Factors affecting duck nesting in the aspen parklands : a spatial analysis
by David William Howerter

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
Habitat fragmentation often has been cited as a cause for reduced reproductive success of grassland-nesting birds, including ducks, though results of many studies have been equivocal. As remotely sensed habitat data become increasingly available, an increased understanding of how habitat configurations affect demographic parameters will allow wildlife managers to make better decisions about habitat preservation and restoration. We used duck (Anas spp.) nesting data from 15 65-km2 study areas (n ≈6300 nests) dispersed throughout the aspen (Populus tremuloides) parklands of south-central Canada, to test hypotheses and build models that predict hatching rates and nest-site distributions in relation to landscape features. We constructed separate models using landscape features generated at 3 different spatial extents and using 3 different habitat classification schemes. Generalized linear mixed-modeling techniques were used to model hatching rates, and logistic regression was used to discriminate between nest location and random points. Information-theoretic techniques were used to select the best models. Hatching rates generally increased with habitat patch size, and with distance from habitat edge and nearest wetland though relationships were complex. Several interactions improved the fit of our models. We used life-history theory and models of hatching rates to construct hypotheses about how birds should choose nest sites. The same covariates that were useful for predicting hatching rates also were useful for discriminating between nest sites and random points; however, birds did not always choose the safest habitats as nest locations. Therefore, fitness may not be maximized by nest choice. In each case, models built from landscape features generated at the smallest spatial extent had the greatest discriminatory ability; however, inclusion of variables from >1 spatial extent significantly improved our models. Finally, we demonstrate how our models can be incorporated into spatially explicit decision support tools to help guide management.. Based on our results, it is clearly important to consider spatial configurations of habitats when planning habitat management.

FACTORS AFFECTING DUCK NESTING IN THE ASPEN PARKLANDS: A SPATIAL ANALYSIS

by

David William Howerter

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

January 2003

APPROVAL

of a dissertation submitted by

David William Howerter

This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Dr. Jay J. Rotella, Committee Chair ______________________ 1/13/03
Date

Approved for the Department of Ecology

Dr. Jay J. Rotella, Department Head ______________________ 1/13/03
Date

Approved for the College of Graduate Studies

Dr. