2001

Landscape ecology of mammalian predators and its relationship to waterfowl nest success in the Prairie Pothole Region of North Dakota

Michael Lee Phillips

Iowa State University

Follow this and additional works at: https://lib.dr.iastate.edu/rtd

Part of the Ecology and Evolutionary Biology Commons, and the Environmental Sciences Commons

Recommended Citation

https://lib.dr.iastate.edu/rtd/447

This Dissertation is brought to you for free and open access by the Iowa State University Capstones, Theses and Dissertations at Iowa State University Digital Repository. It has been accepted for inclusion in Retrospective Theses and Dissertations by an authorized administrator of Iowa State University Digital Repository. For more information, please contact digirep@iastate.edu.
INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®
Landscape ecology of mammalian predators and its relationship to waterfowl nest success in the Prairie Pothole Region of North Dakota

by

Michael Lee Phillips

A dissertation submitted to the graduate faculty in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Animal Ecology
Major Professor: William R. Clark

Iowa State University
Ames, Iowa
2001
Graduate College
Iowa State University

This is to certify that the Doctoral dissertation of

Michael Lee Phillips

has met the dissertation requirements of Iowa State University

Signature was redacted for privacy.

Major Professor

Signature was redacted for privacy.

For the Major Program

Signature was redacted for privacy.

For the Graduate College
# TABLE OF CONTENTS

## ACKNOWLEDGMENTS

**v**

## ABSTRACT

**vi**

## CHAPTER 1. GENERAL INTRODUCTION

- Introduction 1
- Dissertation Organization 3
- Literature Review 3
- Literature Cited 6

## CHAPTER 2. PREDATOR SELECTION OF HABITAT FEATURES IN PRAIRIE LANDSCAPES WITH CONTRASTING GRASSLAND COMPOSITION AND ITS EFFECT ON DUCK NEST SUCCESS

- Abstract 13
- Study Areas 17
- Methods 19
- Results 26
- Discussion 30
- Management Implications 33
- Acknowledgments 34
- Literature Cited 35

## CHAPTER 3. ANALYSIS OF PREDATOR MOVEMENT IN PRAIRIE LANDSCAPES WITH CONTRASTING GRASSLAND COMPOSITION

- Abstract 55
- Introduction 57
- Methods 61
- Results 70
- Discussion 76
- Acknowledgments 80
- Literature Cited 80

## CHAPTER 4. PREDATOR ACTIVITY IN GRASSLAND PATCHES AND ITS EFFECT ON WATERFOWL NEST SUCCESS

- Abstract 111
- Introduction 113
- Methods 116
- Results 124
- Discussion 130
- Acknowledgments 134
- Literature Cited 135
ACKNOWLEDGMENTS

I would like to express deep appreciation to Bill Clark, my major professor, for his guidance and tenacious commitment to excellence in research and my graduate education. I would also like to thank the members of my Program of Study Advisory Committee, Brent Danielson, Diane Debinski, Rolf Koford, and Sarah Nusser for their advice, patience and unique perspectives on this project and research in general.

I am grateful to Dohn Broadwell and David Grohne for providing funding for this project through the Institute for Wetland and Waterfowl Research of Ducks Unlimited. This project was also supported by the Iowa Cooperative Fish and Wildlife Research Unit, the Department of Animal Ecology at Iowa State University, and the Central Flyway Council.

I am indebted to the Northern Prairie Wildlife Research Center (NPWRC, USGS) for their financial and logistic support. Marsha Sovada and Ray Greenwood were tremendous sources of information on practical problems of fieldwork, and on the applied and basic ecology of predators and waterfowl. They greatly enhanced my professional development. Robert "Woody" Woodward provided crucial help in the field and with creating the GIS databases for our study areas. Tom Sklebar recorded the aerial photography and videography used for creating our GIS databases.

I thank the crew members - Brian Allen, Davis Coye, Wayne Cymbaluk, Wade Jones, Kammie Kruse, David Fronczak, Mike Mayer, Rich Olsen, Jim Sparks, and Rachel Wolstenholm - for their hard work tracking predators throughout the long summer nights.
Mark Zahn (Wildlife Services, USDA) assisted with trapping foxes. Chuck Loesche (USFWS) provided Stewart-Kantrud (1971) wetland classifications for the NWI data.

I would like to thank Zuleyma Tang-Martinez who transformed my interest in natural history into the scientific pursuit of ethology and behavioral ecology. I hold deep gratitude for my fellow graduate students for their friendship and for their interest and suggestions about the research. I would like to thank David Horn, my colleague on this project, for making this project a most valuable learning experience. I would especially like to thank Dick Schmitz for his friendship, guidance and encouragement which kept me tied to the mast during a difficult passage.
ABSTRACT

Mammalian predation is a major cause of mortality of breeding waterfowl in the Prairie Pothole Region. However, little is known about how landscape features influence the ability of predators to find waterfowl nests. I analyzed the habitat selection and movement patterns of radiomarked red fox (*Vulpes vulpes*) and striped skunk (*Mephitis mephitis*) in two 41.4 km$^2$ study areas with contrasting compositions of grassland (planted cover, pastureland and hayland). The study areas included either 10-15% (Low Grassland Composition, LGC) or 40-50% (High Grassland Composition, HGC) grassland. Edges of wetlands surrounded by cropland were consistently selected by fox and skunk on both types of landscape. Foxes frequently selected planted cover (both edge and interior areas) in LGC landscapes, whereas they rarely selected the interior areas of planted cover in HGC landscapes. Fractal analysis indicated that fox pathways were slightly straighter in LGC landscapes suggesting increased traveling behavior in the more prevalent cropland. However, there were more frequent sharp turns (characteristic of searching behavior) within planted cover in LGC landscapes. Contrary to predictions, the rate of movement was not slower when animals were in planted cover compared to when they were in cropland in either type of landscape. Furthermore, the frequency of turn angles was highly variable in cropland. In contrast, skunk pathways did not differ between LGC and HGC landscapes. They were more influenced by wetlands than by the landscape composition of grassland. Skunks spent more time in back and forth movement in all habitats. The rate of movement was faster in cropland than in planted cover in LGC but not in HGC landscapes. When I simulated random combinations of predator movement and waterfowl
nests there was essentially no relationship between planted cover patch size and the predicted proportion of nests that would be encountered by predators. However, the observed proportion of nests encountered by predators in intermediate sized patches (50-120 ha) was frequently greater than the proportion predicted by random activity. This study has led to a refined understanding of how predators perceive the landscape and is an important contribution to both predator landscape ecology and waterfowl management.
CHAPTER 1. GENERAL INTRODUCTION

Introduction

Mammalian predation is a major factor influencing waterfowl nest success in the Prairie Pothole Region (PPR) of the Northern Great Plains (Klett et al. 1988, Johnson et al. 1989, Sargeant and Raveling 1992, Sargeant et al. 1993). The PPR is a major source for waterfowl breeding in North America (Bellrose 1980, Batt et al. 1989) and has been the focus of restoration and management of grassland breeding habitat. Native grasslands in the PPR have been dramatically altered through increasing fragmentation and loss due to conversion to agricultural uses (Higgins 1977, Sugden and Beyersbergen 1984, Greenwood et al. 1995, Miller and Nudds 1996). However, since 1985 the Conservation Reserve Program (CRP) of the Federal Farm Security Act and the North American Waterfowl Management Plan have provided incentives for large scale restoration of perennial grassland. The result of these opposing trends is a landscape composed of a mosaic of cover types dominated by agriculture and interspersed with patches of grassland of various sizes and differing degrees of isolation from each other. The restoration of grassland breeding habitat has provided an excellent opportunity to study the spatial interactions between predators and waterfowl. Understanding these interactions is crucial to determining the effectiveness of large scale restoration and management of waterfowl breeding habitat in ways that may ultimately reduce the rate of predation on waterfowl and their nests.
Despite the fact that mammalian predation is a major cause of mortality of breeding waterfowl in the Prairie Pothole Region, little is known about how landscape features influence the ability of predators to find waterfowl nests. There has not been much attempt to consider the well developed theoretical concepts about the profitability and costs of predator searching behavior that would predict how changes in the composition of grassland in the landscape could potentially alter predator movement both between, and within, patches of grassland. For example, if predators spend more time in isolated patches of grassland because of long traveling distances or spend time along the edge of grassland patches as a result of increased profitability, then nests located in these areas would be more vulnerable to predation.

This study was a unique opportunity to examine the effect of landscape features on the interaction between predators and waterfowl by simultaneously recording predator movement and waterfowl nest success at the patch and landscape scale. I analyzed the habitat selection and movement patterns of radiomarked red fox (*Vulpes vulpes*) and striped skunk (*Mephitis mephitis*) in two 41.4 km² study areas with contrasting grassland composition. Each study area contained either 10-15% perennial grassland that included planted cover, pastureland, and hayland (Low Grassland Composition, LGC) or 40-50% perennial grassland (High Grassland Composition, HGC). Both predator species are common waterfowl predators (Sargeant 1972, Sargeant et al. 1984, Greenwood 1986) that have the potential to range widely across many contrasting habitat types and exhibit different movement patterns. My objectives in this study were to: 1) study the relative selection by predators of differing cover types including the physiognomic characteristics
(edge and core area) of patches of planted cover (Chapter 2), 2) study the effect of grassland composition on the overall shape of movement pathways and the effect of contrasting cover types on movement between successive locations (i.e., the rate of speed and turn angle) within a pathway (Chapter 3), 3) study the behavioral response of predators to patches of planted cover of varying sizes (Chapter 4), and 4) examine the relationship between predator movement and duck nesting success (Chapters 2 and 4).

**Dissertation Organization**

This dissertation is composed of five chapters including a General Introduction (Chapter 1), three manuscripts prepared for submission to peer-reviewed scientific journals (Chapters 2-4), and a General Conclusion (Chapter 5). Chapters 2-4 are being prepared for submission to The Journal of Wildlife Management, Ecology, and Ecological Applications. I have received editorial comments on Chapter 1 from personnel at the Northern Prairie Wildlife Research Center and outside reviewers who are listed in the Acknowledgments. All sections of the manuscripts and of this dissertation were written by Michael L. Phillips and edited by W. R. Clark.

**Literature Review**

Movement is fundamental to understanding spatial-temporal patterns of dispersal, habitat selection, and the interactions between predator and prey (Swinglund and Greenwood 1983, Bell 1991, Stenseth and Lidicker 1992). Animal movements are influenced by intrinsic physiological factors (e.g., hunger and reproduction) and the
sensory capabilities of organisms (Bell 1991, Zollner and Lima 1997). They are also influenced by extrinsic factors such as the level of spatial structure of the landscape (Burrough 1981, Kotliar and Wiens 1990). Movement pathways may differ between species as a result of dissimilar ways in which species perceive and respond to the density and distribution of a resource in the landscape (With 1994, Wiens et al. 1995). In contrast, similar movement pathways exhibited by different species may reflect a common underlying mechanism governing behavior.

Foraging theory has been used to make predictions about predator behavior as a function of decision rules whereby a predator will move in relation to the density and distribution of resources in order to maximize its rate of intake of energy or the encounter rate with prey (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976, Stephens and Krebs 1986). The theory recognizes the importance of the rate of return of resources within contrasting habitat types and the distribution of discrete patches of required resources on predator movement in the landscape. The greater the rate of return of resources within a habitat the more time a predator will spend foraging in that habitat. These habitats are more likely to be efficiently searched by predators. The greater the distance between patches of the required habitat in the landscape the more energy a predator must invest in traveling between patches and therefore the more time a predator will spend in the patch.

In a mosaic agricultural landscape, grassland-nesting habitat contains resources potentially attractive to predators (e.g., food resources, Pasitschniak-Arts 1998) and is surrounded by agricultural habitats that are unlikely to contain many resources attractive to
a predator. Based on foraging theory, predator movement is predicted to be faster and straighter as it travels through the agricultural matrix toward a patch of grassland. Simulation studies have demonstrated that relatively straight movement pathways are a more efficient search pattern for an animal that uses widely dispersed patches (Zollner and Lima 1999). Once within a grassland patch, a predator will increase its foraging efficiency by moving in a more tortuous manner and will move more slowly as it spends more time foraging than traveling. In highly fragmented landscapes, predator movement pathways will be relatively straighter as they move long distances between isolated patches. In less fragmented landscapes with large, contiguous patches, predator movement pathways will be relatively more tortuous as the predators have less distance to travel to encounter prey.

Ecologists have suggested that predator movement patterns may be influenced by the physiognomic characteristics of habitat patches (Andren 1995, Ims 1995). The size and shape of a patch will determine the relative amounts of edge and interior ("core area") habitat (Temple 1986). Small or linearly shaped patches have proportionally less core area and more edge habitat than do large, block shaped patches. If predators spend more time along the edge of patches, then nests near edges may be vulnerable to either direct or incidental predation (Gates and Gysel 1978, Angelstam 1986, Vickery et al. 1992, Paton 1994). For grassland nesting birds, the amount of edge habitat in the landscape can affect their mortality (Schmitz and Clark 1999) and the amount of core area can be important in predicting nest success (Pasitschniak-Arts and Messier 1996, Clark et al. 1999).
The patch size of grassland nesting habitat may influence predator movement and foraging efficiency and may be an important mechanism determining the relationship between predators and nest success (Fritzell 1975, Oetting and Dixon 1975, Sargeant et al. 1984, Cowardin et al. 1985, Krasowski and Nudds 1986, Clark and Nudds 1991). It is argued that foraging efficiency will be greatest in small patches since they are easily found and thoroughly searched. Moreover, foraging efficiency will decrease with increasing patch size due to predator satiation or decreased foraging effort by a few predators over a large area (dilution effect). There is evidence that smaller patch size is associated with lower nest success and increased predation in forest songbirds (Whitcomb et al. 1981, Wilcove 1985) and ring-necked pheasants (*Phasianus colchinus*) (Clark et al. 1999). It has been observed that waterfowl nest success is greater in larger patches of CRP for waterfowl in the PPR (Kantrud 1993, Sovada et al. 2000) and is positively correlated with the composition of grassland in the landscape (Greenwood et al. 1987, Reynolds et al. 1994, Horn 2000).

**Literature Cited**


island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.


CHAPTER 2. PREDATOR SELECTION OF HABITAT FEATURES IN PRAIRIE LANDSCAPES WITH CONTRASTING GRASSLAND COMPOSITION AND ITS EFFECT ON DUCK NEST SUCCESS

A paper to be submitted to the Journal of Wildlife Management

Michael L. Phillips, William R. Clark, Marsha A. Sovada, David J. Horn, Rolf R. Koford, and Raymond J. Greenwood

Abstract: We investigated habitat selection by red fox (Vulpes vulpes) and striped skunk (Mephitis mephitis) in North Dakota landscapes with contrasting compositions of waterfowl nesting habitat during the 1996-1997 duck nesting seasons. We used radio telemetry to monitor the nightly movements of red fox and striped skunk on four 41.4 km² study areas. Each year, one study area contained 10-15% perennial grassland that included planted cover, pastureland, and hayland (Low Grassland Composition, LGC) while the other study area contained 40-50% perennial grassland (High Grassland Composition, HGC). We examined the relationship between the level of habitat selection by predators and duck nest success in 3 landscape features associated with planted cover: planted cover core, planted cover edge and planted cover-wetland edge. Agricultural-wetland edges were highly selected by striped skunk and by red fox in both LGC and HGC landscapes. Planted cover was selected more frequently by fox in LGC than in HGC landscapes. The interior portions of planted cover (i.e., the core areas and wetland edges within planted cover) were frequently selected by fox on LGC landscapes, while they were
rarely selected by fox in HGC landscapes. We found only a moderate level of selection for the edge around planted cover by red fox or striped skunk. Striped skunk did not show a strong selection for planted cover in either type of landscape, but they exhibited a strong selection for agricultural-wetland edges. Pastureland was used 5 times more frequently by fox in HGC landscapes than in LGC landscapes and may have contributed to the low selection of planted cover cores. Nest success was found to be greater in HGC landscapes than in LGC landscapes for each of the 3 landscape features associated with planted cover: planted cover core, planted cover edge and planted cover-wetland edge. Observations of predator activity in relation to landscape features will allow us to predict the spatial characteristics of breeding hotspots for waterfowl and suggest landscape level management strategies.

**Key words:** compositional analysis, habitat fragmentation, habitat selection, landscape composition, *Mephitis mephitis*, nest success, North Dakota, Prairie Pothole Region, predation, red fox, striped skunk, *Vulpes vulpes*.

Mammalian predation is an important factor influencing the nest success of waterfowl in the Prairie Pothole Region of the northern Great Plains (Klett et al. 1988, Johnson et al. 1989, Sargeant and Raveling 1992, Sargeant et al. 1993). Although most of these predators are habitat generalists (Fritze 1978, Sargeant et al. 1984, Greenwood 1986), little is known about how the composition of the landscape affects movement patterns and how such movement patterns might influence vulnerability of waterfowl
nests. The conversion of native grasslands to agricultural cropland has led to loss and fragmentation of breeding habitat for upland waterfowl (Sugden and Beyersbergen 1984, Batt et al. 1989), and it is likely this has led to changes in the relationship between predator movements and waterfowl nesting success. We chose to study red fox (hereafter fox) and striped skunk (hereafter skunk). Both species are common waterfowl predators (Korschgen 1959, Sargeant 1972, Sargeant et al. 1984, Greenwood 1986) that have the potential to range widely across many different habitat types and exhibit different movement patterns.

Theoretically, predators should spend more time in isolated grassland patches because of the increased energy investment required to reach the patches (Stephens and Krebs 1986). Furthermore, predators should select habitat features in a mosaic agricultural landscape based on the rate of return of required resources relative to that of surrounding habitat types (Charnov 1976). Predators will remain in, or frequently revisit, a patch as long as the rate of gain in resources remains above the average for that type of habitat. Patches highly selected by predators are more likely to be efficiently searched for prey. In a mosaic agricultural landscape, planted cover contains many resources potentially attractive to predators (e.g., food resources, Pasitschniak-Arts 1998) and is surrounded by agricultural habitats which can contain either moderate resources attractive to predators (e.g., pastureland or hayland) or few resources that are less attractive to predators (e.g., cropland). We predicted that in landscapes with a low grassland composition, predators would disproportionately select the isolated patches of planted
cover. Consequently, waterfowl nests in such habitats would be more vulnerable to predation.

Much theory and supporting data have been developed to predict how predator movement patterns may be influenced by the physiognomic characteristics of nesting habitat (Andren 1995, Ims 1995). The size and shape of planted cover will determine the relative amounts of edge and interior ("core area") habitat (Temple 1986). Small or linearly shaped patches of planted cover have proportionally less core area and more edge habitat than do large block shaped patches. Nests in edge habitat may be vulnerable to either direct or incidental predation (Gates and Gysel 1978, Angelstam 1986, Vickery et al. 1992). For grassland nesting birds, the amount of edge habitat in the landscape can affect their mortality due to predation (Schmitz and Clark 1999) and the amount of core area can be important in predicting nest success (Pasitschnia-Arts and Messier 1996, Clark et al. 1999). The extent to which the edge or the core area of preferred habitat affects nest success may depend on the amount of nesting habitat in the landscape (Donovan et al. 1997, Clark et al. 1999). We predicted that in landscapes with a high grassland composition, predators would be less efficient in searching core areas of large, interconnected blocks of planted cover resulting in greater nest success for waterfowl.

Besides edges around planted cover, edges around wetlands also may have an important effect on predator movement. Wetland edges and wet meadows contain many prey species that are attractive to some predators (Greenwood et al. 1999). Striped skunk have been shown to be attracted to wetland edges (Lariviere and Messier 2000); however, no one has examined whether the landscape context of the wetland edges influences
predator movement. If upland habitat within core areas of planted cover is attractive to predators, then wetland edges within planted cover may not be used as frequently as wetland edges surrounded by cropland.

Our objective was to simultaneously examine the selection of habitats by predators and estimate waterfowl nest success in landscapes with differing amounts of perennial planted cover. Our goal was to determine if predator selection of habitats, as well as the core areas and edges around planted cover and edges around wetlands, are predictably related to duck nesting success.

STUDY AREAS

In 1996 and 1997, we selected two 41.4 km² study areas with contrasting amounts of perennial grassland (planted cover, pastureland, and hayland) in the Prairie Pothole Region of central North Dakota. Study areas we selected with a "Low Grassland Composition" (hereafter LGC) were Litchville, ND (Svea Township in Barnes County) in 1996 (Fig. 1) and Bowdon, ND (Berlin Township in Wells County) in 1997 (Fig. 2). LGC landscapes contained isolated patches of perennial grassland surrounded by cropland. Habitat composition of the Litchville study area was 66.9% cropland, 12.5% planted cover, 2.3% pastureland, 0.3% hayland, and 11.7% wetlands. Habitat composition of the Bowdon study area was 56.4% cropland, 13.8% planted cover, 2.7% pastureland, 3.2% hayland, and 18.5% wetlands.

In contrast, study areas we selected with a "High Grassland Composition" (hereafter HGC) were Medina, ND (Iosco Township in Stutsman County) in 1996 (Fig. 3)
and Hurdsfield, ND (Silver Lake Township in Wells County) in 1997 (Fig. 4). HGC landscapes contained large patches of perennial grassland adjacent to cropland. Habitat composition of the Medina study area was 34.3% cropland, 22.1% planted cover, 19.0% pastureland, 4.1% hayland, and 13.4% wetlands. Habitat composition of the Hurdsfield study areas was 23.0% cropland, 22.5% planted cover, 27.8% pastureland, 1.5% hayland, and 21.1% wetlands.

We used data from the National Wetland Inventory (NWI, U.S. Fish and Wildlife Service, St. Petersburg, Florida) to identify the wetland basins on the study areas. Each study area contained a similar composition of wetland basins (Litchville = 9.3%, Bowdon = 13.9%, Medina = 12.1%, and Hurdsfield = 13.8%). The wetlands were predominantly temporary and seasonal. Differences in the percentages of wetlands in the habitat compositions for the different study areas noted above are mainly the result of flooded margins around wetland basins as a result of the wet conditions. NWI classifications were converted to Stewart and Kantrud (1971) classifications by the Habitat and Population Evaluation Team (U. S. Fish and Wildlife Service, Bismarck, North Dakota).

All study areas also included a square-mile road system (<2%). Other habitat types (<1.0%) included farmsteads, trees, and other miscellaneous habitat types. The Medina study area included a predator exclosure (2.4%) which contained planted cover enrolled in the Conservation Reserve Program and hayland.
METHODS

Capture

We captured fox and skunk in April and May (1996 and 1997) and in June (1997) using either livetraps for skunks or snares with stops and leg hold traps for foxes. A professional trapper from Wildlife Services (United States Department of Agriculture, Bismarck, ND) assisted in capturing fox. We trapped intensively and systematically across all study areas with the goal of capturing all resident animals of both predator species. All captured study animals were sexed, weighed, examined for tooth wear and reproductive status of females, ear tagged and fitted with a telemetry transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) containing a 1 hour mortality switch. The transmitters weighed approximately 60 g for skunk and 110 g for fox. All trapping and handling procedures followed recommendations by the American Society of Mammalogists (1987), the Northern Prairie Wildlife Research Center's Animal Care and Use Guidelines, and were approved by the Iowa State University Committee on Animal Care.

Radiotelemetry

We sampled daytime locations (0800-2000) by recording 1 location for each animal on the study area each day (except Sundays). We recorded predator movements intensively at night (2000-0800) 3 times each week. To ensure complete coverage of the study area and sampling of all animals, we divided each study area into 4 quadrants and systematically rotated our sampling among each of the quadrants. We recorded the
frequency and duration each animal was tracked in order to minimize bias in our tracking effort among the available animals.

Locations for a sampled animal were recorded every 10-15 minutes. Locations were estimated from 2-3 bearings using vehicle-mounted null-peak directional antennas. Bearings were taken from telemetry stations positioned along roads or at other accessible positions with known Universal Transverse Mercator (UTM) coordinates. Locations and their 95% error ellipses were estimated using LOCATE II software (Pacer Truro, Nova Scotia, Canada; Nams 1990). Locations based on 2 bearings were estimated using a fixed standard deviation determined for each crew member based on 2 field tests given before and midway through the field season.

We examined the statistical distribution of the error ellipses and deleted any location with an error ellipse that was greater than 3.0 times the interquartile range above the 75% quantile (an "extreme outlier", Devore and Peck 1986: 94). Animals with fewer than 20 locations (13 skunk and 4 fox) were considered undersampled and were not used in the analysis.

**Habitat and Landscape Variables**

Land cover data were recorded from low altitude aerial photography and videography for each study area plus a 1.6 km wide border around each study area. Habitat types were digitized and classified using the Map and Image Processing System (MicroImages, Lincoln, Nebraska, USA). Habitat classifications were verified by ground observations. We used ARC/INFO (ESRI, 1994, Redlands, California, USA) for management and analysis of the land cover data.
We delineated each study area into nine habitat types: 1) planted cover core, 2) planted cover edge, 3) planted cover-wetland edge, 4) agriculture-wetland edge, 5) pastureland, 6) hayland, 7) cropland, 8) roads (paved and gravel), and 9) miscellaneous habitats. We defined planted cover as areas seeded to perennial grasses and forbs and enrolled in the Conservation Reserve Program (CRP), the Water Bank Program (WBP), or federal Waterfowl Production Areas (WPA). Our definition of a patch of planted cover is similar to that of Sovada, et al. (2000: Fig. 6) except that we allowed gravel and paved roads to divide adjacent areas of planted cover into separate patches. We defined planted cover edge as 50 m on either side of the boundary of planted cover. The core area of the planted cover therefore was defined as interior planted cover > 50 m from the boundary and not included in wetland edges within patches of planted cover. We divided wetland edges into 2 categories: planted cover-wetland edges (habitat ≤ 50 m from the boundary of a wetland that was within planted cover) and agricultural-wetland edge (habitat ≤ 50 m from the boundary of a wetland not within planted cover). If a wetland was adjacent to, or intersected, the boundary of a patch of grassland then the habitat was defined as wetland edge instead of grassland edge.

LGC landscapes contained a smaller composition of cover core area than planted cover in HGC landscapes. Litchville contained 7.7% planted cover core, 4.9% planted cover edge, 2.2% planted cover-wetland edge, and 24.8% agricultural-wetland edge. Bowdon contained 6.4% planted cover core, 4.9% planted cover edge, 5.3% planted cover-wetland edge, and 18.7% agricultural-wetland edge. Medina contained 11.4% planted cover core, 8.0% planted cover edge, 5.6% planted cover-wetland edge, and
19.7% agricultural-wetland edge. Hurdsfield contained 13.6% planted cover core, 5.6% planted cover edge, 5.4% planted cover-wetland edge, and 21.1% agricultural-wetland edge.

Pastures contained grazed perennial grasses. Hayland contained perennial grasses that were disturbed by mowing. Croplands were planted in either row crops (corn, sunflowers, beans, potatoes, or soybeans) or grain crops (wheat, barley, oats, flax, or canola). The miscellaneous category included the remaining habitat types: farmyards, trees, fallow agricultural land, islands, land not in agricultural use, and a predator exclosure on Medina. Trees were usually found in small woodlots, shelterbelts or around farmyards. The open water portions of wetland basins were excluded from the analysis, because we did not consider these areas available habitat for the predators.

**Statistical Analysis**

Selection of habitat types by fox and skunk was evaluated using compositional analysis (Aitchison 1982, Aebischer et al. 1993). For a given number of habitat types, \( D \), a composition is the proportions of each habitat used \( (x_{il}^a, \text{for } i = 1, \ldots, D) \) or the proportions of each habitat available \( (x_{il}^a, \text{for } i = 1, \ldots, D) \) for each animal \( (k = 1, \ldots, n) \) in each landscape type \( (l = \text{LGC or HGC}) \). The proportion of habitat used is the ratio of the number of locations in a habitat type to the total number of locations recorded for an individual. The proportion of habitat available is the ratio of the area of a habitat to the total area for all habitats within a buffer distance (defined below). By focusing the analyses on compositions, animals become the observational unit of our analyses rather than individual locations. Compositional analysis compares the difference, \( d_{il} \), in
selection between one of the habitat types, $S$, relative to each of the remaining habitat types $i (i = 1, ..., D-1)$, such that:

$$d_{ai} = \ln\left(\frac{x^{u}_{ikl}}{x^{u}_{stk}}\right) - \ln\left(\frac{x^{u}_{ikl}}{x^{u}_{stk}}\right).$$

The differences, $d_{ai}$, among habitat types were examined simultaneously using a multivariate analysis of variance (MANOVA, Rencher 1995). We constructed a matrix of the differences, $d_{ai}$, with $D-1$ habitats (i.e., the dependent variables) in columns and $n$ rows (one row for each animal). If an animal used all 9 habitat types at random, then $d_{ai} = 0$ (for all $i = 1, ..., D-1$). We chose an alpha level of 0.10 to evaluate the MANOVA tests for significant nonrandom habitat use. For habitats not used or that were not available, we substituted the value 0.0001 that was an order of magnitude smaller than the smallest observed proportion. Because there was an imbalance in the number of locations recorded for each animal, the differences, $d_{ai}$, were weighted by the square root of the number of locations. Because of insufficient sample size among fox, we pooled animals of the same species from study areas with a similar type of landscape (e.g. foxes on Litchville were pooled with foxes on Bowdon and analyzed as foxes on LGC landscapes).

We used a buffering technique to estimate the composition of habitat available to each predator. Although a home range has frequently been used to define what habitat types are available to an animal (Aebischer et al. 1993), our data were recorded in groups of locations collected along nightly movement paths that would skew the shape and size of a home range estimator. Therefore, we defined available habitat based on a series of concentric buffers around the mean UTM location for each animal. The buffering technique avoided any of the assumptions necessary for calculating a home range and is
independent of individual behavior. We buffered at 500, 1000, 2000, and 3000 m
distances. The distances were determined by examining the range of UTM locations for
all animals. We examined selection of habitat types by fox and skunk at each of the buffer
distances. The smallest buffer distance that indicated nonrandom use by both fox and
skunk was used to rank habitat types. The smallest buffer distance would give the most
conservative estimate of available habitat (i.e., larger buffer distances are likely to contain
more habitat not used by an individual).

We constructed rank matrices to determine the relative use of each of the habitat
types and test for significant differences between each pair of habitat types (Aebischer et
al. 1993). A rank matrix was constructed for each animal (k) by computing the difference,
d_{ijk}, in selection between each ith (row) and jth (column) pair of habitat types as follows:
\[ d_{ijk} = \ln\left(\frac{x_{ik}}{x_{jk}}\right) - \ln\left(\frac{x_{ik}}{x_{jk}}\right).\]
If \( d_{ijk} \equiv 0 \), then the level of selection for the ith and jth habitat are approximately equal for
the kth animal. However, if \( d_{ijk} > 0 \), then the animal showed a greater selection for the
ith habitat compared with the jth habitat, and consequently if \( d_{ijk} < 0 \), then the animal
showed a lower selection for the ith habitat compared with the jth habitat. As above, each
of the \( d_{ijk} \) were weighted by the square root of the number of locations. We then
computed the mean and standard error for each \( d_{ijk} \) element in the matrices for fox and
skunk on landscapes with LGC and HGC, such that:
\[ \bar{d}_{ijl} = \frac{1}{n} \sum_{k=1}^{n} d_{ijk}. \]
To rank habitat types by level of use, we counted the number of positive values in each row of the $\mathbf{d}_{ijlt}$ matrix (Aebischer et al. 1993). The habitats were ranked from 1 (lowest selection) to 9 (highest selection). When the null hypothesis of random habitat use was rejected by the MANOVA, we computed a series of $t$-tests using an alpha level of 0.05 to test for significant differences between the elements in the mean rank matrix, $\mathbf{d}_{ijlt}$, to determine which habitat types contributed most to nonrandom use (Rencher and Scott 1990, Aebischer et al. 1993).

To illustrate the probability of selection for each habitat, $i$, by each species ($s =$ fox or skunk) in the different landscape types, $l$, we computed standardized selection ratios (Manly et al. 1993: 40) such that:

$$B_{i,sl} = \frac{G_{ist}}{\sum_{i=1}^{D} G_{ist}}$$

where $G_{ist}$ is the geometric mean of the selection ratios ($w_{ist}$) among individuals for each species ($s$) in each type of landscape ($l$). A selection ratio, $w_{ist}$, is the proportion of habitat used ($x_{ist}^u$) divided by the proportion of habitat available ($x_{ist}^a$) for each individual ($k$) in landscape type ($l$). For example, for fox #1 on LGC landscapes ($s =$ fox, $k = 1$, and $l = \text{LGC}$),

$$w_{\text{fox},1,\text{LGC}} = \frac{x_{1,\text{fox},1,\text{LGC}}^u}{x_{1,\text{fox},1,\text{LGC}}^a}$$

and for all fox on LGC landscapes ($k = 1, \ldots, n$, where $n = 13$) the geometric mean of the $w_{ist}$ is:

$$G_{ist} = \text{antiloge} \left[ \frac{1}{n} \sum_{k=1}^{n} \ln(w_{ist}) \right]$$
We used geometric means so that the standardized selection ratios would correspond to the ranks of the habitat types as computed above which are based on the log scale. We illustrated the relative strength of selection among the habitat types in Figures 1-4 using the inverse of the number of resources (i.e., $1/9 = 0.11$) (Krebs 1999: 478). Values above 0.11 indicate high levels of selection and values below 0.11 indicate low levels of selection.

Nest Success

We focused assessment of duck nest success in planted cover. We searched for waterfowl nests using a chain dragged between 2 vehicles. Nest searching took place from early May to mid-July. Each field was searched 3 times in 1996 and 4 times in 1997. Nest success was estimated by procedures developed by Mayfield (1975) and modified by Johnson (1979). We used the program CONTRAST (Hines and Sauer 1989) to make comparisons of the estimates of nest daily survival rates (DSR) in planted cover between landscape types. We also compared nest survival in each of the features of planted cover (i.e., edge, core, and wetland edges within planted cover). Further details of the procedures used to find and monitor nests are given in Horn (2000).

RESULTS

Radiotelemetry

We tracked 16 fox and 52 skunk in LGC landscapes and 16 fox and 47 skunk in HGC landscapes. We recorded 23,592 locations over the 2 field seasons. We deleted locations with an error ellipse greater than 3.0 times the interquartile range above the 75%
quantile (= 117,604 m$^2$). The resulting median area for error ellipses was 11,345 m$^2$.

The final data set contained 21,913 locations (3,295 day locations and 18,618 night locations) for 114 individuals. Litchville contained 6 fox and 22 skunk. Bowdon contained 7 fox and 22 skunk. Medina contained 5 fox and 17 skunk. Hurdsfield 10 fox and 25 skunk. For the analyses animals were pooled by study areas with a similar landscape type so that there were 13 fox and 44 skunk in LGC landscapes and 15 fox and 42 skunk in HGC landscapes.

Habitat Selection

Nonrandom habitat use ($P < 0.10$) was consistently observed for fox and skunk on both the LGC and HGC landscapes at only the 2000 and 3000 m buffer distances (Table 1). In LGC landscapes, there was significant nonrandom habitat use by fox at the 1000, 2000, and 3000 m buffer distances, but not at the 500 m distance. In HGC landscapes, there was significant nonrandom habitat use by fox at the 2000 and 3000 m buffer distances, but not at the 500 and 1000 m distances. There was nonrandom habitat use by skunks at all buffer distances in both landscape types; however, at the 2000 and 3000 m distances the relationships were much stronger than at the 500 and 1000 m distances.

We focused on the 2000 m buffer distance for our analysis because it was the smallest buffer distance that revealed nonrandom habitat use for both fox and skunk on both landscape types. The 2000 m distance included 97.8% of the locations (i.e. individuals rarely moved beyond this buffer distance). Therefore, the 2000 m distance closely reflected the range of movement for both fox and skunk. Our inability to detect
nonrandom habitat use for fox at the 500 and 1000 m buffer distances could be due to either an insufficient number of locations, or not enough heterogeneity in available habitat.

For fox in LGC landscapes, the selection of planted cover core areas ranked highest among habitats (Fig. 5). All 3 features of planted cover (i.e., the edge and core areas of planted cover and planted cover-wetland edges) were highly selected by fox. These habitat types were not different from each other in the level of use by fox (P-values ranged from 0.27 to 0.89). Planted cover cores were not different from agricultural-wetland edges (P = 0.33), or cropland (P = 0.06). The use of planted cover cores by fox was greater than pastureland (P = 0.004), hayland (P = 0.05), roads (P = 0.001), and miscellaneous habitats (P = 0.02), which were rarely selected.

For skunk in LGC landscapes, agricultural-wetland edges were the most highly selected habitat and were greater than all other habitat types (P < 0.05 for all comparisons) including planted cover-wetland edges (Fig. 6). Cropland was strongly selected by skunk, but selection was less than agricultural-wetland edges (P < 0.0001). The selection of cropland was greater than the other agricultural habitats such as pastureland (P = 0.01) and hayland (P = 0.04). Cropland was selected more than roads (P = 0.03). Unlike fox, skunk did not show a strong selection for planted cover. The use of planted cover core, planted cover edge and planted cover-wetland edges was not different from agricultural habitats such as cropland (P-values ranged from 0.07 to 0.65), pastureland (P-values ranged from 0.14 to 0.51) and hayland (P-values ranged from 0.32 to 0.99). The selection of features of planted cover was not different from roads (P-values
ranged from 0.25 to 0.87) or other miscellaneous habitats (P-values ranged from 0.38 to 0.92).

