while camouflaging the camera with the vegetation to minimize female abandonment. Abandonment was also minimized by setting the system up in under 20 minutes and between the hours of 1000 and 1600 hr in dry, comfortable temperatures. The system was set up in both the incubation and nestling stages. For the incubation stage the female had incubated for three to five days before a video-system was placed at the nest. In 2004 the female was acclimated to the presence of the video-system by placing the camera 4 m from the nest two days before set-up. The power was obtained by
a connection to a power converter connected to a sealed lead acid battery (King et al 2001). Contents of the nest were checked every 24 hours by connecting a portable monitor to the system. The battery supply and video-cassette were changed at each 24 hour visit.

**Predator Community**

The relative abundance of predators at each site was monitored using standard methods for each group (see below). Only individual predators or predator groups that were found at more than six sites in a given year were included in analyses.

*Mid-sized Mammals.*—

I set up two track stations at each site to monitor mid-sized mammals. Track stations were a 1 m diameter of cleared vegetation, sprayed with glyphosate herbicide, filled with sand, and baited to attract predators (Kuehl and Clark 2002). I baited the track station with a can of fish-flavored cat food in the center. Each station was left for 48 hours before the station was checked for tracks. After 48 hours the station was checked for tracks and the sand was smoothed. The station was checked a second time after another 48 hours. Precipitation interferes with the visibility of the tracks causing survey information to be lost and inequalities in survey information between sites and years. In 2003 each site was successfully surveyed one to four times from June to August. In 2004 each site was successfully surveyed one to six times from May to August. A track index was calculated by taking the number of stations with tracks over the number of track
nights per site. The means of the track indices from each visit were calculated to get a seasonal probability for each site.

*Small Mammals.*

Abundance of small mammals was estimated using ten track tubes at each site. Track tubes consisted of two 30-cm plastic gutters fastened together to form a tube with a binder clip on one side and duct tape on the other (Glennon et al. 2002). Felt inkpads were fastened at both ends and strips of contact paper, sticky side up, were used as a track surface. I preserved and identified tracks on the contact paper by placing it on white paper. For each survey period, tubes were monitored at 48 hour intervals over a four day period so that two samples of tracks were collected at each tube.

In 2003 each site was surveyed twice with four track nights per survey from June to August. In 2004 each site was surveyed twice with four track nights per survey from May to August. Each site had ten tubes. Tracks were identified by separating ground squirrel tracks from other rodent tracks. A track index of small mammal, ground squirrel, and other rodent tracks were calculated by taking the number of tubes with tracks over the total number of tubes. The means of the track indices from each visit were calculated to get a seasonal probability for each site.

*Reptiles.*

Ten coverboards (60 x 180 cm plywood sheets) were placed at each site to monitor reptiles (Parmeleee and Fitch 1995). In 2003 all ten coverboards at each site were checked five to six times from June through August. In 2004 each site was checked ten or 11 times from May through August. Reptiles under boards were captured and
identified. Mean number of snakes per board was calculated for individual sites by dividing the number of snakes by the number of boards at the site and standardized by the number of checks in a given year.

_Birds._

Point counts were used to estimate abundance of avian predators. Four point counts were conducted over two field seasons (Ralph et al. 1995). Point counts were ten minutes in duration and possible avian predators were counted in the grassland site, as flyovers, and on the exterior of the grassland site. Point counts included blue jays (_Cyanocitta cristata_), American crows (_Corvus brachyrynchos_), common grackles (_Quiscalus quiscula_), brown-headed cowbirds, red-tailed hawks (_Buteo jamaicensis_), and American kestrels (_Falco sparverius_).

**Statistics**

I used a Fisher Exact Test to compare the reproductive success of nests with cameras and nests without cameras. The Fisher Exact Test compares the probabilities of predation and fledging between the nests with cameras and those without. If the probabilities do not differ there is not a significant difference in predation between the nests with cameras and nests without cameras.

I used Multivariate Analysis of Variance (MANOVA) to test 1) whether the mean surveys of the predator community differed in relation to the documented predators captured on video (modeled as a sum response), and 2) whether documented predators captured on video were associated with differences in the mean surveys of particular
predators (modeled as an identity response) (JMP version 5, SAS Institute, Inc., Cary, NC). MANOVA tests whether differences in the dependent variables ( predator surveys) exist among groups (presence or absence of documented predators recorded on camera at each site) by creating a new dependent variable that maximizes differences among groups. The null hypothesis for the test is that no differences in the new composite variable occur in relation to the independent variables ( predator events recorded on camera). Based on the documented predators observed at the 15 sites where cameras were used, I categorized camera events into three independent variables for analysis: a) presence or absence of raccoon events, b) presence or absence of snake events, and (c) presence or absence of subsidiary predator events (ground squirrels, Murine rodents, brown-headed cowbirds, and mink). These categories produce similar sample sizes for the presence and absence of predation events within each category.

To determine whether predator surveys at the 36 grassland sites explained variation in probability of survival at each stage of development and in overall reproductive success, I used a model selection approach. I generated hypotheses using seven combinations of the explanatory variables ( predator surveys) derived a priori from knowledge of predators known to influence nesting success and from video data of documented predators found in this study (Table 1). Each combination contained information from the mid-sized mammal, small mammal, reptile, and bird surveys, but varied in categorization of various taxa. The combinations included potential predators, documented predators, and the most common predators on video giving seven models for each stage of development (incubation, nestling, number fledged and overall survival) per
year. Predator groups were included in the evaluations only if they were present at more than 6 sites per year creating a difference between years. Documented and potential predators were evaluated both as broad categories and, where possible, as individual species.

I employed Akaike Information Criterion (AIC) to select the best models for each stage of development (Burnham and Anderson 1998). The value for AIC is,

\[ AIC = -2 \ln(\ell(\hat{\theta}|data)) + 2k \]

where \( \ln(\ell(\hat{\theta}|data)) \) is the value of the maximized log-likelihood over the unknown parameters \( (\theta) \), given the data and the model, and \( k \) is the number of parameters. Other models may have values close to the value of the best model so it is inadequate to only select the model with the lowest AIC. To compensate for model selection uncertainty each alternative model can be evaluated by using the difference between the model AIC and the minimum AIC,

\[ \Delta_i = AIC_i - \min AIC \]

Models with \( \Delta_i \leq 2 \) are considered to have enough support as a candidate model. The smaller the likelihood of a model being the best model the in set of candidate models the higher the \( \Delta \) (Burnham and Anderson 1998).

Akaike weights, \( w_i \),

\[ w_i = \frac{\exp(-\frac{\Delta_i}{2})}{\sum_{r=1}^{k} \exp(-\frac{\Delta_r}{2})} \]
can also be considered as indicators of the strength of the $i$ model. The $w_i$ is the probability that model $i$ is the best model in the set of all models considered (Burnham and Anderson 1998).

To determine the explanatory power of candidate models I used McFadden's $\rho^2$, a value between "0" and "1" which is obtained through a transformation of the likelihood ratio statistic,

$$\text{McFadden's } \rho^2 = 1 - \frac{LL(B)}{LL(0)}$$

where $LL(B)$ is the log-likelihoods of the full model and $LL(0)$ is the log-likelihood of the constant only model. McFadden's $\rho^2$ is analogous to but is much lower than $R^2$ and a value in the 0.2 to 0.4 range can be considered highly satisfactory (Tabachnick and Fidell 2001).

RESULTS

Potential Predators

Potential predators documented at the sites included mid-sized mammals, small mammals, reptiles, and birds (Table 2).

Documented Predators

Animals documented removing eggs or nestlings were considered predators whether or not they consumed what they removed. In 2003, I recorded 14 predation events (four snakes, two raccoons, four ground squirrels, two Murine rodents, and one
brown-headed cowbird) and two fledgling events on video. In 2004, I recorded ten predation events (five snakes, four raccoons, and one brown-headed cowbird) and ten fledging events (Figure 3). In both years combined I recorded two Murine rodents, two ground squirrels, four raccoons, four snakes, one brown-headed cowbird eating eggs, and two raccoons, two ground squirrels, one mink, and five snakes, and one brown-headed cowbird taking nestlings (Figure 4). Video footage of documented predators was digitized and predators were identified (Figure 5).

Nesting Success

Nesting success was calculated for 170 nests in 2003 and 212 nests in 2004, and 90% of nests were found prior to or during incubation. Over the course of two years I placed cameras at 33 nests. Of these, 24 failed due to predators (73%) and nine fledged (27%). Over this same period, 370 nests without cameras were monitored and 249 failed due to predators (67%), while 121 survived to fledge (33%). Using a two tailed test (because predators could be attracted to or repelled by cameras) this difference was not significant (Fisher Exact Test, $P = 0.57$) indicating that presence of camera did not increase or decrease predation rates.

Predator Community and Documented Predators

My first objective was to determine if the community of predators surveyed at a site (potential predators) explained the predators that actually destroyed the nests (documented predators). For the purpose of this analysis I grouped the documented
predators into three categories: snakes, raccoons, and subsidiary predators. Snakes and raccoons accounted for the largest number of predation events. The category "subsidiary predators" includes all other species and was used because the analysis techniques are more robust with a limited number of categories.

The sites possessing video events were categorized based on the presence or absence of each of these documented predator categories. The communities of potential predators were compared among sites where each documented predator was documented and not documented. For example all sites that documented snakes on video were compared to the sites that lacked documented snakes on video; all sites that documented raccoons on video were compared to the sites that lacked raccoons on video; and all sites that documented subsidiary predators on video were compared to the sites that lacked subsidiary predators on video while controlling for the other variables. This was accomplished by using a MANOVA where each of the three documented predator categories was entered as an independent variable with the response being the potential predator community.

I analyzed the association between the predator community and the camera events using two approaches for modeling the composite predator community variable created in MANOVA. First, I tested whether the cumulative predator community (e.g., a single canonical score derived from the sum of the surveys) was associated with the presence of raccoon, snake or subsidiary predation events. I also tested whether an association existed when each predator survey contributed individually to the composite variables representing the predator community (e.g., five canonical scores derived from a linear
combination of the predator surveys). Further inference can be made by examining the predator categories (raccoon, snake, subsidiary) individually to see which survey data (raccoon, documented snake, ground squirrel, other rodent) accounts for the most variation (explained by eigenvalue) among the three predator categories by examining the eigenvectors for each guild in the survey under the highest canonical correlation score. Guilds that explained the most variation will have high positive numbers or low negative numbers depending on direction of effect.

When testing the cumulative predator community, the documented predators on video are associated with the predator surveys (MANOVA, $F = 16.19$, df $= 3$ and $10$, $P = 0.0004$). When a snake was documented on video the cumulative predator community at the corresponding site tends to be different from the sites where no snakes are found on video (MANOVA, $F = 3.72$, df $= 1$ and $10$, $P = 0.08$). When a raccoon was documented on video the cumulative predator community at the corresponding site is significantly different from the sites where no raccoons were found on video (MANOVA, $F = 7.69$, df $= 1$ and $10$, $P = 0.02$). When subsidiary predators are documented on video the cumulative predator community at the corresponding site differed significantly from the sites where no subsidiary predators are found on video (MANOVA, $F = 17.46$, df $= 1$ and $10$, $P = 0.002$). When the MANOVA is run to test the cumulative effect of the predator abundances found in the survey, the abundances of all predator types are combined into one canonical score and the importance of the individual predators are not known. When the test is significant, it tells us that the predator communities are different among sites
but not how they are different; sites with a high canonical score have larger combined abundances of predators.

When correlations among potential predators are controlled, the identification of raccoon, snake, or subsidiary predators from camera tended to be associated with differences in the predator surveys (MANOVA, Wilks’ $\lambda = 0.05$, df = 15 and $16.97 F = 2.14$, $P = .0673$). This trend is due to the effect of subsidiary predators (MANOVA, $F = 3.99$, df = 5 and 6, $P = 0.06$) and not raccoon or snake predation events with most of the variation in the composite variable created from the predator surveys being explained by lower snake numbers and higher cowbird and rodent numbers in the sites with subsidiary predator events (Table 3). Therefore, this suggests that fewer snakes and more cowbirds and rodents are associated with sites where subsidiary predators were identified on camera.

**Predator Community and Nesting Success**

My second objective was to determine what potential predator groupings best explain the probability of survival for dickcissel nests. I used the predator types as dependent variables (Table 1) to explain survivorship at multiple stages of development (incubation, nestling, number fledged) and overall reproductive success. I constructed seven possible models based on *a priori* information of predators known to influence nesting success and the predators I documented on video in this region (Table 1). I used AIC to select candidate models from the set of possible models. AIC compares the explanatory value of the possible models. From the set of possible models the candidate
models are those with a $\Delta_i \leq 2$ and a $w_i \geq 0.1$ and represent the combinations of variables that best explain variance in the dependent variables.

Models containing the potential predator (broad) community were consistently selected as competing candidate models for each stage of development and for overall reproductive success in 2003 (Table 4). The variance explained by these models (estimated as McFadden's $\eta^2$) ranged from 0.10 to 0.29. When incorporating the strength of association, a candidate model of potential predator community explaining nestling survivorship (McFadden's $\eta^2 = 0.29$) and a candidate model of the potential predator community explaining the number of fledglings (McFadden's $\eta^2 = 0.19$) are considered "highly satisfactory" (Table 4).

In 2004 the best models included the potential predator (broad) to explain number fledged and overall survival rate. The variance explained by these models (estimated as McFadden's $\eta^2$) was 0.05 and 0.08 respectively. Two single factor models of raccoons (McFadden's $\eta^2 = 0.02$) and of documented snakes (McFadden's $\eta^2 = 0.02$) and a two-factor model with raccoons and documented snakes (McFadden's $\eta^2 = 0.03$) were selected as candidate models for explaining survival at the incubation stage. For the nestling stage, modeling the effect of raccoons on nestling survival emerged as the single best model with a McFadden's $\eta^2$ of 0.03 (Table 5).

Some predators consistently had negative impacts on measures of dickcissel reproductive success. Ground squirrels and reptiles in 2003 and documented snake predators in 2004 were negatively related to reproductive success when present in selected models (Table 4 and Table 5). However, avian predators as a group as well as
brown-headed cowbirds as a single group positively influenced number fledged and incubation, nestling and overall survival (Tables 4 and 5) in 2003 and 2004 when present in selected models. Similarly, a total ten selected models in 2003 and 2004 contained mid-sized mammals; in nine, the mid-sized mammal grouping positively influenced probability of survival and number fledged. However, it is notable that among selected models containing a species-level grouping of raccoons (only present in 2004), a positive or negative effect appears equally likely. (Table 5).

DISCUSSION

Over the course of the study I documented 24 predation events by ten species (Figure 5). The variety of predators on video lends further evidence to the high diversity of predators saturating small grasslands in an agricultural matrix (Figure 3). The most common predators were snakes, raccoons, and ground squirrels (Figure 3). The prevalence of raccoons and ground squirrels is typical of previous studies of predators on grassland birds (Pietz and Granfors 2000, Renfrew and Ribic 2003). Somewhat unusual is the high predation rates by snakes when compared to other grassland studies (Table 6). Snakes are known to be predators of bird nests (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003, Weatherhead and Blouin-Demers 2004) but have mainly been documented in forests and old fields. My sample size of documented predator events is consistent with previous studies (Pietz and Granfors 2000, Renfrew and Ribic 2003). It is likely that additional predator species would be detected at a low frequency with a larger sample size. However, given the consistency of the of snake events across
years it is unlikely that a larger sample would change the importance of the most common predators documented on video.

My censusing methods provided information on all the predators documented on video (Table 2). Among the most common species were raccoons, garter snakes, fox snakes, brown-headed cowbirds, and Murine rodents (documented predators) as well as skunks, coyotes, American crows and common grackles which, while potential predators based on previous studies, were not observed taking nests.

**Predator Community and Documented Predators**

One question unanswered by previous studies of documented predators is whether different types of predators are equally likely to take nests or if some predators are disproportionately important in relation to their abundance in the community. The first objective of this study was to understand if the predators documented on video were associated with the predator surveys at the same sites. One expectation might be that when a predator is actually documented taking nests at a site, that species will be more prevalent in the community of potential predators than it is at a site where it is not observed taking nests. There is a tendency for this pattern to be supported in my study: sites with snake predation had higher numbers of snakes; sites with raccoon predation had higher numbers of raccoons; sites with subsidiary predation events had higher levels of rodents and brown-headed cowbirds (Table 3). However when the response is modeled as identity in MANOVA it approaches significance for subsidiary predators only (MANOVA, $F = 3.99$, df = 5 and 6, $P = 0.06$). Modeling the response as identity is
important because it identifies which predator guilds in the surveys are accounting for the most variation in the canonical score allowing inferences about the composition of the predator community to be made.

With a high diversity of predators, community interactions may influence the documented predators on video (Figure 1). For example, snakes appear to be a common predator at bird nests in the tallgrass prairie in eastern Nebraska and western Iowa. In grassland sites with decreased snake presence more opportunity is given to other predators such as ground squirrels, mice, and birds to take the nests as well as reduce predation by snakes on those potential predators. My results suggest that this may be the case; snakes were less abundant at sites where predation by subsidiary predators occurred (Table 3). Brown-headed cowbirds may be less likely to interact directly with snakes. However brown-headed cowbirds have been documented to destroy nests at the nestling stage in order to force the host to re-nest. Brown-headed cowbirds may be more likely to contribute to subsidiary predation at sites where egg predation by snakes and subsequent renesting by dickcissels is low (Table 3).

It is possible that video cameras may cause a bias in predator identification by attracting curious predators and deterring wary predators. My results suggest this did not occur. Predation did not differ between nests with and without cameras.

**Predator Community and Nesting Success**

Levels of nest predation in the study tended to be high, especially during the nestling stage (Figure 6). Overall, the types of predators taking the eggs and nestlings
were similar, with the exception of Murine rodents which were only observed taking eggs (Figure 4).

While the results above indicate that the nature of the predator community influences the type of predators actually taking the nests, it is also important to know if the nature of the predator community influences the probability of a nest being destroyed by a predator. Therefore, the second and third objectives of the study were to understand what predator community best explains the probability of survival for nests and to understand what level of detail is needed when investigating predators in relation to probability of survival for bird nests.

In both years of this study, the predators as entities of a community best explain the variation in the number of nestlings fledged by dickcissels and the overall survival of dickcissel nests (Table 4 and Table 5). I found that the predator community as a whole was a better predictor of survival rate than the individual predators in 2003 (Table 5). The answer to the second question I pose: what potential predators best explain the probability of survival for dickcissels varied among years and the stage of the reproductive cycle.

Several lines of evidence demonstrate the importance of snakes as predators in this region of the tallgrass prairie. In the best models, snakes have a negative effect on almost every stage of development in 2004 (Table 5), and snakes were the most common predators on video in the same year (Figure 3). Furthermore, in 2003 best models consistently revealed a negative relationship between reptiles and measures of
reproductive success (Table 4), and snakes were one of the two most common predators on video (Figure 3).

In 2003 the best models showed that four groups had consistent effects on measures of reproductive success. In the best models reptiles and ground squirrels showed a consistent negative effect on nesting success at nearly every stage of development in 2003 (Table 4) and were also the two most common predators on video in 2003 highlighting their importance as documented predators in response to their abundance in surveys (Figure 3). In contrast, avian predators as a group (e.g. common grackle, American crow, blue jay, and brown-headed cowbirds) and brown-headed cowbirds as a species-specific group consistently had positive effects on the survival rate at every stage of development in the selected models (Table 4 and 5) suggesting that sites favorable for dickcissel breeding may also be attractive to other types of birds for reasons such as habitat condition and availability of other food items. In the 2003 and 2004 best models, mid-sized mammals also positively influenced measures of reproductive success at every stage of dickcissel development except at the nestling stage in 2003 (Table 4 and 5). Mid-sized mammals as a group contain many species with differing life histories. In 2003 the majority of the tracks categorizing this group were those of the striped skunk. The preferred food of the striped is small mammals and the increased predation pressure on small mammals such as ground squirrels and other rodents by skunks may alleviate the pressure on bird nests by decreasing the probability of small predation on bird nests (Ackerman 2002). The best models show that mid-sized mammals may only have a
negative influence at the nestling stage when activity levels at the nest increase causing the mammals to be attracted to the nest by increased noise and odor.

The inconsistencies between years can be explained by assessing the variation explained in each model. The variation explained by the models in 2003 was higher than the variation explained by models in 2004 (Table 4 and 5). In 2004 the variation was considerably higher for the models that included the predator community as a whole when compared to models of single predators (Table 5). Even though important predators such as the raccoon and documented snakes appear as the candidate models for incubation and nestling stages in 2004, these models lack the ability to explain substantial variation, in measures of reproductive success among sites. Therefore, these results indicate the absence of other factors, such as combinations of other predators, needed to explain dickcissel nest predation rates. Further support of this statement comes from the fact that an increase in raccoons in 2004 compared to 2003 is contrasted by the increase in survival rate in 2004 when compared to 2003 (unpublished data Figure 6).

My third objective addressed the question of what level of detail from single species studies to studies of the entire predator community is most important for understanding nest predation. A broad grouping of the potential predator community and not species level groupings best explained measures of nest predation in dickcissel, for two candidate models emerged as best models using AIC and also have “highly satisfactory values for the strength of association (Table 4). One of these models explains predator effects on nestling survivorship and the other, on number fledged. Therefore, the strongest models indicate the significance of predation at the nestling
stage, and this result is consistent with the dramatic decreases observed in the survival rate found in the study of this population (unpublished data Figure 6). Although in 2004 single factor models of raccoons and documented snakes appeared for the incubation and nestling stages, the predator community as a whole remained as the candidate model for number fledged and overall survival.

While many researchers have acknowledged the need to study the entire community, most studies have focused on single species. The predator community interactions I have described support the concept that the entire community must be addressed to better understand mechanisms behind predation patterns. My results indicate that the broadest categorization of predators is the most informative (Table 4 and 5). However in 2004 the single factor models of raccoons were candidate models for the incubation stage. In 2004 the variation was considerably better for the models that included the predator community as a whole when compared to models with only single predators.

MANAGEMENT IMPLICATIONS

Regional Variation in Nest Predators in the Tallgrass Prairie

Studies investigating the predator community in the prairies of North America have shown a wide diversity of predators (Table 6). In studies conducted in Nebraska, Iowa (described here), North Dakota (Pietz and Granfors 2000), and Wisconsin (Renfrew and Ribic 2003) the most common predator has varied but the top candidates continue to be snakes, ground squirrels, and raccoons. The variation between the studies may be
explained by sample size where an increase in sample size may dilute the variation or
create a more recognizable pattern. Further comparisons between these studies are
difficult because all studies did not survey the predator community, but speculations can
be made based on information about biogeographical regions and land management
techniques.

As the top trophic level in any ecosystem, predators are the most vulnerable to
anthropogenic disturbance and land use and any changes in the predator community will
greatly impact nesting success in birds. The predator community composition and the
behavior of each predator type may be altered with habitat alteration through land
management tools such as tree removal, grazing and burning (Chapter 3). The changes in
biogeographical region and the differing land management techniques used in different
regions of the Great Plains may explain the variation in the most common predators.

Managing the Predator Community for Increased Avian Nesting Success

Previous nest predation studies and management suggestions have focused on
threats from outside the grassland such as raccoons and brown headed cowbirds.
Management recommendations put forth to minimize the impact of raccoons and brown
headed cowbirds have focused on habitat manipulation that decreases woody cover
eliminating the predator’s preferred habitat and perch sites. Decreasing the numbers of
raccoons and brown headed cowbirds has been supported because they are considered
pests in the tallgrass prairie. Comparative studies before and after habitat manipulations
are needed to see how the predator community was altered and how the changes in the community influence nesting success.

My study emphasizes the importance of snakes and ground squirrels as major predators of grassland birds. Management recommendations aimed at decreasing the influence of these predators is not straightforward; snakes and ground squirrels are natural members of the community and may themselves be legitimate targets of conservation efforts. Future research aimed at grassland obligate species should focus on how land management influences predator community composition and how the resulting community influences predation risk. Both ground squirrels and snakes have been shown to respond to vegetation structure. Research should focus on the degree of heterogeneity needed within a grassland site to maintain ample nesting sites for grassland birds while creating a predator community composition which alters the foraging behavior of predators to favor increased nesting success. My research suggests that indirect management of the predator community through habitat manipulations may be an effective way to increase grassland bird reproductive success.

My results also emphasize that management strategies focused on one predator type are most likely insufficient for decreasing nest predation because of the high diversity of predators and interactions among predators. Attempting to increasing nesting success by directly managing specific species will not be effective due to compensatory predators that are present to take the place of the removed predator. This is emphasized by my result that showed an increase in predation events by subsidiary predators at sites of decreased common predators such as snakes. Studies that simultaneously look at the
predator community’s response to habitat in conjunction with nest predation rates may better explain the value of habitat manipulation for increasing avian reproductive success.

ACKNOWLEDGMENTS

This work was supported by The American Museum of Natural History Frank M. Chapman Memorial Fund, Sigma Xi Grants-In-Aid of Research, Center for Great Plains Studies Grant-In-Aid for Graduate Students, University of Nebraska at Omaha Biology Department, University of Nebraska at Omaha Summer Rhoden Biological Fellowship, University of Nebraska at Omaha Phi Delta Gamma Scholarship, University of Nebraska at Omaha Summer Graduate Scholarship, University of Nebraska at Omaha Graduate Thesis Scholarship, USDA Biotechnology Risk Assessment Research Grants Program, and the U.S. Fish and Wildlife Challenge Grant (Boyer Chute NWR). I thank the refuge managers at Boyer Chute National Wildlife Refuge and DeSoto National Wildlife Refuge for financial and logistical support. I thank the private land owners for permission to work on their land. My gratitude is extended to S. Balint, T. Bean, A. Cade, K. Dougherty, T. Eidem, A. Garton, A. Hanson, J. Henningsen, J. Jorgensen, E. McIntyre, E. Mehsling, M. Ortega, N. Poole, R. Pumphrey, G. Toll, and K. Wells for their work as field assistants. I thank my committee members Dr. Larkin Powell and Dr. Tom Bragg for their comments and suggestions that improved the quality of my thesis.
LITERATURE CITED


Table 1. Potential predator combinations (7) of the explanatory variables explaining nesting success in dickcissels. Predator groups or species were only included if they were present at six or more sites creating a difference between years. Predator groups and species are abbreviated as follows: mid-sized mammals (MMAM), raccoons (PRLO), striped skunks (MEME), small mammals (SMAM), ground squirrels (GRSQ), other rodents (RODT), reptiles (REPT), snakes (SNAK), documented snake predators (DSNK), garter snakes (Thamnophis sp.)(THSP), fox snakes (Elaphe vulpina) (ELVU), birds (BIRD), blue jay (BLJA), common grackle (COGR), brown-headed cowbird (BHCO).

<table>
<thead>
<tr>
<th>Potential Predators</th>
<th>2003</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>Broad</td>
<td>(MMAM SMAM REPT BIRD)</td>
<td>(MMAM SMAM REPT BIRD)</td>
</tr>
<tr>
<td>Moderate</td>
<td>(MMAM RDNT GRSQ SNAK BIRD)</td>
<td>(MMAM RDNT GRSQ SNAK BIRD)</td>
</tr>
<tr>
<td>Detailed</td>
<td>(MEME RDNT GRSQ THSP COGR BHCO)</td>
<td>(PRLO MEME RDNT GRSQ ELVU THSP BLJA COGR BHCO)</td>
</tr>
<tr>
<td>Documented Predators</td>
<td>(PRLO RDNT GRSQ DSNK BHCO)</td>
<td>(PRLO RDNT GRSQ DSNK BHCO)</td>
</tr>
<tr>
<td>Most Common Predators</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First</td>
<td>(DSNK)</td>
<td>(DSNK)</td>
</tr>
<tr>
<td>Second</td>
<td>(GRSQ)</td>
<td>(PRLO)</td>
</tr>
<tr>
<td>First/Second</td>
<td>(DSNK GRSQ)</td>
<td>(DSNK PRLO)</td>
</tr>
</tbody>
</table>
Table 2. Potential predators found in surveys in eastern Nebraska and western Iowa. All predator groupings in the first column were used in analyses. (*) indicates predator species found at six or more sites and included in analyses as individual groups (†) indicates predator species that were documented as documented predators on video.

<table>
<thead>
<tr>
<th>Potential Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mid-sized mammals</strong></td>
</tr>
<tr>
<td>*†raccoons (<em>Procyon lotor</em>), *striped skunks (<em>Mephitis mephitis</em>), Virginia opossums (<em>Didelphis virginiana</em>), coyotes (<em>Canis latrans</em>), red fox (<em>Vulpes vulpes</em>), †mink (<em>Mustela vison</em>), domestic cats and dogs</td>
</tr>
<tr>
<td><strong>Small mammals</strong></td>
</tr>
<tr>
<td>(Ground squirrels)</td>
</tr>
<tr>
<td>†thirteen-lined ground squirrels (<em>Spermophilus tridecemlineatus</em>), †Franklin’s ground squirrels (<em>Spermophilus franklinii</em>), †Murine and other rodents</td>
</tr>
<tr>
<td>(Other rodents)</td>
</tr>
<tr>
<td><strong>Reptiles</strong></td>
</tr>
<tr>
<td>(Snakes)</td>
</tr>
<tr>
<td>†yellow-bellied racers (<em>Coluber constrictor</em>), *red-sided garter snakes (<em>Thamnophis sirtalis</em>), †plains garter snakes (<em>Thamnophis radix</em>), †bullsnakes (<em>Pituophis catenifer</em>), *†fox snakes (<em>Elaph Vulpina</em>), prairie ringneck snakes (<em>Diadophis punctatus</em>), northern brown snakes (<em>Storeria dekayi</em>), northern prairie skinks (<em>Eumeces septentrionalis</em>)</td>
</tr>
<tr>
<td>(Documented snakes)</td>
</tr>
<tr>
<td>(Garter snakes)</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
</tr>
<tr>
<td>*†brown-headed cowbirds (<em>Molothrus ater</em>), *blue jays (<em>Cyanocitta cristata</em>)</td>
</tr>
<tr>
<td>*common grackles (<em>Quiscalus quiscula</em>), American crows (<em>Corvus brachyrhynchos</em>).</td>
</tr>
</tbody>
</table>
Table 3. Least squares means (± SE) of predator surveys at sites according to the presence or absence of predators documented on video. *F*-values reported are from MANOVA with the response variable modeled as a sum (total predator community effect) and as an identity (correlations among predator surveys controlled).

<table>
<thead>
<tr>
<th>Predator Surveys</th>
<th>Video Events from 2003 and 2004</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Snake (n = 9)</td>
</tr>
<tr>
<td></td>
<td>Sum (F = 3.72, P = 0.08)</td>
</tr>
</tbody>
</table>

**Most Common Predators**
- Documented Snakes
  - Snake: 0.05±0.160
  - No Snake: 0.04±0.009
  - Raccoon: 0.03±0.008
  - No Raccoon: 0.05±0.016
  - Subsidiary: 0.03±0.013
  - No Subsidiary: 0.06±0.016

- Raccoons
  - Snake: 0.05±0.040
  - No Snake: 0.13±0.100
  - Raccoon: 0.11±0.070
  - No Raccoon: 0.07±0.050
  - Subsidiary: 0.10±0.080
  - No Subsidiary: 0.08±0.040

**Subsidiary Predators**
- Ground Squirrels
  - Snake: 0.04±0.065
  - No Snake: 0.04±0.038
  - Raccoon: -0.02±0.017
  - No Raccoon: 0.10±0.067
  - Subsidiary: -0.01±0.035
  - No Subsidiary: 0.08±0.073

- Other Rodents
  - Snake: 0.40±0.073
  - No Snake: 0.60±0.110
  - Raccoon: 0.30±0.100
  - No Raccoon: 0.70±0.074
  - Subsidiary: 0.57±0.050
  - No Subsidiary: 0.43±0.098

- Brown-headed Cowbirds
  - Snake: 0.45±0.024
  - No Snake: 0.63±0.220
  - Raccoon: 0.46±0.046
  - No Raccoon: 0.62±0.110
  - Subsidiary: 1.02±0.180
  - No Subsidiary: 0.06±0.027
Table 4. Candidate models for effect of predator community on probability of survival for dickcissel nests in 2003. Only the models with Akaike weights greater than 0.1 are shown with the bold type indicating the largest Akaike weight. The sign ("+" or ".") of $\beta$ from the ordinal logistic regression precedes the variable name in the Model Column and indicates the direction of effect that variable has on Y. Predator groups and species are abbreviated in same manner as Table 1.

<table>
<thead>
<tr>
<th>Y</th>
<th>Model</th>
<th>$\Delta$AIC</th>
<th>$w_i$</th>
<th>$\rho^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incubation</td>
<td>+MMAM-GRSQ-RDNT+SNKE+BIIRD</td>
<td>0.00</td>
<td>0.37</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>-PRLO-GRSQ+RDNT+DSNK+BICO</td>
<td>1.33</td>
<td>0.19</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>+MMAM-SMAM-REPT+BIIRD</td>
<td>0.33</td>
<td>0.31</td>
<td>0.10</td>
</tr>
<tr>
<td>Nestling</td>
<td>-MMAM+SMAM-REPT+BIIRD</td>
<td>0.00</td>
<td>0.81</td>
<td>0.29</td>
</tr>
<tr>
<td>Number Fledged</td>
<td>+MMAM-GRSQ+RDNT-SNAK+BIIRD</td>
<td>0.00</td>
<td>0.51</td>
<td>0.19</td>
</tr>
<tr>
<td>Number Fledged</td>
<td>+MMAM-SMAM-REPT+BIIRD</td>
<td>1.32</td>
<td>0.26</td>
<td>0.13</td>
</tr>
<tr>
<td>Overall Survival</td>
<td>+MMAM-GRSQ-RDNT-SNAK+BIIRD</td>
<td>0.16</td>
<td>0.36</td>
<td>0.17</td>
</tr>
<tr>
<td>Overall Survival</td>
<td>+MMAM-SMAM-REPT+BIIRD</td>
<td>0.00</td>
<td>0.39</td>
<td>0.14</td>
</tr>
</tbody>
</table>
Table 5. Candidate models for effect of predator community on probability of survival for dickcissel nests in 2004. Only the models with Akaike weights greater than 0.1 are shown with the bold type indicating the largest Akaike weight. The sign ("+" or "+") of $\beta$ from the ordinal logistic regression precedes the variable name in the Model Column and indicates the direction of effect that variable has on $Y$. Predator groups and species are abbreviated in same manner as Table 1.

<table>
<thead>
<tr>
<th>Y</th>
<th>Model</th>
<th>$\Delta$AIC</th>
<th>$w_i$</th>
<th>$\rho^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incubation</td>
<td>+PRLO-DSNK</td>
<td>1.33</td>
<td>0.17</td>
<td>0.03</td>
</tr>
<tr>
<td>Incubation</td>
<td>+PRLO</td>
<td>0.00</td>
<td>0.34</td>
<td>0.02</td>
</tr>
<tr>
<td>Incubation</td>
<td>-DSNK</td>
<td>0.67</td>
<td>0.24</td>
<td>0.02</td>
</tr>
<tr>
<td>Nestling</td>
<td>-PRLO</td>
<td>0.00</td>
<td>0.89</td>
<td>0.03</td>
</tr>
<tr>
<td>Number Fledged</td>
<td>-PRLO-MEME-RDNT+GRSQ+ELVU</td>
<td>0.00</td>
<td>0.46</td>
<td>0.17</td>
</tr>
<tr>
<td>Number Fledged</td>
<td>-THSP+BLJA+COGR+BHCO</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number Fledged</td>
<td>+RACCOON-MURINE+GRSQ+DSNAKE+BHCO</td>
<td>1.79</td>
<td>0.19</td>
<td>0.07</td>
</tr>
<tr>
<td>Number Fledged</td>
<td>+MMAM-SMAM+REPTILE+BIRD</td>
<td>1.89</td>
<td>0.18</td>
<td>0.05</td>
</tr>
<tr>
<td>Overall Survival</td>
<td>+MMAM-GRSQ-RDNT+SNAK+BIRD</td>
<td>1.73</td>
<td>0.15</td>
<td>0.08</td>
</tr>
<tr>
<td>Overall Survival</td>
<td>+PRLO-RDNT-GRSQ-DSNK+BHCO</td>
<td>1.11</td>
<td>0.21</td>
<td>0.09</td>
</tr>
<tr>
<td>Overall Survival</td>
<td>+MMAM-SMAM+REPT+BIRD</td>
<td>0.00</td>
<td>0.37</td>
<td>0.08</td>
</tr>
</tbody>
</table>
Table 6. Most common predators documented on video vary by region in the Great Plains: snakes and raccoons are the most common predators in this study (Nebraska and Iowa), (b) ground squirrels are the most common predator in South Dakota (Pietz and Granfors 2000), and (c) raccoons and ground squirrels are the most common predator in Wisconsin (Renfrew and Ribic 2003). The most common predators may be a function of biogeography, land management such as burning and grazing, and degree of fragmentation and woody encroachment. Variation may also be a function of small sample sizes.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Nebraska/Iowa¹</th>
<th>North Dakota²</th>
<th>Wisconsin³</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Snake (Elaphe vulpina, Thamnophis spp., Coluber constrictor, Pituophis catenifer)</em></td>
<td>9</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td><em>Raccoon (Procyon lotor)</em></td>
<td>6</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td><em>Ground squirrel (Spermophilus spp.)</em></td>
<td>4</td>
<td>13</td>
<td>4</td>
</tr>
<tr>
<td>Brown-headed cowbird (<em>Molothrus ater</em>)</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Mouse (<em>Peromyscus sp., Zapus sp.</em>)</td>
<td>2</td>
<td>3</td>
<td>-</td>
</tr>
<tr>
<td>Long-tailed weasel/mink (<em>Mustela spp.</em>)</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>American badger (<em>Taxidea taxus</em>)</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Birds of prey (<em>Buteo sp., Circus cyaneus</em>)</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Fox/coyote/dog (<em>Vulpes vulpes/Canis latrans</em>)</td>
<td>-</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Domestic cat</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Striped skunk (<em>Mephitis mephitis</em>)</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Opossum (<em>Didelphis virginiana</em>)</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>White-tailed deer (<em>Odocoileus virginianus</em>)</td>
<td>-</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>24</strong></td>
<td><strong>26</strong></td>
<td><strong>24</strong></td>
</tr>
</tbody>
</table>

¹This study ²Pietz and Granfors (2000) ³Renfrew and Ribic (2003)
Figure 1. This diagram is a subset of Figure 2 (Nest Predation Variables) in Chapter 1 and illustrates the pathway of influence between the potential predator community and the documented predators taking the nests and the influence on predation rates.

Figure 2. The video-system consisted of an infra-red video camera connected to a 24-hour time lapse VCR. Both devices were powered by a 12-volt 56-amp hour battery by using a 300 watt power converter. A portable television monitor was used to assure operation and check the contents of the nest.
Figure 3. Fates of nests monitored by video. In 2004 more nests fledged and the diversity of predators was lower than in 2003.

Figure 4. Snakes, raccoons, ground squirrels, and brown-headed cowbirds are documented eating both incubation and nestling stages. Murine rodents are documented eating the incubation stage. Of the 23 predation events 13 were at incubation and 10 were at the nestling stage.
Figure 5. Digitized images of predators from video footage: (a) yellow-bellied racer, (b) raccoon, (c) thirteen-lined ground squirrel, (d) Murine rodent (probably a *Peromyscus maniculatus*), (e) brown-headed cowbird, and (f) mink.
Figure 6. Survival curves for Dickcissel offspring from incubation through fledgling life stages in 2003 and 2004 in eastern Nebraska and western Iowa. Day zero is the first day of incubation and day 20 is fledge date. After day 20 the probability of survival is calculated for fledglings after they have left the nest taken from Berkeley (2004).
CHAPTER 3

THE INFLUENCE OF HABITAT AT MULTIPLE LEVELS ON THE
PREDATORS OF GRASSLAND BIRD NESTS*

Abstract: The grasslands of North America are of high conservation concern.
As a result, grassland birds have undergone precipitous declines and are considered the
most threatened group of birds in North America with nest predation as the leading cause
of reproductive failure. Conservation biologists have been concerned that habitat
fragmentation increases predation pressure on grassland birds. A diverse community of
nest predators has been documented in the grasslands of North America. Knowing how
predators respond to habitat as a community is important to conservation biologist in
understanding the mechanisms behind nest predation. I analyzed the predator
community's response to habitat at multiple levels including local vegetation structure
(vegetation of grassland site), local patch variables (size and shape of grassland site),
and landscape variables (habitat composition and diversity surrounding each site within
400, 800, and 1600 m using a Geographical Information System).

I examine the relative importance of the habitat variables and combinations of the
variables using Akaike's Information Criterion. My results indicate that habitat at
multiple levels best explains predator community composition. In both years landscape
variables (increased percent development and decreased surrounding grasslands)
explained the predator community as well as decreased survival. In 2003 the best habitat

*To be submitted to Conservation Biology. Authors: Klug, P.E.; Wolfenbarger, L.L;
McCarty, J.P
model for explaining predator community (percent development, percent grassland, patch size, heterogeneity in litter depth and vegetation height) significantly influenced probability of survival for Dickcissels (Spiza americana) through a significant positive effect of percent grassland within 1600 m and a negative effect of percent development within 1600 m on nestling survivorship. When analyzing the response of individual predator groups to the best habitat models, ground squirrels and other rodents increased with a decrease in grassland and an increase in development. Documented snakes responded in the opposite manner. In 2004 the best habitat model explaining predator community (percent development, percent grassland, patch size, edge to interior ratio, litter depth heterogeneity, and vertical vegetation density) had a significant relationship with the probability of survival for Dickcissels at the incubation stage, through a negative effect of litter depth heterogeneity. When analyzing the predator response to the best habitat models, raccoons and Brown-headed Cowbirds increased with an increase in litter depth heterogeneity.

The importance of percent development and grassland in the landscape is problematic where the availability of conservation land is minimal and development is increasing. The fact that percent development is important in a landscape that has been entirely converted to human use highlights the importance of the nature and intensity of human development on predator communities. Efforts should minimize human development on and surrounding conservation land while increasing the proximity of grasslands in relation to each other.
Key Words: agricultural mosaic, predator community, habitat, landscape, nest predation, fragmentation, grassland birds, Great Plains, tallgrass prairie

Introduction

In the Great Plains, agriculture and urbanization have replaced native prairie and fragmented the landscape. The tallgrass prairie biome of the Great Plains is listed as a critically endangered ecosystem, with less than 2% of the native ecosystem remaining (Noss et al. 1995). The remaining grassland fragments are isolated and embedded in a mosaic of habitat types including woodlots, human development, and agricultural fields. The presence and amount of habitats has an effect on ecological functions of the adjacent grasslands including the reproductive success of grassland birds and their predators.

Habitat loss, fragmentation, and degradation of native prairie are thought to be responsible for the decline in many grassland species and at the same time responsible for the increase in generalist species adapted to human development. The drastic declines of Neotropical migrants have been linked to habitat fragmentation of their breeding grounds (Herkert 1995). In particular, grassland birds have undergone precipitous declines and are considered the most threatened of any group of birds in North America (Knopf 1994; Rich et al. 2004). The fragmentation of remaining habitat can affect avian populations by decreasing suitable breeding habitat and increasing nest failure due to nest predation (Johnson & Temple 1990). Fragmentation and degradation may increase predation risk when changes increase generalist predators such as raccoons (*Procyon lotor*), coyotes (*Canis latrans*), and garter snakes (*Thamnophis* spp.) which adds to predation pressure.
from grassland obligate predators resident in the prairie fragments such as ground
squirrels (*Spermophilus* spp.), fox snakes (*Elaphe vulpina*), and bull snakes (*Pituophis
catenifer*).

Nest predation is the leading cause of reproductive failure in grassland birds and
counts for 80% of nest losses (Martin 1993). Nest predation is an important issue when
aiming to increase populations of Neotropical migrants, and although a great deal of work
has been done to improve the reproductive success of Neotropical migrants, information
on the predator community is limited. Researchers have recognized the importance of
identifying the predator community to better understand the mechanisms of predation, but
despite the general consensus, there is a lack of quantitative studies that include the entire
 predator community. Understanding the predator community is an important gap in our
understanding because little is known about the predator community’s response to habitat
and how this influences predation risk.

Most studies looking at the influence of habitat on nest predators are aimed at a
particular taxonomic group or species (Chalfoun et al. 2002b). Of these studies most are
focused on mid-sized mammals such as raccoons, canines, and skunks (Dijak &
Thompson 2000; Dion et al. 1999; Heske et al. 1999; Lariviere & Messier 2001; Schmidt
2003) bird predators such as Brown-headed Cowbirds and corvids (Andren 1992;
Johnson & Temple 1990), and small mammals (Ackerman 2002; Bradley & Marzluff
2003). Focusing on one predator type may not explain patterns of predation as well as
investigations of the entire predator community.
In the Great Plains the diversity of potential predators highlights the importance of understanding how changes in habitat may influence the entire predator community and ultimately affect predation risk (Pietz & Granfors 2000; Renfrew & Ribic 2003; Thompson et al. 1999; Weatherhead & Blouin-Demers 2004). With a wide array of predators it is unclear how species respond as a community to land use and grassland management. Individual predator groups are influenced by habitat due to its functionality as refuge from predators and productivity of prey. Each predator type responds to landscape depending on its own life history and habitat preferences blurring the relationships between habitat variables and nest predation patterns if only one predator type is examined.

The simultaneous effects of local vegetation structure, local patch variables, and landscape composition on the predator community emphasize the need for an approach that considers multiple levels. Previous work has emphasized the importance of assessing multiple levels in order to accurately explain ecological mechanisms (Donovan et al. 1997; Weins et al. 1993). For example, nest predation studies have mainly focused on “edge effects” (Lahti 2001; Paton 1994) but recently the emphasis has been to understand the context in which increased predation risk occurs by looking at multiple habitat levels, especially the landscape surrounding the site of interest (Chalfoun et al. 2002b; Donovan et al. 1997; Thompson et al. 2002). Winter et al. (2000) found that nest fates were not related to landscape features such as roads, agricultural fields, or forests but were negatively influenced by distance to shrubby areas due to increased exposure to mammalian carnivores. Bergin et al. (2000) found that habitat differed in importance at
different scales and that nest predation was influenced by the surrounding landscape mosaic due to habitat affinities of predator types showing that landscape and internal habitat is integral in shaping the abundance and behavior of predators and has an effect on the reproductive success of birds. The literature suggests that in order to gain a better perspective on the patterns of nest predation, predator guilds in an area must be considered in the context of fragmentation (Heske et al. 2001; Lahti 2001; Pietz & Granfors 2000) and underscore the importance of integrating the effects of habitat on predator presence and abundance.

I am focusing on habitat at multiple levels in relation to the predator community (Figure 1). The landscape variables include the landscape diversity and the percent composition of grassland, row crops, trees, human development, and wetlands surrounding the site of interest. The landscape variables were measured at three distances (400, 800, and 1600 m buffers). The local patch variables include the size of the grassland site in hectares and the shape of the grassland site measured by the edge to interior ratio (m/m²). The local vegetation structure describes vertical and horizontal vegetation structure and includes litter depth, vegetation height, grass density, forb density, and shrub density. In this study I ask two questions: (1) what landscape composition, local patch, and local vegetation structure variables influence the presence and abundance of predators and how does this influence the probability of survival for bird nests? (2) What levels of habitat or combination of levels including landscape composition and diversity, local patch variables, and local vegetation structure best explains predator community composition and individual predator presence?
Methods

Sites

My research is conducted in eastern Nebraska and western Iowa in the Dissected Till Plains physiographic region (Fitzgerald & Pashley 2000). This region consists of intensive agriculture interspersed with small parcels of restored or marginal grasslands. I worked at a total of 36 distinct sites with only select sites used in both years (23 in 2003 and 30 in 2004) spread over an 815 km² area. Grassland sites differed in their isolation, shape, and size ranging from one to 50 ha. Both public and private lands were used under a variety of managements which created habitat differences. The private grasslands in Iowa and Nebraska are characterized by minimal grazing and limited burning, though in some cases woody plants are removed manually or with herbicides. I had 16 farm sites, consisting of one Conservation Reserve Program (CRP) parcel, two switchgrass (*Panicum virgatum*) stands, and 13 sites of agricultural terraces within agricultural fields planted to cool season brome (*Bromus* spp.). I had nine sites (7-110 ha) at the Desoto National Wildlife Refuge (3,166 ha) and six sites (7-45 ha) at the Boyer Chute National Wildlife Refuge (1,295 ha). The refuge sites are restored grasslands managed with prescribed burning and no grazing. The dominant vegetation on the refuges ranged from primarily warm season to primarily cool season and varied in amount of forbs. I had three sites (4-28 ha) at the Allwine Prairie Preserve (65 ha), a 30-year old restored tallgrass prairie managed by the University of Nebraska at Omaha and one site at the Cuming City Cemetery Nature Preserve (4 ha), a remnant native prairie managed by Dana College. All areas containing the grassland sites including the
refuges and preserves are a mosaic of habitat types characterized by agriculture consisting mainly of corn and soybeans. Habitats surrounding the grassland sites of interest included human development, woodlots, forests, wetlands, water, grasslands, and marginal grasslands (terraces, waterways, ditches) but minimal hayfields and pasture.

**Predator Community**

I determined the suite of potential predators by surveying for mid-sized mammals, small mammals, reptiles, and avian predators using two track stations, ten track tubes, ten coverboards and two point counts at each site respectively (Glennon et al. 2002; Kuehl & Clark 2002; Parmelee & Fitch 1995; Ralph et al. 1995). The surveys showed the relative abundance of predators between sites. Only individual predators or predator groups that were found at more than six sites in a given year were included in the analysis.

**Mid-sized Mammals**

Track stations were a one meter diameter area of cleared vegetation, sprayed with glyphosate herbicide and filled with sand (Kuehl & Clark 2002). I staked one can of fish flavored cat food in the center of the track station as bait. Each station was left for 48 hours before the station was checked for tracks. The station was then smoothed over and left for another 48 hours. Precipitation interferes with the visibility of the tracks causing survey information to be lost and inequalities in survey information between sites and years. In 2003 each site was successfully surveyed one to four times from June to August. In 2004 each site was successfully surveyed one to six times from May to August. Track indices of mid-sized mammal, raccoon, striped skunk, canine (coyote,
domestic dog, and fox), and opossum tracks were calculated by taking the number of stations with tracks over the number of track nights at each site. The mean of the probabilities from each visit were calculated to get a mean seasonal probability.

**Small Mammals**

Track tubes consisted of two 30-cm plastic gutters fastened together to form a tube with a binder clip on one side and duct tape on the other (Glennon et al. 2002). The tubes had felt inkpads fastened at both ends and strips of contact paper, sticky side up, were used as a track surface. Small, plastic tubes were filled with a peanut butter and bird seed mixture and placed in the tubes as bait. Track tubes were set up and left for 48 hours. The tubes were then checked; the contact paper, ink pads, and bait were replaced, and left for an additional 48 hours. In 2003 each site was surveyed twice with four track nights per survey from June to August. In 2004 each site was surveyed twice with four track nights per survey from May to August. Each site had ten tubes. Tracks were identified by separating ground squirrels (*Spermophilus* spp.) from other rodents. Track indices of small mammal (ground squirrel and other rodents) tracks, ground squirrel tracks, and other rodent tracks were calculated by taking the number of tubes with tracks over the total number of tubes at each site. The means of the track indices from each visit were calculated to get a mean seasonal probability.

**Reptiles**

Ten individually numbered coverboards (60 cm by 180 cm ply-wood sheets) were placed at each site (Parmelee & Fitch 1995). In 2003 all ten coverboards at each site were checked five or six times from June to August. In 2004 each site was checked ten or 11
times from May to August. Reptiles under boards were captured, identified and measured. Mean number of snakes per board was calculated for individual sites by dividing the number of snakes by the number of boards at the site and standardized by the number of checks in a given year.

**Birds**

A total of four point counts were conducted over two field seasons (Ralph et al. 1995). Point counts were ten minutes in duration and possible avian predators were counted in the grassland, as flyovers, and on the exterior of the grassland. Point counts included Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), Common Grackles (*Quiscalus quiscula*), Brown-headed Cowbirds (*Molothrus ater*), and Red-tailed Hawks (*Buteo jamaicensis*), and American Kestrels (*Falco sparverius*).

**Local Vegetation Structure**

I measured local vegetation structure using the Robel pole method (Robel et al. 1970; Rotenberry & Weins 1980). The Robel pole is a slim pole divided into decimeters and passed vertically through the vegetation at each sample point. The number of vegetation contacts per decimeter was recorded for grass, forbs, and shrubs to calculate vertical vegetation density. Other vegetation variables measured were litter depth and maximum vegetation height. I measured horizontal forb and shrub densities using the point-centered quarter method (Cottam & Curtis 1956) and using methods modified for grasslands by Elzinga (2001) and Rotenberry and Weins (1980). The distance to the nearest forb and shrub in each of the four quadrants using the nest as the center was
measured to estimate densities of forb and shrubs. Six and nine sampling points per site were used in 2003 and 2004 respectively. Each site was systematically divided into six or nine equal quadrant depending on year. The sampling point was then chosen at random from the center of each quadrant.

**Local Patch Variables**

I calculated the site area and edge to interior ratio for each site using ortho-photo quadrangles in ArcGIS 8.1 (ESRI, Redlands, California) by digitizing the sites at a scale of 1:1500 (Figure 2).

**Landscape Composition and Diversity**

I digitized eight habitat types within a 1600 m buffer of each site using 1999 and 2003 digital aerial photographs in ArcGIS 8.1 (ESRI, Redlands, California) at a scale of 1:1500 (Figure 2). I identified eight habitat categories in Washington and Douglas counties in eastern Nebraska and Harrison and Pottawattamie counties in western Iowa: human development (residential, livestock), agricultural row crops, grassland (grazed pasture, hayfield, warm-season, cool-season, road ditches, waterways, terraces, fence lines), trees (forest, riparian, woodlot, development, savanna dominated by trees), wetlands, water (rivers, streams, lakes), and roads (highway, county, access, driveway). I ground-truthed all areas for accuracy during the autumn of 2004 and winter of 2005.

I computed landscape composition and diversity surrounding each site at 400, 800, and 1600 m buffers from the perimeter of the site. Landscape composition included
the proportion of grass, trees, wetland, crops, and development. Landscape diversity was obtained using the Shannon-Weiner index for diversity. The value for diversity is,

\[ H = -\sum_{k=1}^{s} (P_k) \ln(P_k) \]

where \( P_k \) is the proportion of the landscape in habitat \( k \) and \( s \) is the number of habitats observed.

**Statistical Analyses**

*Multiple Analysis of Variance (MANOVA) and Analysis of Variance (ANOVA)*

I used a multiple analysis of variance (MANOVA) to model the effect of habitat on the predator community and an analysis of variance (ANOVA) to model habitat on the individual predators present at 36 grassland sites with landscape composition and diversity, local patch variables, and local vegetation structure data as the explanatory variables representing habitat (JMP version 5, SAS Institute, Inc., Cary, NC). I grouped the predator community into four groups to be analyzed, the broad predator group consisting of four dependent variables (mid-sized mammals, small mammals, reptiles, and avian predators), the documented predator group consisting of five dependent variables (raccoons, documented snakes, ground squirrels, other rodents, and Brown-headed Cowbirds), documented snakes consisting of one dependent variable, raccoons consisting of one dependent variable, and ground squirrels consisting of one dependent variable. Local vegetation structure explanatory variables included vertical vegetation structure (litter depth, maximum vegetation height, and the density of grass, forbs and
shrubs); horizontal vegetation structure (density of forbs and shrubs), and heterogeneity of vegetation (variation in litter depth, variation in vegetation height, and variation in total density). Combinations of explanatory variables were used in each of the three categories (31 models of vertical vegetation, three models of horizontal vegetation, and seven models of heterogeneity). Local patch explanatory variables included combinations of site area (ha) and edge to interior ratio (m/m²) for a total of three models. Landscape explanatory variables (at 400, 800, and 1600 m) included landscape diversity and all combinations of landscape composition (percent grassland, percent trees, percent crops, percent wetlands and percent human development) for a total of 96 models (Table 1).

Predators were analyzed as groups consisting of the broad predator group based on predator survey data and the documented predator group using only the survey information for the predators documented on video in both 2003 and 2004 (see Chapter 2). The top two most common predators from each year were also analyzed individually (for 2003 documented snakes and ground squirrels; for 2004 documented snakes and raccoons). Analyses included the predator groupings (Table 2) in relation to habitat at all levels.