For fox in HGC landscapes, the selection of agricultural-wetland edges was ranked highest among habitats (Fig. 7), but the level of use did not differ from any of the other habitat types (P-values ranged from 0.15 to 0.84). Planted cover core was the lowest ranked habitat. The level of use of both habitats associated with the interior of planted cover (i.e., planted cover core and planted cover-wetland edges) was less than planted cover edge (P < 0.01), but did not differ from any of the other habitat types (P-values ranged from 0.18 to 0.84). The selection of pastureland was ranked high, but it was not different from other habitat types (P-values ranged from 0.21 to 0.89).

For skunk in HGC landscapes, agricultural-wetland edges were ranked highest among habitats (Fig. 8). The selection of agricultural-wetland edges was greater than all other habitat types (P < 0.05 for all comparisons) except planted cover-wetland edges (P = 0.11). In the same manner as fox on HGC landscapes, the level of use of the core areas of planted cover was low. The selection of planted cover core areas was less than planted cover-wetland edges (P < 0.05) and agricultural-wetland edges (P < 0.01), but it was not different from the use of planted cover edges (P = 0.18). The selection for pastureland and hayland is close to the random level of selection on HGC landscapes (Fig. 8) and is proportionally greater than the LGC landscapes (Fig. 6).

Nest Success

We used 1659 duck nests to compute Mayfield estimates of nest success. Litchville contained 270 nests, Bowdon contained 410 nests, Medina contained 741 nests, and
Hurdsfield contained 238 nests. The Mayfield estimate of waterfowl nest survival was greater in HGC landscapes (Medina and Hurdsfield combined) than in LGC landscapes (Litchville and Bowdon combined) in each of the landscape features associated with planted cover and for all features of planted cover combined (Table 2).

DISCUSSION

The composition of the landscape influences habitat selection by fox and skunk. Fox selection of planted cover was altered by the differing compositions of planted cover between the LGC and HGC landscapes. Skunk did not respond to the differing compositions of planted cover in the landscape. Both fox and skunk demonstrated a consistently strong response to agricultural wetland edges that had similar compositions on both LGC and HGC landscapes. These patterns of habitat selection are consistent with foraging theory that predicts a higher level of selection of patches that require great effort by the predator or have a large rate of return (Charnov 1976, Stephens and Krebs 1986). The higher level of selection for a specific habitat could result from intensive searching within a local area over a short period of time (Tinbergen et al 1967) or from multiple return visits over the breeding season. Either activity will increase the opportunity for a predator to find nests.

In LGC landscapes, fox frequently used landscape features associated with the isolated patches of planted cover (i.e., the core and edge of planted cover, as well as, planted cover-wetland edges). This increased selection of planted cover, whether for foraging, denning or marking the territory, gave fox a greater opportunity to find nests.
either directly or incidentally. Mayfield estimates of nest success (as indicated by the
daily survival rates) were low in all landscape features of planted cover in LGC landscapes
compared to HGC landscapes.

In HGC landscapes, there was a low level of selection by fox for the interior
features of planted cover (i.e., the core areas and wetland edges within planted cover).
This may have been due to the increased availability of core areas in the large blocks. It
also may have been due to the greater availability of other perennial grassland habitat such
as pastureland that could have provided resources that were an attractive alternative to
planted cover. There was a higher selection for pastureland by foxes in HGC landscapes
than in LGC landscapes. The low level of selection for the interior areas of planted cover
means fox would have less opportunity to search these areas which would increase the
probability of nest success. The net effect of these patterns of habitat selection may be
viewed as a dilution of the searching effort by fox in the interior of planted cover. This
was consistent with our observation that Mayfield estimates of nest success were higher in
HGC landscapes than in LGC landscapes for the interior features of planted cover.

The level of selection for planted cover edge by fox was similar on both LGC and
HGC landscapes. However, estimates of nest success in planted cover edge were greater
in HGC landscapes than in LGC landscapes. We reexamined the estimates of nest success
for the differing landscapes by comparing estimates of nest success in planted cover edge
for each of the 4 study areas (Fig. 9). One of the HGC landscapes (Medina) has greater
nest success in planted cover edge than all other study areas. The other HGC landscape
(Hurdsfield) is not different from the other 2 LGC landscapes (Litchville and Bowdon).
The estimate of nest success in planted cover edge in the Hurdsfield study area is consistent with the use of edge habitat by fox on both types of landscape. The Medina study area may not have lower nest success because there was 30-40% more planted cover edge on Medina than the other 3 study areas and it had the fewest number of foxes. The effect is a dilution of the foraging efficiency of fox in planted cover edge on Medina leading to a higher nest success.

In contrast to the fox, skunk showed a moderate to low selection for features of planted cover in both the LGC and HGC landscapes. Selection for planted cover was not distinguishable from most of the other habitat types available to skunk. The most striking characteristic of skunk habitat use is the strong selection for agricultural-wetland edges. Although both species showed strong attraction to agricultural-wetland edges, the selection is greater in skunk. Wetland edges usually contain food resources (both vertebrate and invertebrate species) that are attractive to both fox (Henry 1996) and skunk (Greenwood et al. 1999).

We did not find a strong overall selection for the edge of planted cover by predators. This is consistent with Heske’s (1995) track data along forest edges. Fox used planted cover edges more than the core areas in HGC landscapes, but the use of planted cover edges was not different from other landscape features. There has been mixed evidence for the effects of edge habitat on nesting success; however, many studies indicating increased effects of predation within 50 m of a habitat edge have come from forest-field ecotones (Paton 1994, Andren 1995). We found no evidence of a strong edge effect on nest success in planted cover (Horn 2000) which is consistent with observations
of waterfowl nest success in grassland habitat by Pasitschniak-Arts et al. (1998). The lack of a strong edge effect in a prairie ecosystem may be due to vegetation structure along edges that is not different from the core areas or from some grain crops during the growing season.

Differences in the predator community may also be a factor influencing waterfowl nest success. We observed a greater presence of coyotes in HGC landscapes than on LGC landscapes during track surveys conducted at the time of this study. When we examined track data collected during our field seasons (M. A. Sovada, Northern Prairie Wildlife Research Center, unpublished data) it was evident that most of the coyote tracks were found in many patches of planted cover and pastureland. These track surveys were not detailed enough to tell us whether the coyote spent much time in the interior areas of planted cover, but avoidance of coyote by fox may be a contributing factor to the higher nest success of waterfowl in landscapes with a high grassland composition (Sovada et al. 1995).

**MANAGEMENT IMPLICATIONS**

Waterfowl nesting habitat in the northern Great Plains is being restored through direct acquisition of grassland by wildlife agencies and by implementation of agricultural policy like the CRP. Management approaches and policy decisions often focus on the restoration of waterfowl nesting habitat (Reynolds et al. 1994). Our analyses of predator use of habitats may enable wildlife biologists to refine management plans by providing an understanding of the link between habitat selection by predators and nest success and by
suggesting new ways to view landscapes from a predator use perspective. For example, our observations of fox and skunk provide support for the restoration of large blocks of perennial grassland in landscapes that already have a high composition of grasslands, including pastureland. Conversely, the management strategy of restoring small patches of perennial grassland in fragmented agricultural landscapes is less likely to be effective management for waterfowl nesting because of the saturated use of these areas by predators in such landscapes (see also Greenwood et al. 1995 and Sovada et al. 2000). The observation of increased use of the small blocks of CRP in landscapes with a low grassland composition and of agricultural wetland edges in both types of landscapes suggest increased use of perennial grassland along riparian buffer strips that would be established under the proposed buffer initiative. Restoration plans that account for expected response of predator communities will be a more effective management strategy in the long term than one that focuses only on waterfowl nesting habitats.

ACKNOWLEDGMENTS

We are grateful to Mr. Dohn Broadwell and Mr. David F. Grohne for providing funding for this project through the Institute for Wetland and Waterfowl Research of Ducks Unlimited. We would like to thank the Northern Prairie Wildlife Research Center (NPWRC, USGS) for their financial and logistic support. R. Woodward from the NPWRC provided crucial help in the field and with creating the initial GIS database. We thank B. Allen, D. Coye, W. Cymbaluk, W. Jones, K. Kruse, D. Fronczak, M. Mayer, R. Olsen, J. Sparks, and R. Wolstenholm for spending long nights collecting the data. We
thank T. Sklebar (NPWRC) for recording the aerial photography and videography and M. Zahn (Wildlife Services, USDA) for assistance in trapping fox. We thank C. Loesche (USFWS) for providing Stewart-Kantrud (1971) wetland classifications for the NWI data. Dave Howarter, Serge Lariviere, Wes Newton, and Mike Zicus provided valuable suggestions on earlier drafts of this manuscript. This project was also supported by the Iowa Cooperative Fish and Wildlife Research Unit, and the Department of Animal Ecology at Iowa State University. This is Journal Paper No. J-19001 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa, Project No. 3299, and supported by Hatch Act and State of Iowa funds.

LITERATURE CITED


Environmental Systems Research Institute Inc. (ESRI). 1994. ARC/INFO user's guide. ESRI. Redlands, California, USA.


Washington, D. C., USA.


   Auk 96:651-661.

   species of predators on nesting success of ducks in the Canadian Prairie Pothole


   Menlo Park, California, USA.


   animals: statistical design and analysis for field studies. Chapman and Hall, New
   York, New York, USA.

   466.


Pasitschniak-Arts M., and F. Messier. 1996. Predation on artificial duck nests in a
   fragmented prairie landscape. Ecoscience 3:436-441.


Temple, S. A. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301-304 in J. M. Verner, L. Morrison, and C. J. Ralph,

Table 1: Summary statistics from MANOVA tests evaluating nonrandom use of habitats by red fox and striped skunk for each buffer distance on study areas with Low Grassland and High Grassland Composition in North Dakota, 1996-1997.

<table>
<thead>
<tr>
<th>Landscapes</th>
<th>Buffer Distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>500</td>
</tr>
<tr>
<td>Low Grassland Composition (LGC)*</td>
<td></td>
</tr>
<tr>
<td>fox (n = 13)</td>
<td></td>
</tr>
<tr>
<td>Wilks' $\Lambda$</td>
<td>0.2711</td>
</tr>
<tr>
<td>P</td>
<td>0.2942</td>
</tr>
<tr>
<td>skunk (n = 44)</td>
<td></td>
</tr>
<tr>
<td>Wilks' $\Lambda$</td>
<td>0.6871</td>
</tr>
<tr>
<td>P</td>
<td>0.0767</td>
</tr>
<tr>
<td>High Grassland Composition (HGC)*</td>
<td></td>
</tr>
<tr>
<td>fox (n = 15)</td>
<td></td>
</tr>
<tr>
<td>Wilks' $\Lambda$</td>
<td>0.3986</td>
</tr>
<tr>
<td>P</td>
<td>0.3637</td>
</tr>
<tr>
<td>skunk (n = 42)</td>
<td></td>
</tr>
<tr>
<td>Wilks' $\Lambda$</td>
<td>0.6605</td>
</tr>
<tr>
<td>P</td>
<td>0.0540</td>
</tr>
</tbody>
</table>

* Litchville (1996) and Bowdon (1997), ND contained 10-15% grassland and were defined as Low Grassland Composition landscapes. Medina (1996) and Hurdsfield (1997), ND contained 40-50% grassland and were defined as High Grassland Composition landscapes.
Table 2: Daily survival rate (DSR and SE), the number of nests (n), \( \chi^2 \) values, and P-levels for nests in 3 habitat features of planted cover, and all 3 planted cover features combined, comparing study areas with Low Grassland Composition (LGC) to study areas with High Grassland Composition (HGC).

<table>
<thead>
<tr>
<th>Landscape Type</th>
<th>Habitat</th>
<th>LGC</th>
<th>HGC</th>
<th>( \chi^2 )-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>DSR</td>
<td>SE</td>
<td>n</td>
<td>DSR</td>
</tr>
<tr>
<td>planted cover-core</td>
<td>302</td>
<td>0.912</td>
<td>0.005</td>
<td>558</td>
<td>0.952</td>
</tr>
<tr>
<td>planted cover-edge</td>
<td>99</td>
<td>0.909</td>
<td>0.010</td>
<td>208</td>
<td>0.946</td>
</tr>
<tr>
<td>planted cover-wetland edge</td>
<td>152</td>
<td>0.905</td>
<td>0.008</td>
<td>130</td>
<td>0.942</td>
</tr>
<tr>
<td>planted cover - combined</td>
<td>553</td>
<td>0.909</td>
<td>0.005</td>
<td>896</td>
<td>0.947</td>
</tr>
</tbody>
</table>

Figure 1. Low Grassland Composition landscape on the Litchville, North Dakota study area (1996). The red border outlines the 41.4 km\(^2\) study area.

Figure 2. Low Grassland Composition landscape on the Bowdon, North Dakota study area (1996). The red border outlines the 16 mi\(^2\) study area.

Figure 3. High Grassland Composition landscape on the Medina, North Dakota study area (1996). The red border outlines the 16 mi\(^2\) study area.

Figure 4. High Grassland Composition landscape on the Hurdsfield, North Dakota study area (1996). The red border outlines the 16 mi\(^2\) study area.

Figure 5. Standardized selection ratios (B) for fox in LGC landscapes in North Dakota, 1996 and 1997. Values within histogram bars are the rank of each habitat. Habitats with the same letter above the bar are not significantly different from each other (P > 0.05). The solid line represents the level of selection if all habitats were selected at random.

Figure 6. Standardized selection ratios (B) for skunk in LGC landscapes in North Dakota, 1996 and 1997. Values within histogram bars are the rank of each habitat. Habitats with the same letter above the bar are not significantly different from each other (P > 0.05). The solid line represents the level of selection if all habitats were selected at random.
Figure 7. Standardized selection ratios (B) for fox in HGC landscapes in North Dakota, 1996 and 1997. Values within histogram bars are the rank of each habitat. Habitats with the same letter above the bar are not significantly different from each other (P > 0.05). The solid line represents the level of selection if all habitats were selected at random.

Figure 8. Standardized selection ratios (B) for skunk in HGC landscapes in North Dakota, 1996 and 1997. Values within histogram bars are the rank of each habitat. Habitats with the same letter above the bar are not significantly different from each other (P > 0.05). The solid line represents the level of selection if all habitats were selected at random.

Figure 9. Daily survival rate (DSR and SE) for nests in planted cover edge comparing all 4 study areas in North Dakota, 1996-1997: Litchville (n = 34 nests), Bowdon (n = 65 nests), Medina (n = 172 nests) and Hurdsfield (n = 36 nests). DSR with the same letter are not different (P > 0.05).
Figure 1

Litchville, North Dakota

Upland Habitat:
- planted cover
- pastureland
- hayland
- row crop
- grain crop
- sunflowers
- summerfallow
- trees
- farmyard
- other

Wetlands:
- temporary
- seasonal
- semipermanent
- flooded margin

Roads
- paved roads
- gravel roads

Scale - 1:70000

920 1840 meters
Figure 3

Medina, North Dakota

Upland Habitat:
- planted cover
- pastureland
- hayland
- hayland
- predator exclusion
- row crop
- seasonal
- permanent
- flooded margin
- grain crop
- sunflowers
- summerfallow
- trees
- farmyard
- other

Wetlands:
- temporary
- seasonal
- permanent
- lake
- flooded margin

Roads
- paved roads
- gravel roads

Scale - 1:70000
0 920 1840 meters
Hurdsfield, North Dakota

Upland Habitat:
- planted cover
- pastureland
- hayland
- row crop
- grain crop
- sunflowers
- summerfallow
- trees
- farmyard
- island
- other

Wetlands:
- temporary
- seasonal
- semipermanent
- lake
- flooded margin

Roads
- paved roads
- gravel roads

Scale - 1:70000

Figure 4
Low Grassland Landscape
Fox

Figure 5
Figure 6
Figure 7
High Grassland Landscape
Skunk

Figure 8
Figure 9

Daily Survival Rates (+ s.e.)

Litchville  |  Bowdon  |  Hurdsfield  |  Medina

Figure 9
CHAPTER 3. ANALYSIS OF PREDATOR MOVEMENT IN PRAIRIE LANDSCAPES WITH CONTRASTING GRASSLAND COMPOSITION

A paper to be submitted to Ecology

Michael L. Phillips, William R. Clark, Sarah M. Nusser, Marsha A. Sovada, and Raymond J. Greenwood

Abstract. The composition of grassland in the landscape has the potential to alter the behavioral response of predators to patches of waterfowl breeding habitat. We examined the movement patterns of red fox (Vulpes vulpes) and striped skunk (Mephitis mephitis) in relation to landscape features in the Prairie Pothole Region (PPR) of North Dakota landscapes during 1996 and 1997. Based on foraging theory and our previous analyses of habitat selection for these species, we predicted a slow rate of movement and more frequent obtuse turn angles within patches of planted cover or wetland edges (characteristic of foraging behavior), whereas movement would be faster with more frequent acute turn angles in the agricultural matrix (characteristic of traveling behavior). We also predicted movement pathways would be straighter for foxes as they traveled further between isolated patches of planted cover on LGC landscapes, whereas skunk pathways would be similar on both types of landscapes as they focused their movement toward wetland edges. To examine our predictions, we used radiotelemetry to record nightly movement patterns in two study areas containing either 10-15% perennial grassland which included planted cover, pastureland, and hayland (Low Grassland
Composition, LGC) or 40-50% perennial grassland (High Grassland Composition, HGC). We computed the rate of movement and turning angle between successive locations within a movement pathway, as well as the fractal dimension (D) and displacement ratio (Δ) of each pathway. In LGC landscapes, movement patterns of foxes were slightly straighter (D_{LGC} = 1.095, D_{HGC} = 1.139, P = 0.07) and turn angles were more frequently obtuse in planted cover suggesting a more tortuous foraging movement. In contrast to our prediction, fox movement was not faster or more directed in the agricultural matrix. In HGC landscapes, fox movements included more frequent obtuse turns in pasture and cropland but not in the planted cover. Skunk movement pathways did not differ between landscape types (D_{LGC} = 1.120, D_{HGC} = 1.129, P = 0.49). This result reflected the selection by skunk for wetland edges that had a similar composition on all study areas. Movement was directional in planted cover and agricultural matrix; however, the most frequent turn angles occurred along a 0° or 180° axis. The rate of movement was faster in the agricultural matrix on LGC but not HGC landscapes and was greatest for transitions between planted cover or wetland edges and the agricultural matrix for fox and skunk. Fast movement across the boundary between planted cover and cropland might alter the likelihood of edge effects in prairie ecosystems compared to forest-field ecotones.

Understanding the behavioral responses of predators to landscape structure is an essential component of predicting the spatial and temporal population dynamics of generalist predators and waterfowl.
Key Words: displacement ratio, fractal dimension, landscape composition, Mephitis mephitis, movement, North Dakota, Prairie Pothole Region, predation, red fox, striped skunk, trajectories, Vulpes vulpes.

INTRODUCTION

Movement is fundamental to understanding spatial-temporal patterns of habitat selection, foraging behavior, and the interactions between predator and prey (Swinglund and Greenwood 1983, Bell 1991, Stenseth and Lidicker 1992). Animal movements are influenced by intrinsic physiological factors (e.g., hunger and reproduction) and the sensory capabilities of organisms (Bell 1991, Zollner and Lima 1997). They are also influenced by extrinsic factors such as the spatial structure of the landscape (Burrough 1981, Palmer 1988, Kotliar and Wiens 1990). Movement patterns are influenced by habitat heterogeneity and composition in the landscape among both invertebrates (Wiens and Milne 1989, Crist et al. 1992, Crist and Wiens 1994, With 1994, Wiens et al. 1995) and vertebrates (Ferguson et al. 1996, 1998, Bascompte and Vila 1997, Etzenhouser et al. 1998). Spatial structure will influence movement as long as there is a perceived difference in quality of the varying habitats as individuals search for resources such as food, mates or den sites, or use different cover types to avoid interspecific and intraspecific agonistic encounters (Kotliar and Wiens 1990, Zollner and Lima 1997).

Foraging theory provides a framework to make predictions about the effect of landscape composition on the interactions between nesting waterfowl and their generalist predators in the PPR. The theory assumes that behaviors are governed by decision rules
whereby a predator maximizes its rate of intake of some currency, such as the encounter rate with prey (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976). Foraging theory recognizes the importance of the rate of return of resources within patches and the distribution of discrete patches of required resources and on predator movement. The greater the rate of return of resources within a habitat then the more time a predator will spend foraging in that habitat. The greater the distance between patches in the landscape then the more energy a predator must invest in traveling between patches and therefore, the more time a predator will spend in the patch. Assuming a predator perceives a greater reward of resources in patches of grassland than in the agricultural matrix, then predator movement will be faster and straighter as it moves through the agricultural matrix toward a patch of grassland. Straighter movement pathways are a more efficient search pattern for an animal that uses widely dispersed patches (Dusenberry 1989, Zollner and Lima 1999). Once within a grassland patch, a predator will increase its foraging efficiency by moving in a more tortuous manner and will move more slowly as it spends more time foraging than traveling.

Grasslands in the PPR are the focus of waterfowl breeding (Bellrose 1980, Batt et al. 1989) and mammalian predation is a major factor influencing waterfowl nest success in the PPR (Klett et al. 1988, Johnson et al. 1989, Sargeant and Raveling 1992, Sargeant et al. 1993). Dramatic loss and fragmentation of grasslands in the PPR (Higgins 1977, Sugden and Beyersbergen 1984, Greenwood et al. 1995, Miller and Nudds 1996) has very likely altered predator movements both between and within patches of grassland and therefore influenced predation rates.
For example, in landscapes dominated by cropland, predators should move faster and in a straighter direction as they move longer distances between isolated patches of grassland. Displacement (i.e. the distance traveled from the first to the last location) should be large. In contrast, landscapes with large, contiguous patches of grassland, predator movement will be relatively slower and more tortuous because predators find resources or encounter prey more frequently. Predators will spend more time foraging than traveling resulting in decreased displacement.

We examined the movement patterns of red fox (Vulpes vulpes) and striped skunk (Mephitis mephitis) in North Dakota landscapes with contrasting grassland composition. Grasslands and wetland edges contain food resources that are attractive to both foxes and skunks (Pasitschniak-Arts 1998, Lariviere and Messier 2000). Previously, we learned that habitat selection was influenced by the composition of grassland in the landscape for foxes but not for skunks (Phillips et al. 2001). Foxes exhibited a low selection for the interior areas of grassland patches in landscapes with a high grassland composition. Skunks were strongly attracted to edges around wetlands that were embedded within the agricultural matrix in both types of landscape, but did not exhibit a strong selection for grassland in either type of landscape (Phillips et al. 2001).

However, we have not shown how habitat selection by these predators influences movement patterns. Therefore, our objective was to study how movement patterns are influenced by the composition of grassland in the landscape. We examined both small-scale movement patterns (the rate of movement and turn angle between successive steps of
a movement pathway) within patches of different habitat types and large-scale movement patterns (the overall shape of the movement pathway).

We predicted that the small-scale movement patterns of fox and skunk would reflect the behavioral response by predators to different resources in grassland patches compared to the surrounding agricultural matrix in both types of landscapes. We expected predators to move in a more tortuous manner (i.e., more obtuse turn angles) and more slowly while foraging in planted cover in contrast to traveling through the agricultural matrix (Fig. 1). We expected their movements to be faster and more directed (i.e., more acute turn angles) as they travel through the agricultural matrix. Finally, we expected the rate of movement to be intermediate between slow movements in grassland and faster movements in the agricultural matrix and for turning to be more random when predators were making a transition between patches of grassland or wetland edges and the agricultural matrix.

We predicted that the large-scale movement patterns would reflect the composition of the landscape and the habitat selection by predators. Therefore, the large-scale movement patterns of foxes will depend on the composition of grassland in the landscape. We expected fox movements to be straighter and displacements greater in landscapes with a low grassland composition as they moved longer distances between the isolated patches of grassland (Fig. 1). In landscapes with a high grassland composition, foxes need not travel long distances to find resources and therefore their overall movement patterns should be more tortuous and displacements smaller. The overall movement patterns of skunks will depend more on the distribution of specific habitats such as wetland edges in
the landscape and therefore will not be a function of grassland composition in the
landscape (Fig. 1).

METHODS

Study Areas

Each year (1996 and 1997), we selected two 41.4 km² study areas with contrasting
amounts of perennial grassland (planted cover, pastureland, and hayland) in the Prairie
Pothole Region of central North Dakota. Study areas we selected with a "Low Grassland
Composition" (hereafter LGC) were Litchville, ND (Svea Township in Barnes County) in
1996 and Bowdon, ND (Berlin Township in Wells County) in 1997. LGC landscapes
contained small, isolated patches of perennial grassland surrounded by cropland. Habitat
composition of the Litchville study area was 66.9% cropland, 12.5% planted cover, 2.3%
pastureland, 0.3% hayland, and 11.7% wetlands. Habitat composition of the Bowdon
study area was 56.4% cropland, 13.8% planted cover, 2.7% pastureland, 3.2% hayland,
and 18.5% wetlands.

In contrast, study areas we selected with a "High Grassland Composition"
(hereafter HGC) were Medina, ND (Iosco Township in Stutsman County) in 1996 and
Hurdsfield, ND (Silver Lake Township in Wells County) in 1997. HGC landscapes
contained large patches of perennial grassland adjacent to cropland. Habitat composition
of the Medina study area was 34.3% cropland, 22.1% planted cover, 19.0% pastureland,
4.1% hayland, and 13.4% wetlands. Habitat composition of the Hurdsfield study areas
was 23.0% cropland, 22.5% planted cover, 27.8% pastureland, 1.5% hayland, and 21.1% wetlands.

We used data from the National Wetland Inventory (NWI, U. S. Fish and Wildlife Service, St. Petersburg, Florida) to identify the wetland basins on the study areas. NWI classifications were converted to Stewart and Kantrud (1971) classifications by the Habitat and Population Evaluation Team (U. S. Fish and Wildlife Service, Bismarck, North Dakota). Although both 1996 and 1997 were wet years, each study area contained a similar composition of wetlands (Litchville = 9.3%, Bowdon = 13.9%, Medina = 12.1%, and Hurdsfield = 13.8%). Wetlands were predominantly classified as temporary and seasonal.

All study areas also included a square-mile road system (< 2% of the landscape) and other habitat types including farmsteads, trees, and other miscellaneous habitat types (all < 1.0%). The Medina study area included a predator enclosure (2.4%) which contained planted cover enrolled in the Conservation Reserve Program and hayland.

Capture and Handling

We captured foxes and skunks in April and May (1996 and 1997) and in June (1997) using either livetraprs for skunks or snares with stops and leg hold traps for foxes. A professional trapper from Wildlife Services (United States Department of Agriculture, Bismarck, ND) assisted us in capturing fox. We trapped intensively and systematically across all study areas with the goal of capturing all resident animals of both predator species. All captured study animals were sexed, weighed, examined for tooth wear and reproductive status of females, ear tagged and fitted with a telemetry transmitter.
(Advanced Telemetry Systems, Isanti, Minnesota, USA) containing a 1 hour mortality switch. The transmitters weighed approximately 60 g for skunks and 110 g for foxes. All trapping and handling procedures for this project were developed following recommendations by the American Society of Mammalogists (1987), the Northern Prairie Wildlife Research Center's Animal Care and Use Guidelines, and were approved by the Iowa State University Committee on Animal Care.

Locations and movement of predators

Locations were estimated from 2-3 bearings using vehicle-mounted null-peak directional antennas. Locations based on 2 bearings were estimated using a fixed standard deviation determined for each crew member based on 2 field tests given before and midway through the field season. Standard deviations ranged from 1.7-3.0. Bearings were taken from telemetry stations positioned along roads or at other accessible positions with known Universal Transverse Mercator (UTM) coordinates. Locations and their 95% error ellipses were estimated using LOCATE II software (Pacer Truro, Nova Scotia, Canada; Nams 1990).

We recorded predator movements intensively at night (2000-0800) 3 times each week. In order to ensure complete coverage of the study area and sampling of all animals, we recorded how often and how long each animal was tracked. Locations for each of the sampled animals were recorded every 15-20 minutes. We defined a trajectory as a series of locations for one animal for one night of tracking. A step is the movement between 2 successive locations within a trajectory (Turchin, 1996).
We took several steps to minimize error and improve the resolution of movement within a trajectory. We examined the statistical distribution of the error ellipses and deleted any location with an error ellipse that was greater than 3.0 times the interquartile range above the 75% quantile (an "extreme outlier", Devore and Peck 1986: 94). Trajectories with less than 10 locations did not give us enough information on movement patterns and were not included in the analysis. Occasionally more than 60 minutes elapsed between locations. To eliminate these gaps we either deleted locations from the data set if they were at the beginning or end of a trajectory, or the trajectories were split into shorter trajectories. We recorded locations more frequently in 1997 than in 1996. The average time between locations was 19.5 min (S.E. = 0.07) in 1996 and 9.9 min (S.E. = 0.07) in 1997. The time between locations can affect trajectory characteristics such as the rate and turn angle between successive locations and the fractal dimension (Ferguson, et al. 1996). Therefore, to standardized the telemetry between the 2 years we systematically deleted every other location from the 1997 data. After editing the data, the average time between locations for 1997 was 19.4 min (S.E. = 0.15).

Habitat delineation

Land cover data were recorded from low altitude aerial photography and videography for each study area plus a 1.6 km border around each study area. Habitat types were digitized and classified using the Map and Image Processing System (MicroImages, Lincoln, Nebraska, USA). Habitat classifications were verified by ground observations. We used ARC/INFO (ESRI, 1994, Redlands, California, USA) for management and analysis of the land cover and movement data.
We divided perennial grassland into 3 cover types: planted cover, pastureland and hayland. Planted cover was dense nesting cover seeded to perennial grasses and forbs by landowners and enrolled in the Conservation Reserve Program (CRP), the Water Bank Program (WBP), or set aside as federal Waterfowl Production Areas (WPA). Our definition of a patch of planted cover is similar to that of Sovada, et al. (2000: Fig. 2) except that we allowed gravel and paved roads to divide adjacent areas of planted cover into separate patches. Pastureland and hayland are agricultural cover types containing perennial grasses that were frequently disturbed by grazing or mowing.

We focused our analyses of the small-scale movement patterns (i.e., the rate of speed and turn angle between successive locations within a trajectory) on the response of predators to planted cover and wetland edges in contrast to the surrounding agricultural landscape. Wetland edges were defined as habitat ≤ 50 m from the boundary of a wetland. Habitats in the surrounding agricultural landscape included cropland, pastureland, hayland, and miscellaneous habitat types. Croplands were planted in either row crops (corn, sunflowers, beans, potatoes, or soybeans) or grain crops (wheat, barley, oats, flax, or canola). The miscellaneous category included the remaining habitat types: farmyards, trees, fallow agricultural land, islands, land not in agricultural use. Trees were usually found in shelterbelts or around farmyards.

Movement analyses

We examined the rate of movement and turn angle between steps within a trajectory. Both are small-scale measures of movement made by foxes and skunks in response to their immediate environment. The fractal dimension and displacement ratio
were larger scale measures that reflect the overall shape of trajectories in response to landscape composition.

Movement between successive locations within a trajectory were defined as a step and divided into one of four step categories: 1) steps in which both beginning and ending location were located in the surrounding agricultural landscape (agricultural-matrix), 2) steps in which both beginning and ending location were located in planted cover or wetland edge (planted cover-wetland edge), 3) steps that originated in agricultural-matrix and ended in planted cover-wetland edge, and 4) steps that originated in planted cover-wetland edge and ended in agricultural-matrix.

Rate of movement and turn angle. - The rate of movement for a step within a trajectory was computed in meters per minute. The turn angle ($\theta$) was computed as the change in the direction of movement made by an individual from one location to the next (Fig 2). Theta is a right hand turn that ranged from 0 to 360 degrees.

Fractals. - The fractal dimension, $D$, (Mandelbrot 1967, 1983) of a trajectory is a quantifiable measure of the overall shape of the trajectory (Dicke and Burrough 1988). The quantity $D$ is a fractional dimension that ranges from the Euclidean limits of 1.0 (a straight line) to 2.0 (a trajectory so tortuous that eventually it fills a two-dimensional plane). As $D$ increases, the trajectory becomes more tortuous and the likelihood that a trajectory will intersect itself increases. The fractal dimension is a useful index to compare species from different taxa as well as to compare the effect of landscape heterogeneity on movement (Wiens et al. 1995, With 1994).
We used the FractalMean estimator constructed by Nams (1996) to compute a fractal dimension for each of the trajectories. The program uses the divider method (Mandelbrot 1967) to estimate the fractal dimension by estimating the length of the pathway ($L$) over a range of divider sizes ($\lambda$) such that,

$$L(\lambda) = k\lambda^{1-D}$$

where $k$ is a constant and $D$ is the fractal dimension of the pathway.

Since the path length is poorly estimated at large divider sizes, the FractalMean estimator computes a mean path length ($\bar{L}$) for each divider size beginning at a random point along the trajectory. We used 15 replications to estimate ($\bar{L}$) for each divider size. The fractal dimension of a trajectory is computed from the plot of log($\bar{L}$) as a function of log($\lambda$). For comparisons among fox and skunk, $\lambda$ was fixed at 30 divider sizes that range from 5-1500 m. We examined the distribution of distances for steps (Fig.3) and set the minimum nonzero divider size at 5 m (which was approximately the 5% quantile for the distribution). We examined the distribution of the total distance traveled (Fig. 4) and set the maximum divider size to 1500 m (which was approximately the 25% quantile of the distribution for both fox and skunk on both landscape types).

The fractal dimension of a trajectory assumes scale independent behavior that may not be true for animal movement (Turchin 1996). Scale independence requires that the log($\bar{L}$) versus log($\lambda$) plot be linear (i.e., a constant slope for all divider sizes). We examined the linear nature of the log($\bar{L}$) versus log($\lambda$) plot by comparing log($\bar{L}$) and the estimated 95% C. I. at each unique divider scale to a mean slope with its estimated 95% C. I. computed by regressing the log($\bar{L}$) versus log($\lambda$) plot for each trajectory. If the 95%
C. I. overlapped throughout the range of scales we argue that the \( \log(\ell) \) versus \( \log(\lambda) \) plot is sufficiently linear to assume scale independence and validly compute a fractal dimension.

**Displacement ratio** - The trajectories were also analyzed by computing the displacement ratio:

\[
\Delta_{ijk} = \frac{\delta_{ijk}}{\tau_{ijk}}
\]

where \( \delta_{ijk} \) = the displacement (i.e., the distance from the first to the last location in a trajectory) and \( \tau_{ijk} = \sum d_s \), for \( s=1,\ldots,n \) steps in a trajectory (i.e., the total distance traveled) for each animal \( (i) \) of each species \( (j) \) on landscape type \( (k) \) (Fig. 2). The ratio should range from 0 (trajectory started and ended at the same location) to 1 (the trajectory is a straight line).

The displacement ratio is a scale-dependent measure of a trajectory that is related to the fractal dimension. In general, the greater the fractal dimension the smaller the displacement ratio. However, it is possible for trajectories to have the same displacement ratio but have the different fractal dimensions. For example, given 2 species that are both central place foragers, both will tend to have small displacement ratios, but the fractal dimension will depend on whether they travel in a directed, circuitous manner or in a tortuous, back and forth manner. The fractal dimension is an index of the overall shape of a trajectory whereas the displacement ratio is an index of the extent of net movement by an individual.
Statistical models

Data collected on movement patterns where structured in a hierarchical, nested model with each step ($m$) nested within each trajectory ($l$) for each animal ($k$) of a particular species ($s$) in each study area ($j$) of a different landscape type ($i$). The rate of movement of steps, as well as the fractal dimension and displacement ratio of trajectories were treated as mixed effect models with landscape type, study area, species, and step modeled as fixed effects while animal and trajectory were random effects. Locations were treated as repeated measures within trajectories. We used an autoregressive order 1 covariance structure for locations assuming a decreasing correlation over time between locations within a trajectory (Littell et al. 1996). We report pairwise comparisons using t-tests of the adjusted least square means in cases where there is a significant interaction.

The rate of movement for steps was modeled as

$$y_{ijklm} = \alpha + \beta_{ij} + a_{jk} + t_{ijkl} + \sigma_{ijklm} + (\alpha \sigma)_{ijklm} + \epsilon_{ijklm}.$$ 

The term ($\alpha \sigma$) is the interaction between landscape type and step category. Species were modeled separately.

The fractal dimension and displacement ratio of trajectories were modeled as

$$y_{ijklm} = \alpha + \beta_{ij} + a_{jk} + t_{ijkl} + \gamma_{ijkl} + (\alpha \gamma)_{ijkl} + \epsilon_{ijkl}.$$ 

Species were included in the model. The term ($\alpha \gamma$) is the interaction between landscape type and species.

The turn angles were analyzed using circular statistics (Batschelet 1981). We computed the mean turn angle ($\bar{a}$), mean vector length ($m$) and angular dispersion ($s$) for the distribution of turn angles for each step category. The mean vector ($m$) is a measure of
the strength of directionality for circular data that ranges from 0 (when the distribution of turn angles is completely uniform) to 1 (when all turn angles are in the same direction). For circular data, \( m \) may be underestimated if the distribution is not unimodal. Because distribution of the step categories were multimodal (see Figs. 5-12), we converted the distributions to unimodal distribution by doubling all turn angles and subtracting 360° if the turn angle was \( \geq 360° \) (Batschelet 1981: 24 ff). We tested for directionality of movement within each step category using Rayleigh’s \( z \)-statistic (Batschelet 1981). We used the Watson-Williams F-statistic (Batschelet 1981) to compare movement for each species: 1) among step categories in each landscape type (e.g., we compared the 4 step categories for fox in LGC landscapes), and 2) between landscapes for each step category (e.g., we compared steps that began and ended in agricultural-matrix for fox in LGC vs. HGC landscapes).