Akaike Information Criterion (AIC)

I employed Akaike Information Criterion (AIC) to select the best models. The value for AIC is,

\[ AIC = -2 \ln(\ell(\hat{\theta}|\text{data})) + 2k \]
where \( \ln(\ell \theta | \text{data}) \) is the value of the maximized log-likelihood over the unknown parameters \((\theta)\), given the data and the model, and \(k\) is the number of parameters. Other models may have values close to the value of the best model so it is inadequate to only select the model with the lowest AIC value. To compensate for model selection uncertainty each alternative model can evaluated by using the difference between the model AIC and the minimum AIC,

\[
\Delta_i = AIC_i - \min AIC
\]

Models with \( \Delta_i \leq 2 \) are considered to have enough support as a candidate model. The smaller the likelihood of a model being the best model the in set of candidate models the higher the \( \Delta_i \). Akaike weights, \( w_i \), can also be considered as indicators of the strength of the \( i \) model,

\[
w_i = \frac{\exp(-\Delta_i)}{\sum_{r=1}^{R} \exp(-\Delta_r)}.
\]

The \( w_i \) is the probability that model \( i \) is the best model in the set of all models being considered. The variation explained by each model can be shown using a correction for 1-Wilks Lambda \((1-\lambda)\),

\[
\text{partial } \eta^2 = 1 - \lambda^i
\]

I modeled predator community composition using the predator groupings (broad and documented) in response to landscape composition and diversity, local patch, and local vegetation structure variables as well as combinations thereof using methods adapted from Gehring and Swihart (2003). I selected the best models from every
category of explanatory variables based on low AIC values and the amount of variation explained \((1 - \lambda)\). To combine models, I chose the variables from the best models from the landscape and the local patch separately and forced the best landscape models and the best local patch models into the landscape-local patch models in addition to a the subset of local patch models. I repeated this process by forcing the best landscape-local patch models into the best local vegetation models in addition to the subset of local vegetation models. I compared AIC values of the best local vegetation only models, best local patch only models and best landscape only models with the best landscape-local patch models and the best landscape-local patch-local vegetation models. The \(\Delta_i\) values were ranked after each combination with the best model always having \(\Delta_i\) value of 0. Best models at each grouping were chosen based on a \(\Delta_i \leq 2\) and a \((1 - \lambda) > 0.6\). I selected the top best model from each group (landscape, landscape-local patch, and landscape-local patch-local vegetation) to be compared. I ranked the landscape, landscape-local patch, and landscape-local patch-local vegetation to see which group was the best model overall by calculating the \(w_i\) for each group. I determined the relative likelihood of one model being better than another by using \(w_i/w_j\) (Burnham & Anderson 1998).

**Results**

**Predator Community Surveys**

Predators recorded at the sites included mid-sized mammals, small mammals, reptiles, and birds (Table 3). All species detected on surveys were considered potential predators because at least some evidence had found them to be related to nest predation
of grassland birds. The potential predator community was divided into a broadly defined group that included all predators found in the survey lumped into categories based on guild (mid-sized mammals, small mammals, reptiles, and birds). The documented predator group included only those species found on video to be nest predators in this area of the Great Plains.

The Predator Community's Response Landscape Composition and Diversity, Local Patch Variables, and Local Vegetation Structure

I used a hierarchical approach to select the best candidate models. Using this approach I produced candidate models for the local vegetation, local patch, landscape, landscape-local patch combined, and landscape-local patch-local vegetation combined. I calculated final AIC values using the best model from each category to arrive at the best overall model per grouping. I used the parameters of these models to explain whether the predator group responded to the habitat variables positively or negatively.

"Broad" Predator Group

The best habitat model to explain the "broad" predator group in 2003 included heterogeneity of litter depth, human development within 1600 m, and patch size (MANOVA Wilks' $\lambda = 0.279$, partial $\eta^2 = 0.856$, df = 12 and 29.4) (Table 4). Litter depth heterogeneity was the strongest explanatory variable, and the canonical score of the predator group was heavily loaded by a decrease in small mammals and an increase in birds. Therefore, litter depth heterogeneity had a strong negative association with small mammals and was associated with higher point counts of avian predators. Development
within 1600 m was the next strongest explanatory variable of the analysis with the canonical score of the predator group mainly loaded by an increase in birds. Patch size was associated with an increase in mid-sized mammals.

In 2004 the best habitat model to explain the “broad” predator group included human development within 800 m, the edge to interior ratio of the patch, the patch size, and vertical shrub density (MANOVA Wilks’ $\lambda = 0.198$, partial $\eta^2 = 0.885$, df = 16 and 64.8) (Table 5). In this model, the canonical score of the predator group was heavily loaded by an increase in birds, indicating that avian predators increased in association with percent development within 800 m, a higher edge to interior ratio, and patch size. However, vertical shrub density was associated with a canonical score most heavily loaded by an increase in mid-sized mammals.

“Documented” Predator Group

In 2003 the best habitat model to explain the “documented” predator group included percent human development within 1600 m, heterogeneity of litter depth and vegetation height, percent grassland within 1600 m, and the size of the patch (MANOVA Wilks’ $\lambda = 0.077$, partial $\eta^2 = 0.960$, df = 25 and 31.2) (Table 4). Percent development within 1600 m was the strongest explanatory variable, and the canonical score of the predator group was heavily loaded by a decrease in documented snakes and an increase in ground squirrels. Litter depth heterogeneity was the next strongest explanatory variable, and the canonical score of the predator group was mainly loaded by a decrease in Brown-headed Cowbirds. Heterogeneity in vertical vegetation density was associated with a
decrease in raccoons. Patch size had a positive association with documented snakes and Brown-headed Cowbirds and a negative association on ground squirrels.

In 2004 the best habitat model to explain the “documented” predator group included human development within 1600 m, the patch size, heterogeneity of litter depth and vertical vegetation density, the edge to interior ratio, and percent grassland within 1600 m (MANOVA Wilks’ \( \lambda = 0.021 \), partial \( \eta^2 = 0.991 \), df = 30 and 74) (Table 5). Percent development within 1600 m was the strongest explanatory variable, and the canonical score of the predator group was heavily loaded by an increase in ground squirrels. Litter depth heterogeneity was the next strongest explanatory variable, and the canonical score of the predator group was mainly loaded by an increase in Brown-headed Cowbirds and raccoons. Heterogeneity in vertical vegetation density was mainly associated with an increase in Brown-headed Cowbirds and raccoons. Patch size was associated with an increase in Brown-headed Cowbirds. A higher edge to interior ratio was associated with an increase in Brown-headed Cowbirds and decrease in ground squirrels.

"Documented Snakes"

In 2003 the best habitat model to explain the “documented snake” predators was litter depth (ANOVA, \( r^2 = 0.309 \), partial \( \eta^2 = 0.916 \), df = 1 and 20) (Table 6). An increase in litter depth had a negative association with the presence of documented snakes.

In 2004 the best habitat model to explain the “documented snake” predators was edge to interior ratio, landscape diversity within 400 m, and grass density (ANOVA, \( r^2 = 0.039 \),
0.417, partial $\eta^2 = 0.965$, df = 3 and 26) (Table 6). Snakes were negatively associated with all three explanatory variables.

"Ground Squirrels"

In 2003 the best habitat model to explain the "ground squirrel" predators was percent development within 1600 m (ANOVA, $r^2 = 0.325$, partial $\eta^2 = 0.927$, df = 1 and 21) (Table 6). Ground squirrels were positively associated with increased development.

"Raccoons"

In 2004 the best habitat model to explain the "raccoon" predators was percent trees within 1600 m, the size and shape of the patch, and vegetation height (ANOVA, $r^2 = 0.320$, partial $\eta^2 = 0.955$, df = 4 and 25) (Table 6). Raccoons were positively associated with an increase in percent trees, a higher edge to interior ratio, and tall vegetation height and negatively to increased patch size.

The Predator Community's Response to Habitat and the Influence on Nesting Success

Because the ultimate objective of the study was to understand predator effects on grassland birds, I evaluated the influence of habitat on the probability of survival for Dickcissels for each year and used these results to interpret how the effects of the habitat on predators influenced nest predation risk. For example, predator taxa respond both negatively and positively to habitat variables in the best candidate models so that the net effect on grassland birds can not be inferred without incorporating analyses of how survivorship is associated with the habitats used by predators. Management implications
of the predator’s response to habitat cannot be given without knowing the direction of effect on nesting success. An indirect way of assigning direction of effect is relating the habitat variables that most greatly impact the predator groups to the corresponding probability of survival in the same grassland. I predict that if habitat variables impact predators then they should also impact the probability of survival. Habitat may affect the probability of survival for Dickcissels consistent with the effects of habitat on the predator groups. In creating the best habitat models I used an information criterion approach to select the best hypothesis from multiple possible hypotheses. This creates a parsimonious model which represents a scientific hypothesis to aid in the understanding of the system being studied (Burnham & Anderson 1998). I used a Fisherian statistical approach when comparing the best habitat models to survival rate by using only the best habitat models selected as the best working hypothesis in an independent statistical analysis of survival rate. I used the selected habitat model in relation to survival rate because the model was objectively selected and based on valid theory and *a priori* considerations.

In 2003 habitat variables from the best candidate model (percent development, percent grassland, patch size, and heterogeneity in litter depth and vegetation height) significantly influenced the probability of survival for Dickcissels at the nestling stage (ordinal logistic regression, log-likelihood $X^2 = 12.03$, df = 5, $P = 0.03$) (Table 7). The model’s significance was driven by a positive relationship to percent grassland within 1600 m and a negative relationship to percent development within 1600 m.
In 2004 the habitat variables from the best habitat model (percent development, percent grassland, patch size, edge to interior ratio and heterogeneity in litter depth and vertical vegetation density) were significantly related to the probability of survival for Dickcissels at the incubation stage (ordinal logistic regression, log-likelihood $X^2 = 18.65$, df = 6, $P = 0.005$) (Table 7). The significance was driven by a negative relationship to increased heterogeneity of litter depth.

**Predator Community’s Response to Habitat at Multiple Levels**

I used the same hierarchical approach to evaluate which combination of the habitat is most informative for explaining predator abundance. I compare $w_i$ for the best landscape, the best landscape-local patch, and the best landscape-local patch–local vegetation models and determine the relative likelihood of one model being better than another using the ratios of $w_i/w_j$, where $w_i$ is the Akaike weight of model in question and $w_j$ is the smallest Akaike weight of the group.

In 2003 models including all habitat levels provided the best fit for all predator groups except for documented snakes which responded best to the local vegetation model and ground squirrels which responded best to the landscape model (Table 8). The landscape-local patch model was only 1.1 times more likely to be better than the landscape model for the broad predator groups (Table 8). The landscape-local patch model is shown to be 27.45 times more likely than the landscape model for the documented snake group (Table 8). The documented predator group and ground squirrels are not improved by the addition of the local patch variables (Table 8).
broad predator group, the documented predator group, and documented snake predator communities all show superiority for models that include the local vegetation structure variables and show an increase of 8.8, 4.5, 4.7, and 59.1 times, respectively (Table 8).

In 2004 models including all habitat levels provided the best fit for all predator groups except the broad predator group which shows the best fit being the landscape-local patch model (Table 9). The landscape-local patch model was 1704, 1077, 125, and 11 times more likely to be better than the landscape model for broad, documented, documented snake, and raccoon predator communities, respectively. The broad predator group is not improved by the addition of local vegetation variables. The documented predator group, documented snake and raccoon predator groups show superiority for models that include the local vegetation structure variables and show an increase of 1550, 164, and 42 times, respectively (Table 9).

**Discussion**

The region where this study takes place is dominated by agriculture and contains isolated fragments of grassland habitat. However, within the region the study areas surrounding the sites showed significant variation in landscape and habitat variables at all levels evaluated (Figure 2 and Table 1). Sites also had a high diversity of potential predators (Table 3) which may be a direct effect of a diverse landscape and minimal grassland habitat.
The Predator Community’s Response to Landscape Composition and Diversity, Local Patch Variables, and Local Vegetation Structure

The first objective of this study was to understand which habitat variables including landscape composition and diversity, local patch variables, and local vegetation structure, influence the presence and abundance of predators preying on bird nests. When multiple members of the predator community were considered variables from all habitat levels are included in the candidate models (Table 4 and Table 5). Percent development was the consistent landscape variable and patch size was the consistent local patch variable included in the candidate models for both predator groups (broad, documented). Local vegetation structure variables mainly included measures of habitat heterogeneity but differed slightly between predator group categorization and year. Specific variables included heterogeneity of litter depth, heterogeneity of vegetation height, heterogeneity of vegetation density, and vertical shrub density (Table 4 and Table 5).

The consistency of percent development and patch size as important explanatory variables in both models and in both years underscored the importance of the association of these two variables with the predator community. For the broad predator group mid-sized mammals, small mammals, and birds accounted for the variation in the predator group’s canonical score by responding to percent development, patch size, or both. For the documented predator group the canonical score was loaded most heavily by ground squirrels, documented snakes, and Brown-headed Cowbirds, indicating that these three groups responded most to percent development, patch size or both (Table 4 and 5).
The probability of encountering certain predators increased at larger sites. Increased patch size positively influenced mid-sized mammals and birds in the broad grouping of the predator community (Table 4 and Table 5) as well as documented snakes and Brown-headed Cowbirds in the documented predator grouping. In contrast, ground squirrels responded negatively. My results suggest a numerical increase in predators as the patch size increases, specifically an increase in documented snakes. Many studies have found an increase in nesting success with increasing patch size in grasslands and eastern deciduous forest (Paton 1994; Sovada et al. 2000) where a decrease in nesting success was found in western North American shrubland (Tewksbury et al. 1998). If the hypothesis that an increase in patch size results in an increase in nesting success holds true for my study, predator community interactions, predator foraging ability, or some other factor may be affecting the disparity between predator numbers and nesting success. If the opposite is true and nesting success decreases with increased patch size, the relationship may be a factor of regional context and the nature of the habitat fragmentation. In areas dominated by agriculture all grassland fragments are relatively small and isolated. Relatively larger fragments may be attractive not only to birds but to a wide diversity of predators causing higher densities of grassland obligates in the fragments and increased penetrations by wide-ranging predators because any grassland in a row crop dominated landscape is their best or only option.

In 2004 avian predators in the broad predator group and Brown-headed Cowbirds in the documented predator group were more abundant when the edge to interior ratio was high or when grassland edge increased in relation to area (Table 5). The same birds
responded positively to patch size. These results corroborate the idea that avian predators increase in highly fragmented patches or large patches with ample edge habitat (Donovan et al. 1997; Morrison & Hahn 2002; Thompson 1994), which was characteristic of some sites in this study within agricultural fields.

Human development significantly affected the predator community and multiple predators within the community contributed to the effect. Increased development was associated with differences in the predator community due to higher probabilities of ground squirrels, lower probabilities of documented snakes, and higher numbers of avian predators, however, Brown-headed Cowbirds did not contribute to differences in the predator community related to development. (Table 4 and Table 5). Although previous studies have investigated the importance of percent development on Neotropical migrants, these have mainly focused on birds in eastern deciduous forests (Friesen et al. 1995). Therefore, the results presented here represent a unique opportunity to understand the effects of human development on grassland communities.

To manage for increased nesting success in grassland birds, land managers may need to manipulate the habitat to decrease the presence of predators or combinations of predators that decrease nesting success. In areas or regions of expanding human development and minimal hectares of public land in conservation the percent of human development near or encroaching on public land cannot readily be controlled by managers. However, in this study, predators responded to the heterogeneity of local vegetation. To increase nesting success in grassland birds, land managers could focus their efforts on patch size and the heterogeneity of the local vegetation. Before
management suggestions about the magnitude of manipulation can be confidently given, information about the predator community and habitat should be collected simultaneously with the nesting success information.

The Predator Community's Response to Habitat and the Influence on Nesting Success

One approach to evaluate the ecological importance of the relationship between habitat variables and the predator community is to test the hypothesis that the most informative model for explaining predator abundance should have a consistent relationship with survival rate. I analyzed probability of survival using habitat variables from the best models explaining predator community. In 2003 I found survival rate at the nestling stage was heavily influenced by a positive relationship with percent grassland and a negative relationship to development (Table 7). When analyzing the predator response to the same habitat variables, ground squirrels and other rodents are negatively associated with an increase in grassland and positively associated with an increase in development (Table 4). Documented snakes respond in the opposite manner. This result suggests that a decrease in human development and an increase in grasslands in the landscape increase the survival rate at the nestling stage by creating a predator community characterized by a decrease in small mammal predators and an increase in documented snake predators. Although snakes are major predators of bird nests, documented snakes likely prefer the same habitat as grassland birds and the effect of
snakes under conditions of increased grassland may be altered due to foraging behavior or other community interactions.

Based on literature from species-specific studies of nest predators, we might expect raccoons to increase in response to increased development and smaller grasslands due to their history of increasing with human induced fragmentation (Dijak & Thompson 2000). In my study of the entire predator community this is not the case. In my study raccoons never load heavily on the canonical score of the predator community in response to landscape variables. Instead heterogeneity in vegetation density and heterogeneity in vegetation height had a positive and negative influence on raccoons, respectively (Table 4 and 5). Vertical shrub density was shown to positively influence mid-sized mammals when the predator community was analyzed broadly (Table 5). Heterogeneity in vegetation density may be characteristic of grasslands with woody invasion; a habitat preferred by raccoons.

In 2004 I found survival rate at the incubation stage was heavily influenced by a negative relationship to litter depth heterogeneity (Table 7). When analyzing the predator response to the same habitat variables, raccoons and Brown-headed Cowbirds are positively impacted by an increase in litter depth heterogeneity (Table 5). This result suggests that an increase in the heterogeneity of litter depth decreases the survival rate at the incubation stage by increasing raccoon and Brown-headed Cowbird predators occupying those grasslands. This relationship is not evident in 2003 but can be explained by the lack of raccoons in surveys in 2003 and the abundance in 2004; indicating that if raccoons are abundant they will respond to habitat and influence nesting success.
It has been shown in previous work that grassland birds respond to increased forbs and heterogeneity in the vegetation. The raccoon response to local vegetation heterogeneity was only found in the year of high raccoon abundance. The attraction of raccoons and Brown-headed Cowbirds to heterogeneous grasslands may be a function of finding high densities of nesting birds in the grasslands indicating that changing the heterogeneity of the grasslands will only change the behavior of raccoons and Brown-headed Cowbirds in the grassland by changing the density of their prey or hosts. Because of the temporal and spatial variation in populations of raccoons, I suggest land managers maintain heterogeneity in the grasslands and try to eliminate these predators by altering landscape features attractive to these predators.

The general consistency of the relationship between predators and habitat supports the ecological interpretation of my models explaining predator abundance. In understanding how the predator community responds to habitat and the corresponding effect on probability of survival allow statements of direction to be made. More specifically, an increase in percent development and a decrease in percent grasslands are associated with a predator community which decreases nesting success (Table 7).

**Predator Community’s Response to Habitat at Multiple Levels**

The second objective of this study was to understand which habitat levels best explain predator community composition and individual predator presence. The fact that all habitat levels entered as candidate models is the first indicator that a multi-scale approach is needed (Table 4 and Table 5). I evaluated this more formally by using a
hierarchical approach to construct models based on landscape, landscape-local patch, and
landscape-local patch-local vegetation variables (Table 8 and Table 9). When comparing
the relative likelihood ratios, the documented predator group was best explained by the
landscape-local patch-local vegetation model in both years suggesting that models
incorporating multiple levels were the best predictors of predator community
composition. In 2003 the broad predator group was best explained by all levels, but in
2004 it was best explained by the landscape-local patch model (Table 8 and Table 9).
Documented snakes were best explained by local vegetation in 2003 but all levels in 2004
(Table 8 and Table 9). Ground squirrels were best explained by the landscape model in
2003 and the raccoons were best explained by all levels in 2004 (Table 8 and Table 9). A
combination of all levels consistently improved the explanatory power of habitat on
predator presence.

Conservation Implications

My results support the assertions of conservation biologists and wildlife
professionals who advocate a multi-scale approach to understanding grassland bird
densities (Bakker et al. 2002; Herkert 1994; Ribic & Sample 2001), predator
communities (Chalfoun et al. 2002a; Dijak & Thompson 2000; Gehring & Swihart 2003;
Kuehl & Clark 2002), and nesting success of birds (Bergin et al. 2000; Donovan et al.

My research suggests that habitat at multiple levels best explained predator
community composition. Of particular importance is my findings that increased percent
development and decreased surrounding grasslands are important factors in explaining the predator community as well as decreased probability of survival. Manipulating these factors to improve nesting survival is problematic in an area such as eastern Nebraska and western Iowa where the availability of conservation land is minimal and development is increasing. More often than not land managers have little control over the area surrounding the designated conservation land. However, these results do underscore the importance of minimizing human structures on the landscape within public land and increasing the proximity of grasslands in relation to each other.

The predator community responded to patch size and shape complexity especially avian predators. Even though not all predator types responded in a consistent manner and the local patch variables were not the main indicators of increased nest success, an increase in patch size in addition to increasing grasslands surrounding a site of interest may dilute predator impact by minimizing predator abundances and altering their foraging strategy. With a greater grassland area to search, the probability that the predator community will find a nest decreases. I included hayfields and pastures under the category of grassland lending support to the idea that placing agricultural grassland near prairie fragments will increase the value of that fragment.

My findings also suggest that the amount of human development surrounding a site directly affects the predator community creating an environment of increased predation risk. While it is not surprising that development may impact wildlife, the fact that percent development is important in a landscape that has been entirely converted to human use highlights the importance of the nature and intensity of human development
on predator communities. If possible conservation land should be located away from human development.

In this particular region of the Great Plains, snakes, raccoons, ground squirrels, Brown-headed Cowbirds, rodents and mink were documented as predators at Dickcissel nests. Any action taken to manage these species separately should be done with caution because a decrease in any one of these predators may not result in an overall increase in nesting success. For example, raccoons were detected at higher rates in 2004 but these differences were not related to nest predation rates on Dickcissels, indicating that raccoons are not the sole driving force behind decreased nest success. Within individual grasslands raccoons may have had a negative impact on nesting success and methods to reduce their numbers through removal or habitat manipulation may benefit nesting success on a site by site basis.

Snakes were the most common predators of bird nests on the refuges but management recommendations are difficult due to overlap in habitat preferences with grassland birds. Further research is needed on snake and bird interactions, as well as interactions among groups of predators, under various landscapes and management designations to understand how snake foraging behavior may be influenced by vegetation structure and heterogeneity.
Acknowledgements

This work was supported by The American Museum of Natural History Frank M. Chapman Memorial Fund, Sigma Xi Grants-In-Aid of Research, Center for Great Plains Studies Grant-In-Aid for Graduate Students, University of Nebraska at Omaha Biology Department, University of Nebraska at Omaha Summer Rhoden Biological Fellowship, University of Nebraska at Omaha Phi Delta Gamma Scholarship, University of Nebraska at Omaha Summer Graduate Scholarship, University of Nebraska at Omaha Graduate Thesis Scholarship, USDA Biotechnology Risk Assessment Research Grants Program, and the U.S. Fish and Wildlife Challenge Grant (Boyer Chute NWR). I thank the refuge managers at Boyer Chute National Wildlife Refuge and DeSoto National Wildlife Refuge for financial and logistical support. I thank the private land owners for permission to work on their land. My gratitude is extended to S. Balint, T. Bean, A. Cade, K. Dougherty, T. Eidem, A. Garton, A. Hanson, J. Henningsen, J. Jorgensen, E. McIntyre, E. Mehsling, M. Ortega, N. Poole, R. Pumphrey, G. Toll, and K. Wells for their work as field assistants. I especially thank T. Bean and J. Henningsen for assisting with digitizing and ground-truthing the sites. I thank my committee members Dr. Larkin Powell and Dr. Tom Bragg for their comments and suggestions that improved the quality of my thesis.
References


Sovada, M. A., M. C. Zicus, R. J. Greenwood, D. P. Rave, W. E. Newton, R. O.


Table 1. Explanatory habitat variables used to explain relative predator abundance.

<table>
<thead>
<tr>
<th>Local Vegetation Structure</th>
<th>Landscape Composition and Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vertical Structure:</strong></td>
<td>Local patch variables:</td>
</tr>
<tr>
<td>Grass Density</td>
<td>Area</td>
</tr>
<tr>
<td>Forb Density</td>
<td>Edge to Interior Ratio</td>
</tr>
<tr>
<td>Shrub Density</td>
<td></td>
</tr>
<tr>
<td>Litter Depth</td>
<td>Composition:</td>
</tr>
<tr>
<td>Maximum Vegetation Height</td>
<td>% Trees</td>
</tr>
<tr>
<td><strong>Horizontal Structure:</strong></td>
<td>% Grass</td>
</tr>
<tr>
<td>Forb Density</td>
<td>% Crop</td>
</tr>
<tr>
<td>Shrub Density</td>
<td>% Wetlands</td>
</tr>
<tr>
<td><strong>Heterogeneity:</strong></td>
<td>% Development</td>
</tr>
<tr>
<td>Litter Depth</td>
<td></td>
</tr>
<tr>
<td>Maximum Vegetation Height</td>
<td><strong>Structure:</strong></td>
</tr>
<tr>
<td>Vertical Density</td>
<td>Diversity</td>
</tr>
</tbody>
</table>


Table 2. Potential predator combinations from surveys based on *a priori* information about nest predators and video data of documented predators (Chapter 2). The combinations include potential predators, documented predators, and most common predators on video and are used as the dependent variables in the analyses. Predator groups or species were only included if they were present at six or more sites.

<table>
<thead>
<tr>
<th>Predator Community</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potential Predators (Broad)</td>
<td>(Mid-sized Mammal, Small Mammal, Reptile, Bird)</td>
</tr>
<tr>
<td>Documented Predators</td>
<td>(Raccoon, Other Rodent, Ground Squirrel, Documented Snakes, Brown-headed Cowbird)</td>
</tr>
<tr>
<td>First Most Common</td>
<td>(Documented Snakes)</td>
</tr>
<tr>
<td>Second Most Common</td>
<td>(Raccoon)</td>
</tr>
<tr>
<td>Third Most Common</td>
<td>(Ground Squirrel)</td>
</tr>
</tbody>
</table>
Table 3. Potential predators found in surveys in eastern Nebraska and western Iowa. All predator groupings in the first column were used in analyses. (*) indicates predators included in analyses as individual groups (†) indicates predator species that were documented as predators on video.

<table>
<thead>
<tr>
<th>Potential Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mid-sized Mammals</strong></td>
</tr>
<tr>
<td><em>†raccoons (<em>Procyon lotor</em>), striped skunks (<em>Mephitis mephitis</em>), Virginia opossums (</em>) indicates predators included in analyses as individual groups (†) indicates predator species that were documented as predators on video. (Didelphis virginiana), coyotes (<em>Canis latrans</em>), red fox (<em>Vulpes vulpes</em>), †mink (<em>Mustela vison</em>), domestic cats and dogs</td>
</tr>
<tr>
<td><strong>Small Mammals</strong></td>
</tr>
<tr>
<td>(Ground Squirrels)</td>
</tr>
<tr>
<td>†thirteen-lined ground squirrels (<em>Spermophilus tridecemlineatus</em>), †Franklin’s ground squirrels (<em>Spermophilus franklinii</em>), †Murine (<em>Peromyscus sp.</em>), and other rodents</td>
</tr>
<tr>
<td>(Other Rodents)</td>
</tr>
<tr>
<td><strong>Reptiles</strong></td>
</tr>
<tr>
<td>(Snakes)</td>
</tr>
<tr>
<td>†yellow-bellied racers (<em>Coluber constrictor</em>), red-sided garter snakes (<em>Thamnophis sirtalis</em>), †plains garter snakes (<em>Thamnophis radix</em>), †bullsnakes (<em>Pituophis catenifer</em>), †fox snakes (<em>Elaphe vulpina</em>), prairie ringneck snakes (<em>Diadophis punctatus</em>), northern brown snakes (<em>Storeria dekayi</em>), northern prairie skinks (<em>Eumeces septentrionalis</em>)</td>
</tr>
<tr>
<td>(Documented snakes)</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
</tr>
<tr>
<td>*†Brown-headed Cowbirds (<em>Molothrus ater</em>), Blue Jays (<em>Cyanocitta cristata</em>), Common Grackles (<em>Quiscalus quiscula</em>), American Crows (<em>Corvus brachyrhynchos</em>):</td>
</tr>
</tbody>
</table>
Table 4. Summary of MANOVA models selected as the best models for predicting predator group presence in grassland sites in relation to habitat at multiple levels in 2003.

<table>
<thead>
<tr>
<th>Predator Groups</th>
<th>Variables</th>
<th>Eigenvalues</th>
<th>Canonical Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Broad</td>
<td></td>
<td>Mid-sized Mammals</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Small Mammals</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Reptiles</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Birds</td>
<td></td>
</tr>
<tr>
<td>% Development (1600 m)</td>
<td>-0.078</td>
<td>0.126</td>
<td>-0.087</td>
</tr>
<tr>
<td>Patch Size</td>
<td>0.254</td>
<td>-0.054</td>
<td>0.028</td>
</tr>
<tr>
<td>Litter Depth Heterogeneity</td>
<td>0.023</td>
<td>-0.234</td>
<td>-0.032</td>
</tr>
<tr>
<td>WHOLE MODEL</td>
<td>0.057</td>
<td>-0.123</td>
<td>-0.046</td>
</tr>
<tr>
<td>Documented</td>
<td></td>
<td>Raccoons</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ground Squirrels</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other Rodents</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Documented Snakes</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Brown-headed Cowbirds</td>
<td></td>
</tr>
<tr>
<td>% Development (1600 m)</td>
<td>-0.120</td>
<td>0.551</td>
<td>0.110</td>
</tr>
<tr>
<td>% Grass (1600 m)</td>
<td>0.035</td>
<td>-0.308</td>
<td>-0.200</td>
</tr>
<tr>
<td>Patch Size</td>
<td>-0.020</td>
<td>-0.449</td>
<td>0.023</td>
</tr>
<tr>
<td>Litter Depth Heterogeneity</td>
<td>0.017</td>
<td>-0.029</td>
<td>0.072</td>
</tr>
<tr>
<td>Veg Height Heterogeneity</td>
<td>-0.202</td>
<td>0.008</td>
<td>0.011</td>
</tr>
<tr>
<td>WHOLE MODEL</td>
<td>-0.130</td>
<td>0.500</td>
<td>0.104</td>
</tr>
</tbody>
</table>
Table 5. Summary of MANOVA models selected as the best models for predicting predator group presence in grassland sites in relation to habitat at multiple levels in 2004.

<table>
<thead>
<tr>
<th>Predator Groups</th>
<th>Variables</th>
<th>Eigenvectors</th>
<th>Canonical Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Broad</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mid-sized Mammals</td>
<td>Small Mammals</td>
<td>Reptiles</td>
</tr>
<tr>
<td>% Development (800 m)</td>
<td>0.054</td>
<td>0.069</td>
<td>0.045</td>
</tr>
<tr>
<td>Patch Size</td>
<td>-0.137</td>
<td>0.097</td>
<td>0.028</td>
</tr>
<tr>
<td>Edge to Interior Ratio</td>
<td>0.072</td>
<td>0.063</td>
<td>0.068</td>
</tr>
<tr>
<td>Vertical Shrub Density</td>
<td>0.239</td>
<td>-0.056</td>
<td>0.113</td>
</tr>
<tr>
<td>WHOLE MODEL</td>
<td>0.087</td>
<td>0.057</td>
<td>0.069</td>
</tr>
</tbody>
</table>

| Documented       |                                |              |                       |
|                 | Ground Squirrels               | Other Rodents| Documented Snakes    | Brownheaded Cowbirds| Canonical Correlation |
| % Development (1600 m) | -0.032                         | -0.245       | -0.059               | -0.005              | -0.026               | 0.827                 |
| % Grassland (1600 m) | 0.147                          | -0.160       | -0.091               | 0.056               | 0.371               | 0.491                 |
| Patch Size      | 0.003                          | -0.160       | -0.016               | -0.007              | 0.337               | 0.814                 |
| Edge to Interior Ratio | 0.092                          | -0.289       | 0.064                | -0.020              | 0.245               | 0.553                 |
| Litter Depth Heterogeneity | 0.228                          | -0.312       | -0.203               | 0.049               | 0.267               | 0.781                 |
| Veg. Density Heterogeneity | 0.272                          | -0.196       | -0.176               | 0.145               | 0.211               | 0.733                 |
| WHOLE MODEL     | -0.158                         | 0.423        | 0.057                | -0.052              | -0.230              | 0.904                 |
Table 6. Summary of ANOVA models selected as the best models for predicting individual predator presence in grassland sites in relation to habitat at multiple levels in 2003 and 2004.

<table>
<thead>
<tr>
<th>Year</th>
<th>Candidate Model</th>
<th>$r^2$</th>
<th>partial $\eta^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>Documented Snakes</td>
<td>(-Litter Depth)</td>
<td>0.309</td>
</tr>
<tr>
<td></td>
<td>Ground Squirrels</td>
<td>(+ Development 1600 m)</td>
<td>0.325</td>
</tr>
<tr>
<td>2004</td>
<td>Documented Snakes</td>
<td>(-Diversity 400 m -Edge to Interior Ratio -Grass Density)</td>
<td>0.417</td>
</tr>
<tr>
<td></td>
<td>Raccoons</td>
<td>(+Vegetation Height -Patch Size +Edge to Interior Ratio +Percent Trees 1600 m)</td>
<td>0.320</td>
</tr>
</tbody>
</table>
Table 7. The selected best habitat models to explain the documented predator community were related to survival rate for each stage of Dickcissel development in both 2003 and 2004 using ordinal logistic regression. The habitat model was selected as the best working hypothesis using a selection criterion to explain predators and is related to survivorship to understand how the resulting predator community impacts nest success. Direction of effect is noted with (-) or (+) for the variables that had a significant effect on Dickcissel survivorship.

<table>
<thead>
<tr>
<th>Best Habitat Models for Documented Predators</th>
<th>Incubation DSR</th>
<th>Nestling DSR</th>
<th>Number Fledged</th>
<th>Overall DSR</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003: % Development (-), % Grassland (+), Patch Size, Litter Depth Heterogeneity, Vegetation Height Heterogeneity</td>
<td>Log-likelihood $X^2 = 2.78$ df = 5 $P = 0.73$</td>
<td>Log-likelihood $X^2 = 12.03$ df = 5 $P = 0.03$</td>
<td>Log-likelihood $X^2 = 5.25$ df = 5 $P = 0.39$</td>
<td>Log-likelihood $X^2 = 4.11$ df = 5 $P = 0.53$</td>
</tr>
<tr>
<td>2004: % Development, % Grassland, Patch Size, Edge to Interior Ratio, Litter Depth Heterogeneity (-), Vertical Vegetation Density Heterogeneity</td>
<td>Log-likelihood $X^2 = 18.65$ df = 6 $P = 0.005$</td>
<td>Log-likelihood $X^2 = 6.68$ df = 6 $P = 0.35$</td>
<td>Log-likelihood $X^2 = 5.26$ df = 6 $P = 0.51$</td>
<td>Log-likelihood $X^2 = 3.13$ df = 6 $P = 0.80$</td>
</tr>
</tbody>
</table>
Table 8. Spatial models for 2003 are ranked using AIC and compare predator responses to habitat at multiple levels. When compared hierarchically the models begin with landscape and the subsequent model is landscape-local patch. The full model is landscape-local patch-local vegetation. *the relative likelihood is only used to compare the hierarchical models (landscape, landscape+local patch, landscape+local patch+local vegetation). * indicates the hierarchical model with the lowest Akaike weight ($w_i$). † indicates model with lowest AIC value overall.

<table>
<thead>
<tr>
<th>Predator Groups</th>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>$w_i$</th>
<th>Relative Likelihood ($w_i/w_j$)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Broad&quot;</td>
<td><em>Local vegetation</em></td>
<td>73.64</td>
<td>9.32</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Local patch</em></td>
<td>75.53</td>
<td>11.21</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>68.67</td>
<td>4.35</td>
<td>0.090</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch</td>
<td>68.40</td>
<td>4.08</td>
<td>0.104</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch+Local vegetation †</td>
<td>64.32</td>
<td>0.00</td>
<td>0.796</td>
<td>8.8</td>
</tr>
<tr>
<td>&quot;Documented&quot;</td>
<td><em>Local vegetation</em></td>
<td>30.10</td>
<td>10.43</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Local patch</em></td>
<td>33.87</td>
<td>14.20</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>22.74</td>
<td>3.07</td>
<td>0.160</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch</td>
<td>23.83</td>
<td>4.16</td>
<td>0.093</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch+Local vegetation †</td>
<td>19.67</td>
<td>0.00</td>
<td>0.743</td>
<td>8.0</td>
</tr>
<tr>
<td>&quot;Documented Snakes&quot;</td>
<td><em>Local vegetation</em> †</td>
<td>-208.96</td>
<td>0.00</td>
<td>0.503</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Local patch</em></td>
<td>-200.73</td>
<td>8.23</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>-199.96</td>
<td>9.00</td>
<td>0.006</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch</td>
<td>-206.59</td>
<td>2.38</td>
<td>0.153</td>
<td>27.4</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch+Local vegetation</td>
<td>-208.12</td>
<td>0.84</td>
<td>0.330</td>
<td>59.1</td>
</tr>
<tr>
<td>&quot;Ground Squirrels&quot;</td>
<td><em>Local vegetation</em></td>
<td>-122.816</td>
<td>13.36</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Local patch</em></td>
<td>-124.284</td>
<td>11.89</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape †</td>
<td>-136.178</td>
<td>0.00</td>
<td>0.624</td>
<td>6.2</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch</td>
<td>-134.525</td>
<td>1.65</td>
<td>0.273</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>Landscape+Local patch+Local vegetation</td>
<td>-132.526</td>
<td>3.65</td>
<td>0.100</td>
<td>†</td>
</tr>
</tbody>
</table>
Table 9. Spatial models for 2004 are ranked using AIC and compare predator responses to habitat at multiple levels. When compared hierarchically the models begin with landscape and the subsequent model is landscape-local patch. The full model is landscape-local patch-local vegetation. *the relative likelihood is only used to compare the hierarchical models (landscape, landscape+local patch, landscape+local patch+local vegetation). * indicates the hierarchical model with the lowest Akaike weight ($w_i$). † indicates model with lowest AIC value overall.

<table>
<thead>
<tr>
<th>Predator Groups</th>
<th>Models</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>$w_i$</th>
<th>Relative Likelihood $(w_i/w_0)$*</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Broad&quot;</td>
<td>Local vegetation</td>
<td>50.00</td>
<td>20.66</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local patch</td>
<td>46.75</td>
<td>17.40</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>44.22</td>
<td>14.88</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch †</td>
<td>29.34</td>
<td>0.00</td>
<td>0.714</td>
<td>1704.2</td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch + Local vegetation</td>
<td>31.17</td>
<td>1.83</td>
<td>0.286</td>
<td>681.8</td>
</tr>
<tr>
<td>&quot;Documented&quot;</td>
<td>Local vegetation</td>
<td>-2.10</td>
<td>18.40</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local patch</td>
<td>-17.71</td>
<td>2.79</td>
<td>0.128</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>-5.81</td>
<td>14.69</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch</td>
<td>-19.77</td>
<td>0.73</td>
<td>0.357</td>
<td>1076.5</td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch + Local vegetation</td>
<td>-20.50</td>
<td>0.00</td>
<td>0.515</td>
<td>1550.0</td>
</tr>
<tr>
<td>&quot;Documented Snakes&quot;</td>
<td>Local vegetation</td>
<td>-139.99</td>
<td>11.57</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local patch</td>
<td>-136.55</td>
<td>15.01</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>-141.35</td>
<td>10.20</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch</td>
<td>-151.01</td>
<td>0.54</td>
<td>0.430</td>
<td>125.2</td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch + Local vegetation</td>
<td>-151.56</td>
<td>0.00</td>
<td>0.564</td>
<td>164.2</td>
</tr>
<tr>
<td>&quot;Raccoons&quot;</td>
<td>Local vegetation</td>
<td>-86.16</td>
<td>6.78</td>
<td>0.025</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local patch</td>
<td>-86.79</td>
<td>6.16</td>
<td>0.034</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>-85.45</td>
<td>7.49</td>
<td>0.017</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch</td>
<td>-90.26</td>
<td>2.69</td>
<td>0.191</td>
<td>11.0</td>
</tr>
<tr>
<td></td>
<td>Landscape + Local patch + Local vegetation</td>
<td>-92.95</td>
<td>0.00</td>
<td>0.733</td>
<td>42.4</td>
</tr>
</tbody>
</table>
Figure 1. This diagram is a subset of Figure 3 (Nest Predation Variables) in Chapter 1 and illustrates the pathway of influence between habitat variables including the landscape, local patch, and local vegetation variables on predator community composition.
Figure 2. Example of digitized GIS image of 1600 m buffers around three study sites. (a) Site with a patch size of 7.4 ha, an edge to interior ratio of 0.02, and a surrounding landscape diversity (at 1600 m) of 1.3. (b) Site with a patch size of 9.0 ha, an edge to interior ratio of 0.27, and a surrounding landscape diversity (at 1600 m) of 1.5. (c) Site with a patch size of 1.5 ha, an edge to interior ratio of 0.042, and a surrounding landscape diversity (at 1600 m) of 0.21.
CHAPTER 4

MANAGEMENT IMPLICATIONS AND FUTURE DIRECTIONS

CURRENT MANAGEMENT GUIDELINES FOR THE DICKCISSEL IN THE TALLGRASS PRAIRIE.

Dickcissels (Spiza americana) are a grassland species of conservation concern to both the state and federal agencies (Knopf 1994, Rich et al. 2004). Although Dickcissels remain abundant in the core of their range their populations are still declining and management to improve their reproductive success is still needed. The core range of the Dickcissel includes both Iowa and Nebraska making it an ideal study location because conservation efforts may be more beneficial where the study species remains relatively abundant. In this chapter I provide a brief overview of current management recommendations for the Dickcissel and note where my results support those recommendations or form new recommendations managers should consider.

A number of conservation groups have worked to synthesize the literature on the ecology of grassland birds, including Dickcissels, to formulate recommendations for land managers (Dechant et al. 1999 (revised 2002), Fitzgerald and Pashley 2000). The recommendations have focused on local vegetation structure within the grassland site of interest along with methods to manipulate the grassland heterogeneity and vegetation structure. Current recommendations also emphasize the importance of patch size and shape and have more recently included recommendations incorporating the landscape
context. One observation that emerges from my research is that predators do not just respond to their environment at a single habitat level but to multiple habitat levels simultaneously (Chapter 3).

**Local Vegetation Structure: Grassland Heterogeneity and Vegetation—**

Vegetation structure is known to influence grassland birds and should be managed to meet the needs of the species of interest (Zimmerman 1982, Temple 2002). Dickcissels prefer warm season grasslands and respond positively to dense grass, moderate litter, and forbs but will nest in a variety of vegetation types and structures (Dechant et al. 1999 (revised 2002), Engberg 2004). Management tools such as burning and grazing can be used to achieve desired vegetation structure in the off season to control for woody encroachment and to create desired habitat structure.

I found that local vegetation structure influenced the predator community and nesting success suggesting that habitat manipulations within grasslands may be an accessible for way for land managers to influence the predator community (Chapter 3). I found that heterogeneity in litter depth negatively impacts nesting success. I hesitate to make recommendations to reduce the heterogeneity of vegetation in grasslands based on the fact the other studies have found that avian settlement and reproductive success increase in heterogeneous grasslands characterized by an increase in forbs (Zimmerman 1982, Berkeley 2004). In my study heterogeneity in litter depth negatively impacted nesting success through the increase of raccoons (*Procyon lotor*) and Brown-headed Cowbirds (*Molothrus ater*). Both of these species may be drawn to heterogeneous
grasslands based on the density of prey and not the vegetation structure. Maintaining heterogeneous grasslands for grassland birds while decreasing other landscape features such as woodlots and trees may be a more productive way to decrease raccoon and Brown-headed Cowbird influence.

Local Grassland Patch Variables: the Size and Shape of Grasslands-

The size and shape of the grassland patch are known to influence grassland bird populations (Herkert 1994, Helzer and Jelinski 1999). Dickcissels will use small fragments such as fence lines, road ditches, and other marginal grassland habitat but exhibit greater densities and productivity in larger patches (> 10 ha) (Temple 2002, Engberg 2004). Recommendations to optimize the value of grasslands for Dickcissels suggest grassland areas should be at least 10 ha if not larger to support increased abundance and productivity of Dickcissels. The shape of the grassland sites should be simplified to maintain a low edge to interior ratio.

My results support recommendations of increasing grassland size and decreasing the edge to interior ratio (Chapter 3). The predator community was shown to respond to grassland size and shape but predator types did not responded in a consistent manner. Even though grassland size and shape were not the main indicators of increased nest success, an increase in grassland size in addition to increasing grasslands surrounding a site of interest may dilute predator impact by minimizing predator abundances and altering their foraging strategy. With a greater grassland area to search, the probability that the predator community will find a nest decreases (Phillips et al. 2003).
Landscape Context: Habitat Composition Surrounding Grasslands

The field of landscape ecology has brought new emphasis to the importance of considering not just the local vegetation and patch variables but also the importance of the landscape mosaic on the ecological processes within the grassland (Turner 1989, Wcins et al. 1993, Donovan et al. 1997, Thompson et al. 2002). Current recommendations emphasize that surrounding landscape should include grasslands to mitigate any patch size restrictions.

My findings also suggest that the amount of human development surrounding a site directly affects the predator community creating an environment of increased predation risk (Chapter 3). My results show that human structures such as homes, barns, animal confinement areas, and industrial development are important human structures in explaining the predator community as opposed to agricultural crop fields. While it is not surprising that development may impact wildlife, the fact that percent development is important in a landscape that has been entirely converted to human use highlights the importance of the nature and intensity of human development on predator communities. If possible conservation land should be located away from human development.

Regionally, changes in land use are likely to change the degree of human development. In primarily agricultural areas, my results suggest that ongoing consolidation of farmland and subsequent decline in the rural population may decrease the impact of human development within the agricultural landscape as buildings are removed (US Census Bureau 1995). In areas near larger metropolitan areas such as Washington County in Nebraska, an increase in human population and homes associated with rural development
of "acreages" and hobby farms is likely to have a disproportionate negative effect on grassland birds as buildings are added to the landscape (US Census Bureau 2005).

**SITE-BASED CONSERVATION: DeSoto National Wildlife Refuge and Boyer Chute National Wildlife Refuge.**

The recommendations above are directly applicable to the refuge managers at DeSoto National Wildlife Refuge and Boyer Chute National Wildlife Refuge. National wildlife refuges are placing increasing emphasis on management that promotes the habitat needs and reproductive success of non-game wildlife, especially migratory birds such as the Dickcissel. One of the main motivations of my research was to answer land manager's site-based questions that are unique to highly fragmented grasslands. The goal of the management at both refuges is to reduce fragmentation. At DeSoto National Wildlife Refuge they are decreasing fragmentation by converting habitat (U.S. Fish and Wildlife Service 2001) and at Boyer Chute NWR they are decreasing fragmentation by the acquisition of land (U.S. Fish and Wildlife Service in prep).

At Boyer Chute National Wildlife Refuge and DeSoto National Wildlife Refuge snakes, raccoons, ground squirrels, Brown-headed Cowbirds, rodents and mink were documented as predators at Dickcissel nests. Any action taken to manage these species separately should be done with caution because a decrease in any one of these predators may not result in an overall increase in nesting success. For example, the year of increased raccoon abundance did not influence overall survival curves of Dickcissels indicating that raccoons are not the sole driving force behind decreased nest success.
Only select grassland sites had decreased nesting success associated with raccoon abundance when viewing raccoon predation on a site by site basis. Raccoons have a negative impact on nesting success and methods to reduce raccoon numbers through habitat manipulation may benefit nesting success at certain sites.

Raccoons are expected nest predators of grassland bird nests but at Boyer Chute National Wildlife Refuge and DeSoto National Wildlife Refuge snakes are the most common predators of bird nests. Management recommendations are difficult to develop since snake habitat preferences overlap those of grassland birds. Although snakes are major predators of bird nests, the negative interaction between birds and snakes was lessened under conditions of increased grassland and decreased development (Chapter 3). My results indicate that the negative interaction between snakes and birds can be minimized in certain environments and may be a function altered foraging behavior in snakes or other predator community interactions.

Of particular importance are my findings that increased percent development and decreased surrounding grasslands are important factors in explaining the predator community as well as decreased probability of survival. The importance of these factors is problematic in an area such as eastern Nebraska and western Iowa where the availability of conservation land is minimal and development is increasing. More often than not land managers have little control over the area surrounding the designated conservation land. I suggest minimizing human structures on the landscape within the refuge and increasing the proximity of grasslands in relation to each other.
REGIONAL IMPLICATIONS FOR CONSERVATION OF GRASSLAND BIRDS IN THE GREAT PLAINS

My research is directly applicable to the area surrounding the Missouri River valley along the border of Nebraska and Iowa where the work was conducted. While site-based studies are of great value to managers of conservation lands such as Boyer Chute National Wildlife Refuge and DeSoto National Wildlife Refuge, a goal of conservation should be to draw broader generalizations.

My study benefits conservation by combining information on fragmentation and predators which includes documentation of nest predators on video. In particular, my study appears to be the only study the only grassland study of these parameters in the Great Plains of North America. The first step toward formulating general recommendations is to integrate information from other studies in the region.

There have now been three studies documenting predators of grassland bird nests in the Great Plains. Renfrew and Ribic (2003) found raccoons to be the most common predator in southeast Wisconsin. Pietz and Granfors (2000) found ground squirrels to be the most common predator in North Dakota. I found snakes to be the most common predator in Nebraska and Iowa (Table 1). Several explanations exist to explain the differences among the three studies including sample size, geographic region, degree of fragmentation, and land management techniques.

One factor affecting predator presence is the sample sizes of all three studies. The sample sizes ranged from 24 to 26 predation events documented on video for each study (Table 1). In increasing the sample size the ranking of the most common predators could
be altered. The predator type captured on video could have also been influenced by the location of the video monitored nests and how the nests were selected for monitoring. Even though the predators documented on video may be influenced by a small sample size, I speculate that the driving force behind the differences may be due to factors that characterize the geographical region.

One factor characterizing geographical region is the extent of species' ranges. Species' range may explain why the North Dakota study lacked snake predators (Pietz and Granfors 2000). For example, the fox snake's (*Elaphe vulpina*) range does not extend to North Dakota but is found in Nebraska, Iowa, and Wisconsin (Conant and Collins 1998). Five of the nine snake predation events in Nebraska were fox snakes (Chapter 2); and the fox snake was also responsible for nest predation in the Wisconsin study (Renfrew and Ribic 2003). Although snake predation occurs in North Dakota it is less prevalent than in areas with a higher diversity of snakes (Table 1).

Another factor distinguishing geographical region is the landscape context and degree of fragmentation. The landscape context of different regions within the Great Plains differ in the degree of grassland fragmentation, the amount of human development, and the prevalence of encroaching forests and amount of woodlots. Regional landscape context may affect raccoon abundance and may explain the lack of raccoons in the North Dakota study (Pietz and Granfors 2000). Raccoons were by far the most common predator in the Wisconsin study and were the second most common in my study (Table 1) (Renfrew and Ribic 2003). Forests, woodlots, and woody encroachment may be
greater in Wisconsin and in the Missouri river valley of Nebraska and Iowa than in North Dakota and would explain the differences in raccoon predation events.

In addition to species' geographical range and landscape context, the management practices of grasslands are another factor that varies by region. For example, the Wisconsin study was conducted on grazed pastures dominated by cool season grasses (Renfrew and Ribic 2003) whereas my study took place on ungrazed, restored grasslands dominated by tallgrass prairie grasses. Predator presence may be influenced by the microclimate created by the grassland vegetation. The study in Wisconsin may have lacked snake predators because the study was conducted on grazed pastures where the decrease in litter depth and vegetation structure may create an unfavorable microclimate for snakes.

The ability to draw inferences from differences among the three studies above is limited by the lack of consistent information about the predator community. My research emphasized the link between the predator community and the predators documented on video (Chapter 2). The lack of information about the entire predator community in all three studies limits the ability to draw inferences from the conflicting findings.

**FUTURE DIRECTIONS**

In understanding predation we will have a better understanding of reproductive success of grassland birds. My results raise several new questions about how best to improve the value of conservation lands for grassland birds. Future research should look at nest predation not only from assessing the predator community but also looking at the
land management factors that influence the predator community. Studies quantifying the predator community and predation risk for grassland birds in differing landscapes, degrees of fragmentation, and land management will aid in understanding the importance of specific predators between geographical regions in the same ecosystem. In understanding how the behavior of predators changes regionally, local effort and modification in land management techniques can be employed to decrease the threat of particular predators.

My work found a diversity of predators including both grassland species such as fox snakes and Franklin’s ground squirrels (*Spermophilus franklinii*) and habitat generalists such as raccoons. Management to decrease predation from grassland specialist will be more problematic and is an area where further research efforts might be directed.

Previous nest predation studies have focused on threats from outside the grassland site such as raccoons and Brown-headed Cowbirds. Management recommendations put forth to minimize the impact of these predators are well established and focus on habitat manipulation that decreases woody cover eliminating the predator’s preferred habitat and perch sites. Management efforts are also straightforward because decreasing the numbers of raccoons and Brown-headed Cowbirds has been viewed in a positive light because they are considered pests in a tallgrass prairie. My results show that efforts to decrease raccoons and Brown-headed Cowbirds may not be enough to increase reproductive success in grassland birds.
My study emphasizes the importance of snakes and ground squirrels as major predators of grassland birds. Management recommendations aimed at decreasing the influence of these predators is not straight forward; snakes and ground squirrels are natural members of the community and may themselves be legitimate targets of conservation efforts. Future research aimed at grassland obligate species should focus on how land management influences predator community composition and how the resulting community influences predation risk. Both ground squirrels and snakes have been shown to respond to vegetation structure. Research should focus on the degree of heterogeneity needed within a grassland site to maintain ample nesting sites for grassland birds while creating a predator community composition which alters the foraging behavior of predators to favor increased nesting success.

The importance of snakes as nest predators raises special concern. Both grassland birds and snakes have been shown to respond to vegetation structure. It was shown that Dickcissels (*Spiza americana*), Grasshopper Sparrows (*Ammodramus savannarum*), and Eastern Meadowlarks (*Sturnella magna*) respond positively to high grass density and deep litter cover and negatively to increasing horizontal heterogeneity (Rotenberry and Weins 1980). Snakes that utilize grasslands have also been shown to respond to vegetation structure. Snakes have been shown to prefer habitat with tall vegetation and deep litter in order to avoid predators and better control temperature and moisture fluctuations for thermoregulation (Setser and Cavitt 2003). Research will benefit by understanding the intersection of snake habitat selection and avian habitat selection and how this influences the reproductive success of grassland birds.
One approach that may present valuable insights is to focus on the behavior of snake predators. Snake behavior may better explain their importance as predators under differing land management schemes. Grassland management techniques may alter snake abundance or activity through the presence of alternate prey or the presence of certain predators. Snakes will also respond to vegetation for thermoregulation needs and foraging strategy. In areas known to have snakes as nest predators researchers should focus their effort in understanding snake behavior in response vegetation structure and predator community resulting from diverse managements.

My long term objective is to focus on the effects of land management on the predator community and how it increases or decreases the reproductive success of grassland birds. For example, grazing and burning influence the abundance and activity of the predator community and may indirectly alleviate or exacerbate nest predation.

Both fire and grazing have the potential to alter habitat and influence on both bird populations and their predators (Madden et al. 1999, Cavitt 2000, Setser and Cavitt 2003, Weatherhead and Blouin-Demers 2004). Changes in vegetation will influence grassland birds by altering prey availability, predator abundance, and suitable nesting site availability. Such changes will also affect the predator community. A more detailed understanding the predator community is important because potential nest predators may interact. As the top trophic level in any ecosystem, predators are the most vulnerable to anthropogenic disturbance and land use and any changes in the predator community will greatly impact nesting success in birds.
REFERENCES

Berkeley, L. I. 2004. The postfledging ecology of Dickcissels (Spiza americana). MS Thesis, University of Nebraska at Omaha, Omaha, NE.


Engberg, S. E. 2004. Landscape and Habitat Effects on Grassland Birds. MS Thesis, University of Nebraska at Omaha, Omaha, NE.


Table 1. Documented predators of grassland bird nests in the Great Plains, USA. For each study the number of occurrences of predation by each predator type is given.

<table>
<thead>
<tr>
<th>Predator Type</th>
<th>Nebraska/Iowa</th>
<th>North Dakota</th>
<th>Wisconsin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snake (<em>Elaphe vulpina, Thamnophis</em> spp., <em>Coluber constrictor, Pituophis catenifer</em>)</td>
<td>9</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Raccoon (<em>Procyon lotor</em>)</td>
<td>6</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td>Ground squirrel (<em>Spermophilus</em> spp.)</td>
<td>4</td>
<td>13</td>
<td>4</td>
</tr>
<tr>
<td>Brown-headed cowbird (<em>Molothrus ater</em>)</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Mouse (<em>Peromyscus</em> sp., <em>Zapus</em> sp.)</td>
<td>2</td>
<td>3</td>
<td>-</td>
</tr>
<tr>
<td>Long-tailed weasel/mink (<em>Mustela</em> spp.)</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>American badger (<em>Taxidea taxus</em>)</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Birds of prey (<em>Buteo</em> sp., <em>Circus cyaneus</em>)</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Fox/coyote/dog (<em>Vulpes vulpes/Canis latrans</em>)</td>
<td>-</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Domestic cat</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Striped skunk (<em>Mephitis mephitis</em>)</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Opossum (<em>Didelphis virginiana</em>)</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>White-tailed deer (<em>Odocoileus virginianus</em>)</td>
<td>-</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>24</strong></td>
<td><strong>26</strong></td>
<td><strong>24</strong></td>
</tr>
</tbody>
</table>

1This study  
2Pietz and Granfors (2000)  
3Renfrew and Ribic (2003)