RESULTS

Radiotelemetry

We tracked 16 fox and 52 skunk in LGC landscapes and 16 fox and 47 skunk in HGC landscapes. We recorded 23,592 locations over the 2 field seasons. Locations recorded at night (\( n = 19,986 \)) were grouped into 1,064 trajectories.

Deleting locations with an estimated error ellipse > 3.0 times the interquartile range above the 75% quantile placed an upper limit of 11.7 ha for locations used in the analysis. Trajectories with less than 10 locations (\( n = 155 \)) were not included in the analysis. The resulting trajectories averaged 17.7 locations (S.E. = 0.30) and ranged
from 10-40 locations. For trajectories with gaps of > 60 minutes we either deleted locations from the data set if they were at the beginning or end of a trajectory (n=185 trajectories), or the trajectories were split into shorter trajectories (n=164 trajectories).

For our analyses we used 9,977 locations grouped within 608 trajectories for 105 individuals. The resulting median area for error ellipses for locations was 1.09 ha. There were 5 foxes and 21 skunks in Litchville, 5 foxes and 16 skunks in Medina, 7 foxes and 20 skunks in Bowdon, and 9 foxes and 22 skunks in Hurdsfield. For comparisons between landscape types we pooled study areas of similar composition of planted cover resulting in 12 fox and 41 skunk in LGC landscapes and 14 fox and 38 skunk in HGC landscapes.

*Rate of movement between locations*

The rate of speed should be interpreted cautiously because of large sample size of steps (Steidel et al. 1997). Large sample sizes may increase the probability of Type I error. We argue that the observed statistics for the rate of speed are biological meaningful and not an artifact of large sample size.

There was no overall difference in the rate of speed for red foxes (Table 1A) between the 2 landscape types ($F_{1,24} = 2.66, P = 0.12$). There was a difference between step categories ($F_{3,2537} = 31.92, P = < 0.0001$) and an interaction between landscape type and step category ($F_{3,2537} = 3.20, P < 0.02$) (Table 1B). The differences between step categories is the result of speeds in the transition categories that were faster than if foxes remained in planted cover-wetland edges or in the agricultural matrix. The mean rate of speed for a step that is a transition from planted cover-wetland edge to agricultural-matrix
is greater than if the step remained in agricultural-matrix \( (t_{2537} = -4.13, P < 0.0001 \) for LGC; \( t_{2537} = -6.18, P < 0.0001 \) for HGC), or if the step remained in planted cover-wetland edge \( (t_{2537} = 2.74, P < 0.01 \) for LGC; \( t_{2537} = 8.00, P < 0.0001 \) for HGC).

Furthermore, the mean rate of speed for a step that is a transition from agricultural-matrix to planted cover-wetland edge is greater than if the step remained in agricultural-matrix \( (t_{2537} = -4.77, P < 0.0001 \) for LGC; \( t_{2537} = -4.83, P < 0.0001 \) for HGC), or if the step remained in planted cover-wetland edge \( (t_{2537} = 3.51, P < 0.001 \) for LGC; \( t_{2537} = 6.57, P < 0.0001 \) for HGC).

The rate of speed for striped skunk is faster on LGC landscapes than on HGC landscapes \( (F_{1.77} = 12.09, P = 0.0008) \) (Table 2A). There were differences between step categories \( (F_{3.6183} = 118.81, P = < 0.0001) \) and an interaction between landscape type and step category \( (F_{3.6183} = 9.36, P = < 0.0001) \)(Table 2B). There were significant differences \( (P < 0.05) \) between landscape type and step categories for nearly all pairwise comparisons. Of all possible pairwise combinations, the only comparisons that were not significant were: 1) steps that remained in planted cover-wetland edge for HGC vs. LGC landscapes \( (t_{6183} = 0.80, P = 0.42) \), 2) steps that remain in agricultural-matrix in HGC landscapes vs. steps that remain in planted cover-wetland edge in LGC landscapes \( (t_{6183} = -0.98, P = 0.33) \), and 3) transition steps from agricultural-matrix to planted cover-wetland edge vs. transition steps from planted cover-wetland edge to agricultural-matrix in LGC landscapes \( (t_{6183} = -0.83, P = 0.41) \), or in HGC landscapes \( (t_{6183} = -0.48, P = 0.64) \).
Turning angle between locations

There was a wide distribution of turn angles in all step categories for foxes and skunks (Figs. 5-12). All mean vector lengths \( (m) \) were < 0.2 and the angular dispersion \( (s) \) ranged from 55.7° to 68.2° (Table 3). By definition a completely uniform distribution has an angular dispersion of approximately 81°. Except for fox in LGC landscapes, most mean angles \( (\bar{\alpha}) \) were close to 0° indicating that the most frequent turn angles were directed along an axis of 0° or 180°. The relatively small values for \( m \) indicated a lack of strong directionality.

For foxes, the only step categories in which there were significant directional movement were for steps that began and ended in planted cover-wetland edges in LGC landscapes and for steps that began and ended in the agricultural matrix in HGC landscapes (Table 3). In contrast, skunks exhibited directional movement in all step categories except for steps that began in planted cover-wetland edge and ended in the agricultural matrix.

The difference among step categories for foxes in LGC landscapes (Table 4) was most likely the result the larger mean vector \( (m = 0.1199; \text{ Table 3}) \) for steps that began and ended in planted cover-wetland edge. There were no differences among step categories for fox in HGC landscapes (Table 4). The difference among step categories for skunks in HGC landscapes (Table 4) was most likely due to the larger mean vector \( (m = 0.1440) \) for transition steps that began in agricultural-matrix and ended in planted cover-wetland edges (Table 3). There were no differences among step categories for skunks in LGC landscapes (Table 4).
The only differences between landscapes were observed for transition step categories (Table 5). For foxes, the mean turn angle for transitions from planted cover-wetland edge to the agricultural matrix was greater on LGC than HGC landscapes (Table 3). The frequency of turn angles was bimodal in HGC landscapes whereas there were more frequent obtuse turn angles in LGC landscapes (Fig. 8). For skunks, the mean turn angle for both transition step categories was greater on HGC than LGC landscapes (Table 3). For transition steps from the agricultural matrix to planted cover-wetland edge, there was a higher frequency of turn angles that range from 20-59° and from 200-239° in HGC than LGC landscapes (Fig. 11) that led to a greater mean turn angle in the HGC landscapes. For transition steps from planted cover-wetland edge to the agricultural matrix, there was a higher frequency of turn angles that ranged from 140-199° (Fig. 12) that may have biased the mean angle more toward an axis along the 0° and 180° direction in the LGC landscape than in the HGC landscape. However, in both step categories, the overall distributions (bimodal in Fig. 11 with the highest frequency of turn angles along the 0° or 180° axis) were similar on both landscapes (i.e., this may be a distinction without a difference).

Analysis of trajectories

Fractal dimension of trajectories. - We did not observe a major departure from a linear relationship for the log(\(L\)) vs. log(\(\lambda\)) plot (Fig. 13). The relationship became slightly more curvilinear at the larger range of scales for fox on HGC landscapes. Although the mean of the observed values dropped below the mean regressed line, the 95% C.I. for both lines
continue to overlap. We concluded that estimates of the fractal dimension of the trajectories was valid for these range of scales.

The fractal dimension ranged from 1.0001 to 1.505 for both fox and skunk on both types of landscape (Table 6). The 3 observed skunk trajectories in Fig. 14 illustrate differences in the shape of trajectories for fractal dimensions that range from 1.1-1.5. The overall mean for fox and skunk on both landscapes was 1.128 (i.e., the average trajectory closely resembled the trajectory in Fig. 14A).

The fractal dimension of trajectories were marginally higher in HGC landscapes than LGC landscapes ($F_{1,101} = 3.63, P = 0.0595$) (Table 6). There was no difference in the fractal dimension between the 2 species ($F_{1,101} = 0.30, P = 0.59$). Although we did not observe a strong interaction ($F_{1,101} = 1.48, P = 0.23$), the results suggest the slight difference between landscapes is due to foxes. The fractal dimension of fox trajectories was higher in HGC landscapes than in LGC landscapes ($t_{101} = 0.30, P = 0.07$) whereas there was no difference in the fractal dimension of skunk trajectories between LGC landscapes and HGC landscapes ($t_{101} = 0.69, P = 0.49$).

*Displacement ratios of trajectories* - The displacement ratios were greater in skunks than in red foxes ($F_{1,101} = 4.68, P = 0.03$)(Table 7). Displacement ratios were slightly higher in LGC landscapes than in HGC landscapes ($F_{1,101} = 2.86, P = 0.09$). Although we did not observe a strong interaction ($F_{1,101} = 1.89, P = 0.17$), the difference in species was the result of a marginally lower displacement ratio for red foxes in HGC than in LGC landscapes ($t_{101} = -1.79, P = 0.07$), whereas there is no difference for striped skunk between LGC and HGC landscapes ($t_{101} = -0.30, P = 0.76$).
DISCUSSION

Predator movement patterns were influenced by the habitat structure of the landscape. Predators responded to different habitats and contrasting composition of grassland in the landscape. These patterns reflected how an organism perceives habitat heterogeneity in the landscape (Wiens et al. 1995, Zollner and Lima 1997). However, foxes and skunks responded differently to landscapes with contrasting grassland composition. Differences in movement patterns were determined by differences in habitat selection.

Foxes strongly selected planted cover in LGC landscapes (Phillips et al. 2001). As predicted, large-scale movement patterns were influenced by spatial distribution of the more isolated patches of planted cover. In LGC landscapes, fox trajectories were slightly straighter (i.e., lower fractal dimension and higher displacement ratio). Foxes had to travel further between grassland patches within their home range. Straighter movement pathways are a more efficient search pattern in landscapes where patches of quality habitat are widely dispersed (Dusenberry 1989, Zollner and Lima 1999). In HGC landscapes, fox trajectories tended to be more tortuous (i.e., higher fractal dimension and lower displacement ratio). Foxes did not have to travel as far before encountering prey in the large, interconnected blocks of grassland. Grassland included planted cover, pastureland and hayland cover types. Fox movement patterns in HGC landscapes were more likely influenced by the presence of pastureland rather than planted cover or hayland because foxes exhibited a strong selection for pastureland and low selection for hayland and for the interior areas of planted cover in HGC landscapes (Phillips et al. 2001).
Skunk trajectories had a consistent shape and displacement on both types of landscape. Skunks strongly selected wetland edges regardless of proximity to grassland or composition of grassland in the landscape (Phillips et al. 2001). Our study areas contained a similar wetland composition. The distribution of wetland edges was fairly uniform across all study areas. Therefore, it is not surprising that skunks displayed similar large-scale movement patterns in landscapes with contrasting grassland composition as they focused their movement among wetland edges.

Large-scale movement patterns clearly depended on the distribution of planted cover or wetlands in the landscape. Small-scale movement patterns reflect habitat selection by predators, but showed greater variability than expected. The relatively small values for $m$ indicated a lack of strong directionality in each of the step categories. In these cases the statistical analyses were not as powerful and should be interpreted cautiously. However, the analyses indicated important trends in the data about movement patterns. The directed movement by foxes in planted cover (i.e., more obtuse turn angles) in LGC landscapes was consistent with greater selection of planted cover. The more obtuse turn angles in planted cover could have increased foraging efficiency by concentrating movement within a restricted area (Tinbergen et al. 1967). However, fox movement within the agricultural matrix of LGC landscapes was not as directed as predicted. Conflicting behavioral motivations (e.g., foraging, exploring and marking territories, risk avoidance, denning) influencing movement across many habitat types may have resulted in increased variability of turn angles. The directed movement by foxes in pastureland within the agricultural
matrix of HGC landscapes was consistent with foraging behaviors in selected pastureland
in contrast to the interior areas of planted cover that were not strongly selected.

As with large-scale movement patterns, skunk exhibited consistent small-scale
movement patterns on both types of landscapes. In LGC landscapes, movement in the
agricultural matrix was faster and more directed with the most frequent turn angles close
to 0°. However, in HGC landscapes movement was slower and the distribution of turn
angles was bimodal with an increased frequency of turn angles in the direction of 180°.
As with foxes, this was very likely the result of skunk foraging behavior in the pastureland
portion of the agricultural matrix. Pastures may contain food resources used by skunks
(Greenwood et al. 1999). Although movement transition from planted cover-wetland
edges to the agricultural matrix was not directional it exhibited the same bimodal
distribution.

The rate of movement was similar in planted cover-wetland edges and in the
agricultural matrix for foxes in both types of landscape. This suggested the use of spatial
memory. Predators may use spatial memory to improve searching efficiency by revisiting
profitable patches (Mellgren and Roper 1986). If a predator has no information about the
spatial distribution of patches or prey within patches then movement patterns will be
slower (and more tortuous) as the animal spends time searching in a random fashion in an
effort to maximize its searching efficiency (Sugihara and May 1990). However, if a
predator uses spatial memory to revisit patches or profitable areas within patches then
faster more directed movement, both between and within patches, would be more efficient
than a random search pattern (Tinbergen et al. 1967, Mellgren and Roper 1986).
The rate of movement for foxes and skunks was greater for transitions at the edges between habitat categories than the rates of movement for steps than remain within a habitat of the same type. Many studies have indicated an increased effect of predation on nest success within 50 m of a habitat edge for forest-field ecotones (Paton 1994, Andren 1995). In an earlier study, we did not find a strong selection for the edge of planted cover by predators (Phillips et al. 2001). In this prairie ecosystem, these predators did not appear to focus their movement along the edge habitat but instead appeared move quickly across the boundary between planted cover and the agricultural matrix. This would reduce the potential for edge effects on nest success due to a decreased opportunity for either direct or incidental predation along edges (Vickery et al. 1992).

Our observations of foxes and skunks demonstrated that habitat heterogeneity at both the patch and landscape scale influenced predator movement patterns. Movements may be influenced by foraging or mating behavior, as well as by behaviors to avoid predation or reduce intraspecific agonistic encounters. Changes in the structure of the landscape can alter the behavioral response of predators to contrasting cover types depending on the perceived costs or rewards associated with differing cover types. However, an understanding of the behavioral responses of these generalist predators to the structure of the landscape is an essential component of predicting the consequences of an increasingly fragmented prairie landscape on the spatial and temporal interactions between predators and prey.
ACKNOWLEDGMENTS

We are grateful to D. Broadwell and D. Grohne for providing funding for this project through the Institute for Wetland and Waterfowl Research of Ducks Unlimited. We would like to thank the Northern Prairie Wildlife Research Center (NPWRC, USGS) for their financial and logistic support. R. Woodward from the NPWRC provided crucial help in the field and with creating the initial GIS database. We thank B. Allen, D. Coye, W. Cymbaluk, W. Jones, K. Kruse, D. Fronczak, M. Mayer, R. Olsen, J. Sparks, and R. Wolstenholm for spending long nights collecting the data. We thank T. Sklebar (NPWRC) for recording the aerial photography and videography and M. Zahn (Wildlife Services, USDA) for assistance in trapping fox. We thank C. Loesche (USFWS) for providing Stewart-Kantrud (1971) wetland classifications for the NWI data. This project was also supported by the Iowa Cooperative Fish and Wildlife Research Unit, and the Department of Animal Ecology at Iowa State University. This is Journal Paper No. J-19275 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa, Project No. 3299, and supported by Hatch Act and State of Iowa funds.

LITERATURE CITED


York, USA.

prairie potholes by North American ducks. Pages 204-227 in A. G. van der Valk,
editor. Northern prairie wetlands. Iowa State University Press, Ames, Iowa, USA.

Chapman and Hall, London, UK.

Harrisburg, Pennsylvania, USA.


Biology 9:129-136

heterogeneous landscapes: an experiment with Eleodes beetles in shortgrass prairie.

Crist, T. O., and J. A. Wiens. 1994. Scale effects of vegetation on forager movement and

Publishing Company, St. Paul, Minnesota, USA.

Dicke, M., and P. A. Burrough. 1988. Using fractal dimensions for characterizing the


Table 1: Means and standard errors for the rate of speed (m/min) for the different step categories for red fox in LGC and HGC landscapes (1996 and 1997).

<table>
<thead>
<tr>
<th>Step Categories</th>
<th>LGC</th>
<th>HGC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \bar{x} )</td>
<td>S.E.</td>
</tr>
<tr>
<td>A. Step categories combined</td>
<td>16.1</td>
<td>1.18</td>
</tr>
<tr>
<td>B. Step categories</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agricultural-matrix to Agricultural-matrix</td>
<td>11.2</td>
<td>1.69</td>
</tr>
<tr>
<td>Planted cover/wetland to Planted cover/wetland</td>
<td>14.4</td>
<td>1.31</td>
</tr>
<tr>
<td>Agricultural-matrix to Planted cover/wetland</td>
<td>20.0</td>
<td>1.64</td>
</tr>
<tr>
<td>Planted cover/wetland to Agricultural-matrix</td>
<td>18.7</td>
<td>1.63</td>
</tr>
</tbody>
</table>
Table 2: Means and standard errors for the rate of speed (m/min) for the different step categories for striped skunk in LGC and HGC landscapes (1996 and 1997).

<table>
<thead>
<tr>
<th>Step Categories</th>
<th>LGC</th>
<th>HGC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x}$</td>
<td>S.E.</td>
</tr>
<tr>
<td>A. step categories combined</td>
<td>10.7</td>
<td>0.35</td>
</tr>
<tr>
<td>B. step categories</td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to agricultural-matrix</td>
<td>9.0</td>
<td>0.50</td>
</tr>
<tr>
<td>planted cover/wetland to planted cover/wetland</td>
<td>7.1</td>
<td>0.38</td>
</tr>
<tr>
<td>agricultural-matrix to planted cover/wetland</td>
<td>13.2</td>
<td>0.51</td>
</tr>
<tr>
<td>planted cover/wetland to agricultural-matrix</td>
<td>13.6</td>
<td>0.51</td>
</tr>
</tbody>
</table>
Table 3: Number of turn angles (n), mean angle (\(\bar{a}\)), mean vector length (m), angular dispersion (s), and Rayleigh's z-statistic for distributions within each step category for A) red fox and B) striped skunk on the two landscape types (1996-1997).

<table>
<thead>
<tr>
<th>A. Fox</th>
<th>n</th>
<th>(\bar{a})</th>
<th>m</th>
<th>s</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGC landscape</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>155</td>
<td>18.6</td>
<td>0.0672</td>
<td>66.6</td>
<td>0.7008</td>
<td>n.s.(^A)</td>
</tr>
<tr>
<td>agricultural-matrix</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>planted cover/wetland to</td>
<td>426</td>
<td>1.2</td>
<td>0.1199</td>
<td>59.0</td>
<td>6.1291</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>137</td>
<td>10.4</td>
<td>0.0761</td>
<td>65.0</td>
<td>0.7929</td>
<td>n s.(^A)</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>144</td>
<td>20.3</td>
<td>0.0989</td>
<td>61.6</td>
<td>1.4093</td>
<td>n.s.(^A)</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. HGC landscape</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>326</td>
<td>4.6</td>
<td>0.1089</td>
<td>60.3</td>
<td>3.8640</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>agricultural-matrix</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>planted cover/wetland to</td>
<td>687</td>
<td>2.4</td>
<td>0.0620</td>
<td>67.6</td>
<td>2.6436</td>
<td>n.s.(^B)</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>221</td>
<td>4.4</td>
<td>0.0589</td>
<td>68.2</td>
<td>0.7666</td>
<td>n.s.(^A)</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Striped Skunk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>463</td>
<td>4.1</td>
<td>0.1513</td>
<td>55.7</td>
<td>10.5931</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>agricultural-matrix</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>planted cover/wetland to</td>
<td>1348</td>
<td>2.2</td>
<td>0.0722</td>
<td>65.7</td>
<td>7.0184</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>301</td>
<td>5.7</td>
<td>0.1223</td>
<td>58.7</td>
<td>4.5020</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. HGC landscape</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to</td>
<td>633</td>
<td>5.1</td>
<td>0.1068</td>
<td>60.6</td>
<td>7.2179</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>agricultural-matrix</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>planted cover/wetland to</td>
<td>2119</td>
<td>2.5</td>
<td>0.0992</td>
<td>61.6</td>
<td>20.8349</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>planted cover/wetland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n.s.(^A) 0.20 &lt; P &lt; 0.50</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n.s.(^B) 0.05 &lt; P &lt; 0.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4: Number of turn angles and Watson-Williamson F-statistic for comparisons among step categories for A) red fox and B) striped skunk on the two landscape types (1996-1997).

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Fox</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscapes</td>
<td>862</td>
<td>6.616</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>HGC landscapes</td>
<td>1451</td>
<td>1.116</td>
<td>0.3414</td>
</tr>
<tr>
<td><strong>B. Striped skunk</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscapes</td>
<td>2422</td>
<td>1.625</td>
<td>0.1815</td>
</tr>
<tr>
<td>HGC landscapes</td>
<td>3393</td>
<td>6.874</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Table 5: Number of turn angles (LGC and HGC landscapes combined) and Watson-Williamson F-statistic comparing step categories for A) red fox and B) striped skunk between the two landscape types (1996-1997).

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Fox</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to agricultural-matrix</td>
<td>481</td>
<td>3.075</td>
<td>0.080</td>
</tr>
<tr>
<td>planted cover/wetland to planted cover/wetland</td>
<td>1113</td>
<td>0.641</td>
<td>0.423</td>
</tr>
<tr>
<td>agricultural-matrix to planted cover/wetland</td>
<td>358</td>
<td>3.117</td>
<td>0.078</td>
</tr>
<tr>
<td>planted cover/wetland to agricultural-matrix</td>
<td>361</td>
<td>4.408</td>
<td>0.037</td>
</tr>
<tr>
<td><strong>B. Striped skunk</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>agricultural-matrix to agricultural-matrix</td>
<td>1096</td>
<td>0.057</td>
<td>0.811</td>
</tr>
<tr>
<td>planted cover/wetland to planted cover/wetland</td>
<td>3467</td>
<td>3.142</td>
<td>0.076</td>
</tr>
<tr>
<td>agricultural-matrix to planted cover/wetland</td>
<td>622</td>
<td>10.507</td>
<td>0.001</td>
</tr>
<tr>
<td>planted cover/wetland to agricultural-matrix</td>
<td>630</td>
<td>6.163</td>
<td>0.013</td>
</tr>
</tbody>
</table>
Table 6: Number of trajectories (n), mean, standard error, and range for the fractal dimension (D) of trajectories for red fox and striped skunk in LGC and HGC landscapes (1996 and 1997).

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>( \bar{x} )</th>
<th>S.E.</th>
<th>minimum</th>
<th>maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Landscape type</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td>255</td>
<td>1.107</td>
<td>0.0102</td>
<td>1.000</td>
<td>1.505</td>
</tr>
<tr>
<td>HGC landscape</td>
<td>353</td>
<td>1.134</td>
<td>0.0095</td>
<td>1.001</td>
<td>1.434</td>
</tr>
<tr>
<td><strong>B. species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fox</td>
<td>172</td>
<td>1.117</td>
<td>0.0120</td>
<td>1.000</td>
<td>1.318</td>
</tr>
<tr>
<td>striped skunk</td>
<td>436</td>
<td>1.125</td>
<td>0.0070</td>
<td>1.000</td>
<td>1.505</td>
</tr>
<tr>
<td><strong>C. landscape type*species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. red fox</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td>66</td>
<td>1.095</td>
<td>0.0177</td>
<td>1.000</td>
<td>1.318</td>
</tr>
<tr>
<td>HGC landscape</td>
<td>106</td>
<td>1.139</td>
<td>0.0162</td>
<td>1.000</td>
<td>1.245</td>
</tr>
<tr>
<td>2. striped skunk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td>189</td>
<td>1.120</td>
<td>0.0099</td>
<td>1.000</td>
<td>1.505</td>
</tr>
<tr>
<td>HGC landscape</td>
<td>247</td>
<td>1.129</td>
<td>0.0098</td>
<td>1.001</td>
<td>1.434</td>
</tr>
</tbody>
</table>
Table 7: Number of trajectories, means, standard errors and ranges for the displacement ratios ($\Delta$) of trajectories for red fox and striped skunk in LGC and HGC landscapes (1996 and 1997).

<table>
<thead>
<tr>
<th></th>
<th>$n$</th>
<th>$\bar{x}$</th>
<th>S.E.</th>
<th>minimum</th>
<th>maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Landscape type</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td>255</td>
<td>0.298</td>
<td>0.0170</td>
<td>0.000</td>
<td>0.767</td>
</tr>
<tr>
<td>HGC landscape</td>
<td>353</td>
<td>0.260</td>
<td>0.0146</td>
<td>0.003</td>
<td>0.998</td>
</tr>
<tr>
<td><strong>B. species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>fox</td>
<td>172</td>
<td>0.255</td>
<td>0.0191</td>
<td>0.003</td>
<td>0.998</td>
</tr>
<tr>
<td>striped skunk</td>
<td>436</td>
<td>0.304</td>
<td>0.0116</td>
<td>0.000</td>
<td>0.838</td>
</tr>
<tr>
<td><strong>C. landscape type*species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. red fox</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td>66</td>
<td>0.289</td>
<td>0.0292</td>
<td>0.003</td>
<td>0.741</td>
</tr>
<tr>
<td>HGC landscape</td>
<td>106</td>
<td>0.221</td>
<td>0.0247</td>
<td>0.007</td>
<td>0.998</td>
</tr>
<tr>
<td>2. striped skunk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGC landscape</td>
<td>189</td>
<td>0.307</td>
<td>0.0174</td>
<td>0.000</td>
<td>0.767</td>
</tr>
<tr>
<td>HGC landscape</td>
<td>247</td>
<td>0.300</td>
<td>0.0155</td>
<td>0.003</td>
<td>0.838</td>
</tr>
</tbody>
</table>
Figure 1: Predictions for the influence of planted cover (square blocks) on movement pathways for A) fox and B) skunk in LGC and HGC landscapes.

Figure 2: Components of a trajectory. The turn angle (θ), the distance (di) traveled for each step, the total distance traveled (τ = Σ di) for a trajectory and the displacement, δ (the distance from the first to the last location in a trajectory).

Figure 3: Distribution for step distance for A) red fox in LGC landscapes (x = 271.8, S.E. = 9.67 and median = 162.8 m), B) red fox in HGC landscapes (x = 290.8, S.E. = 7.99 and median = 184.6 m), C) striped skunk in LGC landscapes (x = 150.8, S.E. = 3.18 and median = 95.0 m) and D) striped skunk in HGC landscapes (x = 150.8, S.E. = 2.67 and median = 96.4 m).

Figure 4: Distribution for total distance traveled by A) red fox in LGC landscapes (x = 4164.1, S.E. = 380.31 and median = 3692.9 m), B) red fox in HGC landscapes (x = 4755.0, S.E. = 307.57 and median = 4193.7 m), C) striped skunk in LGC landscapes (x = 2196.7, S.E. = 110.67 and median = 1928.8 m) and D) striped skunk in HGC landscapes (x = 2357.1, S.E. = 98.66 and median = 1985.70 m).

Figure 5: Frequency histogram of turn angles for red fox in LGC and HGC landscapes for steps that begin and end in the agricultural matrix (1996-1997).
Figure 6: Frequency histogram of turn angles for red fox in LGC and HGC landscapes for steps that begin and end in planted cover-wetland edge (1996-1997).

Figure 7: Frequency histogram of turn angles for red fox in LGC and HGC landscapes for steps that begin in the agricultural matrix and end in planted cover-wetland edge (1996-1997).

Figure 8: Frequency histogram of turn angles for red fox in LGC and HGC landscapes for steps that begin in planted cover-wetland edge and end in the agricultural matrix (1996-1997).

Figure 9: Frequency histogram of turn angles for striped skunk in LGC and HGC landscapes for steps that begin and end in the agricultural matrix (1996-1997).

Figure 10: Frequency histogram of turn angles for striped skunk in LGC and HGC landscapes for steps that begin and end in planted cover-wetland edge (1996-1997).

Figure 11: Frequency histogram of turn angles for striped skunk in LGC and HGC landscapes for steps that begin in the agricultural matrix and end in planted cover-wetland edge (1996-1997).
Figure 12: Frequency histogram of turn angles for striped skunk in LGC and HGC landscapes for steps that begin in planted cover-wetland edge and end in the agricultural matrix (1996-1997).

Figure 13: $\log(\bar{L})$ vs. $\log(\lambda)$ plots with the 95% C.I. for $\bar{L}$ and the mean regressed line computed for foxes on LGC landscapes (A), foxes on HGC landscapes (B), skunks on LGC landscapes (C) and skunks on HGC landscapes (D).

Figure 14: Observed skunk trajectories with fractal dimensions of A) 1.148 ($n = 30$ locations), B) 1.308 ($n = 30$ locations) and C) 1.505 ($n = 32$ locations).
A) Fox

B) Skunk

Figure 1
Figure 4

Figure showing the frequency distribution of total distance (m) for different categories labeled A, B, C, and D.
Figure 5
Fox: planted cover-wetland edge --> planted cover-wetland edge

Figure 6
Fox: agricultural-matrix --> planted cover-wetland edge

Figure 7
Fox: planted cover-wetland edge --> agricultural matrix

Figure 8
Figure 9
Skunk: planted cover-wetland edge --> planted cover-wetland edge

Figure 10

LGC landscape
HGC landscape
Skunk: agricultural-matrix --> planted cover-wetland edge

- LGC landscape
- HGC landscape

Figure 11
Skunk: planted cover-wetland edge → agricultural matrix

Figure 12
CHAPTER 4. PREDATOR ACTIVITY IN GRASSLAND PATCHES AND ITS EFFECT ON WATERFOWL NEST SUCCESS

A paper to be submitted to Ecological Applications

Michael L. Phillips, William R. Clark, Marsha A. Sovada, David J. Horn, Rolf R. Koford, and Raymond J. Greenwood

Abstract. Loss and fragmentation of waterfowl breeding habitat in the Prairie Pothole Region (PPR) has created a mosaic landscape dominated by agriculture interspersed with patches of breeding habitat of various sizes. This fragmentation has led to declines waterfowl nest success due to increased predation. However, little is known about how patch size influences the potential for mammalian predators to find waterfowl nests. For 2 breeding seasons (1996-1997), we estimated the activity of red fox (Vulpes vulpes) and striped skunk (Mephitis mephitis) in North Dakota landscapes in terms of the proportion and density of locations in planted cover. We also estimated the proportion of nests within 50 m of a predator location. These nests were potentially encountered by a predator. We simultaneously collected information on waterfowl nest success within each patch. We compared observed levels of predator activity and observed nest sites to a null model of a random process that predicted that the proportion of predator locations would be proportional to patch size whereas the density of predator locations and the potential for encountering nests would be constant over all patch sizes. We expected a low mean but highly variable proportion of encountered nests in small patches because some patches are
not visited by predators, whereas those that are visited are thoroughly searched. We expected a high proportion of encountered nests in moderately size patches as predators focused activity in patches with more abundant resources. We expected a low proportion of encountered nests in large patches as a result of increased search time in abundant nesting cover and decreased foraging effort by a few predators over a large area (dilution effect). Our comparison of simulated versus observed behavior indicated that the potential for increased predator activity and increased proportion of encountered nests was greatest in moderately sized patches (50-120 ha). This result was consistent with a quadratic regression of observed daily survival rates (DSR) that illustrated a lower predicted DSR in moderately sized patches with the lowest survival rate (DSR = 0.9196) in a 55 ha patch. For patches smaller than 50 ha, the observed level of predator activity was not distinguishable from random activity and the proportion of encountered nests was highly variable. In many patches either all or none of the nests were encountered in both the simulation study and among the observed data which is consistent with the higher observed nest DSR with large variances. In patches larger than 120 ha, we observed that the predator activity level and proportion of encountered nests were less than, or similar to, random levels that was consistent with the higher observed nest DSR with smaller variances among patches. Differences in predator activity were more evident among foxes than among skunks and reflected the stronger attraction to planted cover by foxes. Our modeling approach is a valuable first approximation to understanding the response by predators to waterfowl because it illustrated the nonrandom manner in which predators responded to the distribution of resources.
Key Words: habitat selection, landscape composition, Mephitis mephitis, movement pathways, nest success, patch size, Prairie Pothole Region, predator activity, predation, red fox, striped skunk, Vulpes vulpes.

INTRODUCTION

Native grasslands in the PPR have been dramatically altered through increasing fragmentation and loss due to conversion to agricultural uses (Higgins 1977, Sugden and Beyersbergen 1984, Greenwood et al. 1995, Miller and Nudds 1996). The PPR is a major source for waterfowl breeding (Bellrose 1980, Batt et al. 1989) and has been the focus of habitat management on the breeding grounds (Reynolds et al. 1994). The Conservation Reserve Program (CRP) of the 1985 Federal Food Security Act and the 1986 North American Waterfowl Management Plan have provided incentives for large scale restoration of perennial grassland. The result of these opposing trends in the PPR is a landscape composed of a mosaic of cover types dominated by agriculture and interspersed by patches of grassland of various sizes.

Waterfowl nest success is heavily influenced by mammalian predation in the PPR (Klett et al. 1988, Johnson et al. 1989, Sargeant and Raveling 1992, Sargeant et al. 1993). Wildlife ecologists suggest that as the patch size of breeding habitat decreases waterfowl nests are concentrated in small areas and predator foraging efficiency increases such that small patches are easily found and thoroughly searched (Fritzell 1975, Oetting and Dixon 1975, Sargeant et al. 1984, Cowardin et al. 1985, Krasowski and Nudds 1986, Clark and Nudds 1991). There is evidence that smaller patch size is associated with lower nest
success and increased predation in forest songbirds (Whitcomb et al. 1981, Wilcove 1985) and ring-necked pheasants (Phasianus colchicus) (Clark et al. 1999). Waterfowl nest success is greater in larger patches of CRP in the PPR (Kantrud 1993, Sovada et al. 2000) and is positively correlated with the composition of grassland in the landscape (Greenwood et al. 1987, Reynolds et al. 1994, Horn 2000). However, the relationship between nest success and patch size is unclear. More importantly, almost nothing is known about how patch size influences the potential for mammalian predators to find waterfowl nests.

Our objective was to investigate the relationship between patch size and nest predation by comparing the level of predator activity to waterfowl nest success and the proportion of nests potentially encountered by a predator in patches of waterfowl breeding habitat (planted cover enrolled in the CRP). Our study is unique in that we simultaneously recorded predator activity and the fate of waterfowl nests in the same patches. We studied activity of red fox (Vulpes vulpes) and striped skunk (Mephitis mephitis). Both are common waterfowl predators (Korschgen 1959, Sargeant 1972, Sargeant et al. 1984, Greenwood 1986) that have the potential to range widely across the landscape.

We estimated predator activity using radiotelemetry and recorded the proportion of all telemetry locations and the density of locations in patches of grassland. We estimated the proportion of nests potentially encountered by a predator by assuming that nests would be encountered if nests were within 50 m of a predator location. We compared observed behavior to a null model of random predator activity and random nest sites within patches of planted cover. If predator foraging behavior was a random process then the proportion of telemetry locations would be proportional to patch size, whereas the density of locations
and the potential for encountering nests would be constant over all patch sizes. We expected that there would be a nonrandom functional response by predators to perceived differences in resources among patches. We expected a low mean but highly variable proportion of encountered nests in small patches because some patches are not visited by predators whereas those patches that are visited are thoroughly searched. We expected a high proportion of encountered nests in moderately size patches as predators focused activity in patches with more abundant resources. We expected a low proportion of encountered nests in large patches as a result of increased search time in the abundant nesting cover or decreased foraging effort by a few predators over a large area (dilution effect). These changes in predator activity should mirror the relationship between patch size and duck nest success such that there is a critical range of patch sizes in which waterfowl have an increased chance to escape predation.

Based on our previous analysis of habitat selection and movement pathways, we also predicted that fox and skunk would not respond to patches of breeding habitat in the same manner because of differences in life histories. We observed that foxes were strongly attracted to the edge and interior areas of planted cover in landscapes with a low grassland composition, whereas they rarely selected the interior areas of planted cover in landscapes with a high grassland composition (Phillips et al. 2001a). In contrast, selection of planted cover and movement patterns by skunk were similar regardless of the composition of grassland in the landscape (Phillips et al. 2001a,b). Sovada et al. (2000) did not find a correlation between patch size and skunk activity. We expected that the
smaller extent of movement (i.e., rate of movement and length of pathways, Phillips et al. 2001b) would make skunks less responsive to patch size.

METHODS

Study Areas

Each year (1996 and 1997), we selected two 41.4 km² study areas with contrasting amounts of perennial grassland (planted cover, pastureland, and hayland) in the Prairie Pothole Region of central North Dakota. Study areas we selected with a "Low Grassland Composition" (hereafter LGC) were Litchville, ND (Svea Township in Barnes County) in 1996 and Bowdon, ND (Berlin Township in Wells County) in 1997. LGC landscapes contained small, isolated patches of perennial grassland surrounded by cropland. Habitat composition of the Litchville study area was 66.9% cropland, 12.5% planted cover, 2.3% pastureland, 0.3% hayland, and 11.7% wetlands. Habitat composition of the Bowdon study area was 56.4% cropland, 13.8% planted cover, 2.7% pastureland, 3.2% hayland, and 18.5% wetlands.

In contrast, study areas we selected with a "High Grassland Composition" (hereafter HGC) were Medina, ND (Iosco Township in Stutsman County) in 1996 and Hurdsfield, ND (Silver Lake Township in Wells County) in 1997. HGC landscapes contained large patches of perennial grassland adjacent to cropland. Habitat composition of the Medina study area was 34.3% cropland, 22.1% planted cover, 19.0% pastureland, 4.1% hayland, and 13.4% wetlands. Habitat composition of the Hurdsfield study areas
was 23.0% cropland, 22.5% planted cover, 27.8% pastureland, 1.5% hayland, and 21.1% wetlands.

We used data from the National Wetland Inventory (NWI, U.S. Fish and Wildlife Service, St. Petersburg, Florida) to identify the wetland basins on the study areas. NWI classifications were converted to Stewart and Kantrud (1971) classifications by the Habitat and Population Evaluation Team (U. S. Fish and Wildlife Service, Bismarck, North Dakota). Although both 1996 and 1997 were wet years, each study area contained a similar composition of wetlands (Litchville = 9.3%, Bowdon = 13.9%, Medina = 12.1%, and Hurdsfield = 13.8%). Wetlands were predominantly temporary and seasonal.

All study areas also included a square-mile road system (< 2% of the landscape). Other habitat types (all < 1.0% of the landscape) included farmsteads, trees, and other miscellaneous habitat types. The Medina study area included a predator enclosure (2.4% of the landscape) which contained planted cover enrolled in the Conservation Reserve Program and hayland.

**Habitat delineation**

Land cover data were recorded from low altitude aerial photography and videography for each study area plus a 1.6 km wide border around each study area. Habitat types were digitized and classified using the Map and Image Processing System (MicroImages, Lincoln, Nebraska, USA). Habitat classifications were verified by ground observations. We used ARC/INFO (ESRI, 1994, Redlands, California, USA) for management and analysis of the land cover and movement data.
We focused on the response of predators to patches of planted cover. We used ARC/INFO to measure the area ($m^2$) of the 48 patches of planted cover on the four study areas. Planted cover was seeded to perennial grasses and forbs and enrolled in the Conservation Reserve Program (CRP), the Water Bank Program (WBP), or set aside as federal Waterfowl Production Areas (WPA). Our definition of a patch of planted cover is similar to that of Sovada et al. (2000: Fig. 2) except that we allowed gravel and paved roads to divide adjacent areas of planted cover into separate patches. Habitats in the surrounding agricultural landscape included cropland, pastureland, hayland, wetlands, and miscellaneous habitat types. Pastureland contained grazed perennial grasses. Hayland contained perennial grasses that were disturbed by mowing. Croplands were planted in either row crops (corn, sunflowers, beans, potatoes, or soybeans) or grain crops (wheat, barley, oats, flax, or canola). The miscellaneous category included the remaining habitat types: farmyards, trees, fallow agricultural land, islands, land not in agricultural use. Trees were usually found in shelterbelts or around farmyards.

**Capture and Handling**

We captured foxes and skunks in April and May (1996 and 1997) and in June (1997) using either livetrap for skunks or snares with stops and leg hold traps for foxes. A professional trapper from Wildlife Services (United States Department of Agriculture, Bismarck, ND) assisted us with capturing fox. We trapped intensively and systematically across all study areas with the goal of capturing all resident animals of both predator species. All captured study animals were sexed, weighed, examined for tooth wear and reproductive status of females, ear tagged and fitted with a telemetry transmitter.
(Advanced Telemetry Systems, Isanti, Minnesota, USA) containing a 1 hour mortality switch. The transmitters weighed approximately 60 g for skunks and 110 g for foxes. All trapping and handling procedures for this project were developed following recommendations by the American Society of Mammalogists (1987), the Northern Prairie Wildlife Research Center’s Animal Care and Use Guidelines, and were approved by the Iowa State University Committee on Animal Care.

Movement Analysis

Observed trajectories - We define a trajectory as a series of locations for one animal for one night of tracking. Locations for each of the sampled animals were recorded every 15-20 minutes. Locations were estimated from 2-3 bearings using vehicle-mounted null-peak directional antennas. Locations based on 2 bearings were estimated using a fixed standard deviation determined for each crew member based on 2 field tests given before and midway through the field season. Bearings were taken from telemetry stations positioned along roads or at other accessible positions with known Universal Transverse Mercator (UTM) coordinates. Locations and their 95% error ellipses were estimated using LOCATE II software (Pacer Truro, Nova Scotia, Canada; Nams 1990).

We recorded predator movements intensively at night (2000-0800) 3 times each week. In order to insure complete coverage of the study area and sampling of all animals, we recorded how often and how long each animal was tracked.

We took several steps to minimize error and improve the resolution of movement within a trajectory. We examined the statistical distribution of the error ellipses and deleted any location with an error ellipse that was greater than 3.0 times the interquartile
range above the 75% quantile (an "extreme outlier", Devore and Peck 1986: 94). Trajectories with less than 10 locations did not give us enough information on movement patterns and were not included in the analysis. Occasionally more than 60 minutes elapsed between locations. To eliminate these gaps we either deleted locations from the data set if they were at the beginning or end of a trajectory, or the trajectories were split into shorter trajectories. We recorded locations more frequently in 1997 than in 1996. The average time between locations was 19.5 min (S.E. = 0.07) in 1996 and 9.9 min (S.E. = 0.07) in 1997. The time between locations can affect trajectory characteristics such as the rate and turn angle between successive locations and the fractal dimension (Ferguson, et al. 1996). Therefore, to standardize the telemetry data between the 2 years we systematically deleted every other location from the 1997 data. After editing the data, the average time between locations for 1997 was 19.4 min (S.E. = 0.15).

*Simulated trajectories* - We computed summary statistics (mean, SE and range) for the distance (m) moved between successive locations from each observed trajectory for fox and skunk on each study area (Table 1A). We then simulated a null trajectory by first selecting a random point from a uniform distribution within a study area as a starting location for a simulated trajectory. The distance an animal moved between successive locations within a trajectory was selected from a normal distribution of observed distances. Any simulated distance from the normal distribution that was < 0 was truncated to 0. The turning angle between successive locations was then selected from a uniform circular distribution. The number of locations from a simulated trajectory was determined by rounding the mean number of locations for observed trajectories (Table 1). The number
of simulated trajectories equaled the number of observed trajectories for each species on each study area during the field season (Table 1). We replicated 10 field seasons of simulated trajectories. We used SAS functions (SAS Institute 1989) to create the normal and uniform distributions for the simulated trajectories. We used ARC/INFO to associate a cover type for each location by overlaying the simulated trajectories on the habitat map for each study area.

We analyzed predator activity levels by examining the proportion \( p_i \) and the density \( d_i \) of locations that were within each patch \( i \) of planted cover. The proportion of locations was computed as the ratio of the number of locations \( n_i \) within a patch \( i \) of planted cover to the number of locations within the 48 patches of planted cover such that

\[
p_i = \frac{n_i}{\sum_{i=1}^{48} n_i}.
\]

The density \( d_i \) of locations was computed as the ratio of the number of locations \( n_i \) within a patch \( i \) of planted cover to the area \( a_i \) of the patch measured in \( m^2 \) such that

\[
d_i = \frac{n_i}{a_i}.
\]

We computed the mean, minimum and maximum proportions and densities of locations for the 10 simulated replications in planted cover for each patch size.

We used a validation statistic \( V_2^* \) to test for a difference between observed and simulated movement patterns (Reynolds et al. 1981). The \( V_2^* \) statistic allowed for the comparison between a single observation (i.e., a proportion or density of locations, or proportion of nests encountered) for each patch size with \( m \) simulated observations over the same range of patch sizes. The observed value was ranked among the simulated values. The \( V_2^* \) statistic did not test for each patch \( i \) but tested over the entire range of
patch sizes. The $V_{z^*}$ statistic was compared with the appropriate critical value from the standard normal distribution. If the statistic indicated a difference, we then described where the observed values were greater than the maximum or below the minimum simulated value. Observed values greater than the maximum simulated value indicated that predators were using these patches much greater than would be expected at random. Observed values less than the minimum simulated values indicated that predators were using these patches much less than would be expected at random. If the observed values fell within the range of simulated values then use of these patches by predators could not be distinguished from a random process.

*Nest Success*

*Observed nests* - We searched for waterfowl nests in planted cover using a chain dragged between 2 vehicles. Nest searching took place from early May to mid-July. Each patch was searched 3 times in 1996 and 4 times in 1997. The UTM coordinates for each nest were recorded using a Trimble GPS instrument. Further details of the procedures used to find and monitor nests are given in Horn (2000).

We searched a total of 41 patches of planted cover on the 4 study areas (Litchville = 12 patches, Medina = 10 patches, Bowdon = 12 patches and Hurdsfield = 7 patches). We did not have permission to search 7 patches of planted cover used in the analysis of movement patterns ($n = 48$ patches). These included 4 patches in Medina (10.9, 14.1, 105.2, and 182.5 ha), 2 patches on Bowdon (17.8 and 59.1 ha) and 1 patch in Hurdsfield (374.1 ha).
Nest success (NS) was estimated by procedures developed by Mayfield (1975) and modified by Johnson (1979). We modeled the relationship between the daily survival rate (DSR = \( \sqrt{N_{\text{S}}} \)) of nests within each patch as a function of log-transformed patch size using a nonlinear, quadratic regression (D. J. Horn, unpublished data). The DSR for each patch was arsine transformed and weighted by the proportion of exposure days.

**Proportions of encountered nests**

*Simulated duck nests* - We simulated a random distribution of duck nests in planted cover by first using SAS to create a bivariate uniform distribution of UTM locations within a study area. These locations were plotted on the study area and a subset of points within patches of planted cover that were searched (n = 41 patches) were selected from the sample using ARC/INFO. We generated 10 replications of the simulated duck nests. We used only those replications in which the number of simulated nests equaled the number of observed nests found in each study area.

*Observed and simulated proportion of encountered nests* - We used ARC/INFO to identify nests in planted cover that were within 50 m of a predator location. Any nests within this distance were considered likely to be encountered by a predator. This distance accounts for the potential perceptual capabilities of the predators (M. Sovada and S. Lariviere pers. comm.) and telemetry error in estimating predator locations. Only patches that were searched (n = 41 patches) were used in the analysis. We computed the proportion of encountered nests as the ratio of the number of nests within 50 m of a predator location to the number of nests within each patch. We computed the proportion of nests encountered by fox only, skunk only, and those encountered by either fox or skunk.
The proportion of nests classified as encountered by using the observed nest locations and the observed trajectories was contrasted to the proportions of nests classified as encountered using simulated nests and trajectories. We generated 10 replications of these simulated encounters. We computed the mean, minimum and maximum proportion of encountered nests for the 10 simulated replications in planted cover for each patch size.

We used a validation statistic $V_2^*$ to test for a difference between observed and simulated proportions of encountered nests over the range of patch sizes (Reynolds et al 1981). If the statistic indicated a difference, we then described where the observed proportions appeared to deviate from the simulated proportions. Observed proportions greater than the maximum simulated proportions indicated that predators were using these patches much greater than would be expected at random and therefore were more likely to encounter a nest. Observed values less than the minimum simulated values indicated that predators were using these patches much less than would be expected at random and were therefore less likely to encounter a nest. If the observed values fell within the range of simulated values then use of these patches by predators could not be distinguished from a random process.

RESULTS

Movement Analysis

*Observed trajectories* - We recorded trajectories for 5 foxes and 21 skunks in Litchville, 5 foxes and 16 skunks in Medina, 7 foxes and 20 skunks in Bowdon, and 9 foxes and 22 skunks in Hurdsfield. Deleting locations with an estimated error ellipse $> 3.0$ times the interquartile range above the 75% quantile placed an upper limit of 11.7 ha for locations
used in the analysis. Trajectories with less than 10 locations (n = 155 trajectories) were not included in the analysis. The remaining trajectories averaged 17.7 (S.E. = 0.30) locations and ranged from 10-40 locations. For trajectories with gaps of > 60 minutes, we either a) deleted locations from the data set if they were at the beginning or end of a trajectory (n = 185 trajectories), or b) the trajectories were split into shorter trajectories (n = 164 trajectories). For our analyses we used 9,977 locations grouped within 608 trajectories for 105 individuals. The resulting median area for error ellipses for locations was 1.09 ha.

Simulated trajectories - We simulated 9,999 locations grouped within 608 trajectories for each replication of a simulated trajectory. As a result of truncating distances moved between successive locations in a trajectory to 0, the range of simulated mean distances were greater than observed mean distances (Table 1). Ranges for the SE and maximum distance moved are smaller for simulated trajectories than in observed trajectories (Table 1).

Proportion of locations

A greater proportion of observed fox locations (642 out of a total of 2,916 observed locations) were recorded in planted cover (Z = 9.0, P < 0.0001) compared with simulated fox locations (\( \bar{x} = 486.3 \pm 17.3 \) S.E out of a total 2,900 simulated locations among 10 replications). A greater proportion of observed skunk locations (1,916 out of a total 7,061 observed locations) were recorded in planted cover (Z = 19.6, P < 0.0001) when compared to simulated skunk locations (\( \bar{x} = 1,237.8 \pm 34.6 \) S.E out of a total of 7,099 simulated locations among 10 replications).
**Foxes** - The observed proportion of fox locations in different patch sizes of planted cover was significantly different from the simulated proportions ($V_2* = 2.72$, $P = 0.003$). As predicted, the proportion of random locations increased with increasing patch size (Fig. 1). The proportion of observed locations were within the range of simulated random proportions for the majority of patch sizes (33/48 patches)(Fig. 1). However, there were 9 patches in which the observed proportion of locations was greater than the maximum simulated proportion. These patches were 3.5, 10.6, 10.9, 51.3, 59.1, 76.0, 120.7, 258.9, and 340.6 ha. Four of the 9 patches were between 50 - 120 ha. Three of these 4 patches (51.3, 59.1 and 76.0 ha patches) were in landscapes with a low grassland composition. The patches < 50 ha that were frequently used by foxes were each within 500 m of a known den site. The 10.6 ha patch also included a large semipermanent wetland. The 6 patches that were less than the minimum simulated proportion were 49.8, 105.2, 182.5, 252.0, 477.3 and 605.7 ha and were found only in landscapes with a high grassland composition.

**Skunks** - The observed proportion of skunk locations in different patch sizes was significantly different from the simulated proportions ($V_2* = 2.63$, $P = 0.004$). The proportion of random locations increased with increasing patch size (Fig. 2). The proportion of observed locations for a majority of patches (36/48 patches) were within the range of simulated random proportions (Fig. 2). However, there were 8 patches in which the observed proportion of locations was greater than the maximum simulated proportion. These patches were 6.4, 10.6, 17.8, 25.1, 49.8, 59.6, 72.6 and 182.5 ha in size. Of these patches, half were in landscapes with a low grassland composition (6.4, 10.6, 17.8 and
25.1 ha patches) and the other half were in landscapes with a high grassland composition (49.8, 59.6, 72.6 and 182.5 ha patches). The 4 patches that were less than the minimum simulated proportion were 120.7, 252.0, 275.6 and 477.3 ha in size and all were in landscapes with a high grassland composition.

**Density of locations**

**Foxes** - The observed density of fox locations in different patch sizes was significantly different from the simulated density ($V_z^* = 3.36, P = 0.0004$). As predicted, the density of random locations did not change with increasing patch size (Fig. 3). The density of observed locations showed a similar pattern of use for patches by fox as the proportion of observed locations (Fig. 1). The density of observed locations in the majority of patches (30/48 patches) were within the range of simulated random density (Fig. 3). However, there were 13 patches in which the observed density of locations was greater than the maximum simulated density. These patches were 3.5, 10.6, 10.9, 51.3, 56.3, 59.0, 68.1, 76.0, 120.7, 185.5, 258.9, 340.6 and 374.1 ha. Six of the 13 patches were between 50 - 120 ha and included 4 patches (51.3, 59.1, 76.0 and 120.7 ha) with large differences between observed and random densities. As before, the 3 patches < 50 ha that were frequently used by foxes were within 500 m of a known den site. The 5 patches that were less than the minimum simulated density were 49.8, 105.2, 182.5, 252.0, and 605.7 ha in size and all were in landscapes with a high grassland composition.

**Skunks** - The observed density of skunk locations in different patch sizes was significantly different from the simulated density ($V_z^* = 5.09, P < 0.0001$). The density of random locations did not change with increasing patch size (Fig. 4). The density of observed
locations (Fig. 4) showed a different pattern of use by skunks compared to the proportion of locations (Fig. 2). The majority of patches (28/48 patches) were within the range of simulated random density. However, there were 17 patches (more than twice as many than observed for proportion of locations) in which the observed density of locations was greater than the maximum simulated density and covered a wide range of patch sizes. These patches were 6.4, 8.9, 9.4, 10.6, 17.8, 25.1, 34.6, 36.0, 49.8, 55.1, 59.6, 72.6, 163.5, 182.5, 185.5, 258.9, and 374.1 ha. Ten of the 17 patches (6.4, 8.9, 9.4, 10.6, 17.8, 25.1, 34.6, 36.0, 163.5 and 185.5 ha) were in low grassland landscapes. The 3 patches that were less than the minimum simulated density were 252.0, 275.6 and 477.3 ha in size and were in landscapes with a high grassland landscape.

Nest Success

Observed nests - We estimated the UTM location for 1,534 nests in 41 patches of planted cover in the 4 study areas (Litchville = 217, Medina = 691, Bowdon = 385 and Hurdsfield = 241 nests).

There was a slight improvement in the fit of DSR to patch size for the quadratic regression ($R^2 = 0.50$, $P < 0.0001$; D. J. Horn unpublished analysis) compared to a linear regression ($R^2 = 0.47$, $P < 0.0001$; Horn 2000). The lowest predicted value for DSR (DSR = 0.9196) occurred in a 55 ha patch (Fig. 5; DSR and patch sizes used in the regression were back transformed). For patches < 55 ha there was an increasing DSR with an increasing variance among patches. In contrast, for patches > 55 ha, there was an increasing DSR with a decreasing variance among patches.
Proportion of encountered nests

Either fox or skunk - The observed proportions of nests encountered by either fox or skunk in different patch sizes of planted cover was different from the simulated proportions ($V_2^* = 3.63, P < 0.0001$). As expected, the proportion of encountered nests for random predator activity and random nest sites did not change with increasing patch size (Figs. 6-8). For the proportion of encountered nests for observed predator activity and observed nest sites, the majority of patches (28/41 patches) were within the range of simulated random proportions (Fig. 6). However, there were 9 patches in which the observed proportion of encountered nests was greater than the maximum simulated proportion. These patches were 6.3, 10.6, 36.0, 49.8, 51.3, 59.6, 68.1, 120.7 and 163.5, ha. Five of the 9 patches ranged from approximately 50 - 120 ha. Only 3 of these patches were in low grassland landscapes (49.8, 59.6 and 120.7 ha patches). For the 2 patches < 50 ha, one patch (6.3 ha patch) was within 500 m of a known fox den site and frequently used by foxes and the other patch (10.6 ha patch) included a large semipermanent wetland. The 4 patches that were less than the minimum simulated proportion were 15.2, 17.3, 252.0, and 477.3 ha and all were in landscapes with a high grassland composition.

Fox only - The observed proportions of nests encountered by a fox (Fig. 7) in different patch sizes was not significantly different from the simulated proportions ($V_2^* = 0.12, P = 0.452$). The large variation in simulated proportions together with a small sample of observed trajectories made it difficult to distinguish between observed and simulated proportions.
**Skunk only** - The observed proportions of nests encountered by a skunk (Fig. 8) in different patch sizes was significantly different from the simulated proportions ($V_z^* = 2.90$, $P = 0.002$). The majority of patches (28/41 patches) were within the range of simulated random proportions (Fig. 8). However, there were 10 patches in which the observed proportion of locations was greater than the maximum simulated proportion. These patches were 6.3, 7.5, 10.6, 23.0, 25.1, 36.0, 49.8, 59.6, 72.6 and 163.5, ha. Only 6 of the 10 patches were in landscapes with a low grassland composition. The 3 patches that were less than the minimum simulated proportion were 15.2, 275.6 and 477.3 ha and all were in high grassland landscapes.

**DISCUSSION**

We demonstrated that predators responded to the size of grassland patches used by breeding waterfowl in a nonrandom fashion. Increased predator activity was associated with patch sizes that had the lowest nest success. Predator response to patch size was more evident among foxes than among skunks which suggests that fox behavior will be influenced more than skunks by the loss and fragmentation of waterfowl breeding habitat.

Although the observed behavioral patterns are only suggestive, they are consistent with the nest success data and our knowledge of predator life history. For example, the comparatively larger amount of time spent in medium sized patches (approximately 50-120 ha) decreased nest success due to the greater opportunity for foxes to encounter nests. In patches < 55 ha there was an inverse trend in the DSR with a corresponding increase in variance among patches. It is likely that patches smaller than 55 ha can be quickly and
thoroughly searched and they are unlikely to be revisited. In several small patches either none or all of the nests were within 50 m of recorded predator activity so nest success in small patches may simply depend on whether or not the patch is visited by a predator.

The predicted DSR of waterfowl nests increased as patch size increased above 55 ha. Several factors may influence predator activity in large patches that decreases foraging efficiency and therefore decreases the probability of finding a nest. Foraging efficiency may decline because of increased search time (MacArthur and Pianka 1966) in large patches simply because large patches cannot be easily and thoroughly searched and nests are likely to be widely spaced. Foraging efficiency may decline due to a dilution of searching effort by a few predators over a large area. Larger patches of planted cover are often located in landscapes with a high grassland composition that also contain attractive alternative cover types that potentially divert some foraging effort (Phillips et al. 2001a). By increasing the composition of grassland on a landscape, predators are no longer focused on the planted cover that is selected by nesting waterfowl (Phillips et al. 2001a). Furthermore, dense nesting cover is frequently planted in large fields. Among the motivations for planting dense nesting cover is that waterfowl would be better able to conceal nests (Clark and Nudds 1991) and that travel would be difficult for predators. Obviously these patch and landscape level influences are not independent but in either case predators are unlikely to invest the amount of time necessary to completely search large patches.

Skunk activity levels could not be distinguished from random activity levels for the majority of patch sizes. This is not consistent with Sovada et al. (2000) that found no
correlation between patch size and skunk activity using passive track counts. If skunk were randomly using different cover types, then their activity levels should increase proportionately with the composition of planted cover in the landscape. Sovada et al. (2000) proposed that environmental conditions (e.g., increased rainfall) and a rabies epidemic may have contributed to dramatic spatial heterogeneity in skunk populations during the span of their study that could have influenced measured activity levels. We observed that the level of selection for planted cover (Phillips et al. 2001a) and movement patterns (Phillips et al. 2001b) by skunks did not differ in landscapes with contrasting amounts of grassland. Skunk movement patterns were influenced most by agricultural wetland edges that were distributed widely across our study areas. It is likely that the level of skunk activity in planted cover depends on factors such as the size and distribution of wetlands both within patches of planted cover and in the surrounding cropland.

Large differences in predator activity levels within patches that are very close to the same size could be due to several factors. First, the territoriality of foxes could determine the proximity of an individual patch. Similarly sized patches may have very different predator activity levels depending on whether or not the patch is within the core area of activity of a fox. We observed that some small patches (< 50 ha) were frequently used by foxes. These small patches were often close to den sites or contained features such as wetland edges, treelines or farmsteads that were attractive to foxes. Furthermore, foxes can be displaced by the presence of coyotes (Voigt and Earle 1983, Sargeant et al. 1987a, Sovada et al. 1995) which will limit the availability of some patches.
A second factor is that similar sized patches may contain different prey communities that reflect different profitabilities to predators. Generalist predators such as the fox and skunk can encounter prey types with widely varying search and handling times that range from small immobile invertebrates to relatively large active hens (Verts 1967, Henry 1996, Greenwood et al. 1999). There is potential for great spatial heterogeneity in the types of prey species present between patches of similar size.

Thirdly, patches of similar size can be embedded within landscapes with vastly different grassland composition. The landscape context of the patch may determine the level of activity within an individual patch. In this study, patches that ranged from 50-120 ha in size were found in landscapes that contained as little as 15% and as much as 52% perennial grassland cover. Within this range, the majority of patches with the highest levels of predator activity were located within landscapes with a low grassland composition. All patches in this range with low predator activity were located within landscapes with a high grassland composition. High grassland landscapes are more likely to contain attractive alternative cover types that distract predators from planted cover (Phillips et al. 2001a) and they are more likely to contain large patches of planted cover which are used more frequently by coyotes (Sovada et al. 2000).

Finally, the dynamic human-induced alterations of the landscape have created nonequilibrium interactions between predators and prey that could prevent a long-term stable distribution of predators and prey at the landscape scale. Clark et al. (1999) proposed that maintaining such a nonequilibrium state through the spatial and temporal
rotation of blocks of breeding habitat may improve overall nest success for grassland nesting birds.

Understanding the interaction between patch size of breeding habitat, predator activity and waterfowl nest success is of considerable relevance for management efforts to preserve or restore waterfowl breeding habitat. Agricultural and wildlife policies have created opportunities for large landscape modifications for wildlife habitat in the PPR. These modifications will influence the behavioral patterns (e.g., the selection of feeding and nesting sites, finding mates, avoiding predation) of both predator and prey. We agree with Clark and Nudds (1991) and Sovada et al. (2000) that a definitive experiment will be difficult, but we argue that our modeling approach is a valuable first approximation in understanding the response by predators to waterfowl breeding habitat in an increasingly dynamic landscape.

ACKNOWLEDGMENTS

We are grateful to D. Broadwell and D. Grohne for providing funding for this project through the Institute for Wetland and Waterfowl Research of Ducks Unlimited. We would like to thank the Northern Prairie Wildlife Research Center (NPWRC, USGS) for their financial and logistic support. R. Woodward from the NPWRC provided crucial help in the field and with creating the initial GIS database. We thank B. Allen, D. Coye, W. Cymbaluk, W. Jones, K. Kruse, D. Fronczak, M. Mayer, R. Olsen, J. Sparks, and R. Wolstenholm for spending long nights collecting the data. We thank T. Sklebar (NPWRC) for recording the aerial photography and videography and M. Zahn (Wildlife Services,
USDA) for assistance in trapping fox. We thank C. Loesche (USFWS) for providing Stewart-Kantrud (1971) wetland classifications for the NWI data. This project was also supported by the Iowa Cooperative Fish and Wildlife Research Unit, and the Department of Animal Ecology at Iowa State University. This is Journal Paper No. J-19276 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa, Project No. 3299, and supported by Hatch Act and State of Iowa funds.

LITERATURE CITED


island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.

Table 1: Number of trajectories and mean number of locations per trajectory with mean, standard error, minimum and maximum distance moved (m) between successive locations of observed trajectories (A) and the for the 10 simulated trajectories (B). Ranges are given for the mean, standard error, minimum and maximum distance of simulated trajectories.

There were 5 foxes and 21 skunks in Litchville, 5 foxes and 16 skunks in Medina, 7 foxes and 20 skunks in Bowdon, and 9 foxes and 22 skunks in Hurdsfield.

A. Observed trajectories

<table>
<thead>
<tr>
<th>Location</th>
<th>n (trajectories)</th>
<th>(\bar{x}) (locations/trajectory)</th>
<th>(\bar{x}) distance(m)</th>
<th>SE</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litchville</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fox</td>
<td>30</td>
<td>17.8</td>
<td>261.0</td>
<td>13.3</td>
<td>0.0</td>
<td>1855.0</td>
</tr>
<tr>
<td>Skunk</td>
<td>127</td>
<td>15.6</td>
<td>155.4</td>
<td>4.0</td>
<td>0.0</td>
<td>1429.0</td>
</tr>
<tr>
<td>Medina</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fox</td>
<td>62</td>
<td>18.1</td>
<td>291.8</td>
<td>10.8</td>
<td>0.0</td>
<td>2121.0</td>
</tr>
<tr>
<td>Skunk</td>
<td>123</td>
<td>17.1</td>
<td>170.0</td>
<td>4.2</td>
<td>0.0</td>
<td>1400.8</td>
</tr>
<tr>
<td>Bowdon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fox</td>
<td>36</td>
<td>15.1</td>
<td>282.6</td>
<td>14.0</td>
<td>0.0</td>
<td>1845.6</td>
</tr>
<tr>
<td>Skunk</td>
<td>62</td>
<td>15.6</td>
<td>139.5</td>
<td>5.2</td>
<td>0.0</td>
<td>1162.4</td>
</tr>
<tr>
<td>Hurdsfield</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fox</td>
<td>44</td>
<td>16.3</td>
<td>289.4</td>
<td>11.6</td>
<td>0.0</td>
<td>2422.5</td>
</tr>
<tr>
<td>Skunk</td>
<td>124</td>
<td>16.2</td>
<td>130.8</td>
<td>3.2</td>
<td>0.0</td>
<td>1155.3</td>
</tr>
<tr>
<td>Location</td>
<td>Species</td>
<td>n (trajectories)</td>
<td>$\bar{x}$ (locations/trajectory)</td>
<td>$\bar{x}$ distance(m)</td>
<td>SE</td>
<td>Minimum</td>
</tr>
<tr>
<td>-----------</td>
<td>---------</td>
<td>------------------</td>
<td>----------------------------------</td>
<td>----------------------</td>
<td>------</td>
<td>---------</td>
</tr>
<tr>
<td>Litchville</td>
<td>Fox</td>
<td>30</td>
<td>18</td>
<td>264.8 - 297.9</td>
<td>9.4</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Skunk</td>
<td>127</td>
<td>16</td>
<td>161.6 - 172.5</td>
<td>2.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Medina</td>
<td>Fox</td>
<td>62</td>
<td>18</td>
<td>304.8 - 329.9</td>
<td>7.4</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Skunk</td>
<td>123</td>
<td>17</td>
<td>179.2 - 190.4</td>
<td>3.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Bowdon</td>
<td>Fox</td>
<td>36</td>
<td>15</td>
<td>291.0 - 313.8</td>
<td>9.9</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Skunk</td>
<td>62</td>
<td>16</td>
<td>143.6 - 156.6</td>
<td>3.6</td>
<td>0.0</td>
</tr>
<tr>
<td>Hurdsfield</td>
<td>Fox</td>
<td>44</td>
<td>16</td>
<td>291.1 - 323.4</td>
<td>9.1</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Skunk</td>
<td>124</td>
<td>16</td>
<td>139.3 - 146.0</td>
<td>2.5</td>
<td>0.0</td>
</tr>
</tbody>
</table>
Figure 1. Proportion ($p_i$) of locations for observed fox trajectories and simulated random trajectories ($n = 10$ replications) with mean, minimum and maximum simulated proportions in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).

Figure 2. Proportion ($p_i$) of locations for observed skunk trajectories and simulated random trajectories ($n = 10$ replications) with mean, minimum and maximum simulated proportions in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).

Figure 3. Density ($d_i$) of locations for observed fox trajectories and simulated random trajectories ($n = 10$ replications) with mean, minimum and maximum simulated densities in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).

Figure 4. Density ($d_i$) of locations for observed skunk trajectories and simulated random trajectories ($n = 10$ replications) with mean, minimum and maximum simulated densities in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).

Figure 5. Nonlinear regression for daily survival rates of waterfowl nests in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).
Figure 6. Proportion of nests within 50 m of a fox or skunk location for observed predator and nest locations and for simulated (n = 10 replications) random predator and nest locations with mean, minimum and maximum simulated proportions in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).

Figure 7. Proportion of nests within 50 m of a fox location for observed fox and nest locations and for simulated (n = 10 replications) random fox and nest locations with mean, minimum and maximum simulated proportions in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).

Figure 8. Proportion of nests within 50 m of a skunk location for observed skunk and nest locations and for simulated (n = 10 replications) random skunk and nest locations with mean, minimum and maximum simulated proportions in patches of planted cover of various sizes on the 4 North Dakota study areas (1996-1997).
Figure 1
Figure 2

- • observed skunk proportion > maximum random proportion
- ○ observed skunk proportion < maximum random proportion and > minimum random proportion
- ▲ observed skunk proportion < minimum proportion

- - - - mean random proportion
- - - - maximum random proportion
- - - - minimum random proportion

proportion of locations within a patch

patch size (ha)
Figure 3
observed skunk density > maximum random density
○ observed skunk density < maximum random density and > minimum random density
△ observed skunk density < minimum random density

---

Figure 4
Figure 5: Daily Survival Rate vs. Patch Size (ha) for high and low grassland composition.
Figure 6
Figure 7

- • observed proportion > maximum random proportion
- ○ observed proportion < maximum random proportion > minimum random proportion
- ▲ observed proportion < minimum random proportion
- —— mean random proportion
- - - - minimum random proportion
- - - - maximum random proportion

proportion of nests encountered by fox

patch size (ha)

1.2
1.0
0.8
0.6
0.4
0.2
0.0
2.00 3.56 6.27 7.49 9.42 14.16 15.56 17.29 23.02 28.73 36.01 49.79 52.61 56.28 68.09 76.01 163.51 192.27 238.88 340.64 605.74
Figure 8
CHAPTER 5. GENERAL CONCLUSIONS

General Discussion

The analyses of habitat selection and movement patterns by predators indicated that landscape features such as habitat heterogeneity, as well as the composition and configuration of grassland nesting habitat, can influence predator-prey spatial interactions. The observed patterns of habitat selection and movement by predators are consistent with foraging theory that predicts a higher level of selection for patches that is related to the effort expended by the predator to exploit a patch and the relative rate of return of required resources among habitat types (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976, Stephens and Krebs 1986). Although multiple (even contradictory) behavioral motivations (e.g. foraging versus risk avoidance) may have led to highly variable and complex movement patterns, predators behaved in ways that suggest they are influenced by spatial structure of profitable patches (planted cover or wetland edges) in the landscape. Spatial structure will influence movement as long as there is a perceived difference in quality of the varying habitats. Differences in movement patterns and habitat selection coupled with differences in extent of movement suggest these predators perceived the landscape in a dissimilar manner.

Wetland edges surrounded by agricultural cover types were consistently selected by both fox and skunk on both types of landscape. The composition of grassland in the landscape influenced the selection by fox for the planted cover. Foxes frequently selected the edge and interior areas of planted cover in LGC landscapes, while rarely selecting the interior areas of planted cover in HGC landscapes. Pastureland was used more frequently
by fox in HGC landscapes than in LGC landscapes and may have contributed to the low
selection of planted cover cores. Decreased fox activity in the interior of planted cover in
HGC landscapes would have decreased the opportunity to find nests. Nest success was
found to be greater in HGC landscapes than in LGC landscapes for each of the 3 landscape
features associated with planted cover: planted cover core, planted cover edge and planted
cover-wetland edge.

The analysis of movement patterns indicated that movement patterns are influenced
by habitat selection that reflects differences in resource use between predator species. Fox
pathways were slightly straighter (lower fractal dimension) in LGC landscapes as they
traveled between the more isolated patches of planted cover. Once inside a patch, foxes
exhibited more frequent obtuse turn angles (characteristic of foraging behavior). This is
consistent with foxes frequently selecting all patch features of planted cover in LGC
landscapes. In contrast to predictions, the rate of movement did not differ between planted
cover and the agricultural matrix and the frequency of turn angles was highly variable in
the agricultural matrix in both types of landscape. The agricultural matrix included
pastureland that was frequently selected by fox in HGC landscapes and may provide
resources that are attractive to foxes that elicit foraging behavior.

In contrast, skunk pathways did not differ between LGC and HGC landscapes.
They were more influenced by wetland edges than by the landscape composition of
grassland. Skunks spent more time in back and forth movement in all habitats as
evidenced by a higher frequency of turn angles that were close to 0° or 180° (characteristic
of foraging behavior). The rate of movement was faster in the agricultural matrix than in
planted cover in LGC but not HGC landscapes. As with fox, this may be influenced by the presence of pastureland in the agricultural matrix.

The edges of planted cover were not strongly selected by predators and both moved quickly across the boundary between planted cover-wetland edge and the agricultural matrix. These movement patterns would decrease the opportunity for predators to find prey close to planted cover edge. This is consistent with the lack of a strong edge effect on nest success in planted cover (Pasitschniak-Arts et al. 1998, Horn 2000) in contrast to observed edge effects in forest-field ecotones (Paton 1994, Andren 1995).

The nonlinear relationship between nest success and patch size illustrated a lower nest success in moderately size patches of approximately 55 ha. A comparison of observed predator activity and nest success to a null model of random predator activity and nest locations indicated that predator activity increased in patches approximately the same size. The increased predator activity probably reflected an increased attractiveness of these patches and created a greater opportunity for predators to find and destroy nests. For patches smaller than 50 ha, we observed lower predator activity and a higher variability among patches in the proportion of encountered nests. Some small patches are quickly searched and not likely revisited while others escape predation entirely. This is consistent with the high overall nest success and large variance among the few waterfowl in small patches. In patches larger than 120 ha, we observed both a lower predator activity and a lower proportion of encountered nests which is consistent with the high nest success with lower variance in large patches. Predator foraging efficiency may decline in large patches due to an increased search time in abundant nesting cover, a decreased foraging effort by a
few predators over a large area (dilution effect), or because large patches of planted cover are more likely located in landscapes with a high grassland composition in which attractive alternative cover types (e.g. pasture) are more commonly found.

This study has led to a better understanding of the behavioral responses of foxes and skunks to the structure of habitats in the landscape. Understanding these behaviors is crucial to determining the effectiveness of controlling the rate of predation through large scale restoration and management of waterfowl breeding habitat. These landscape modifications will influence the behavioral patterns (e.g., the selection of feeding and nesting sites, finding mates, avoiding predation) of both predator and prey. The differences in movement patterns between foxes and skunks illustrate the importance of understanding the role of the predator community in the spatial interactions between predators and prey. Predators should respond differently to changes in landscape structure depending on their unique life histories and how they perceive the landscape. However, our results suggest the responses will be governed by perceived costs or rewards associated with the structure of the landscape. Understanding the behavioral responses of predators in a dynamic prairie landscape is a key component in predicting areas of successful waterfowl breeding.

Literature Cited


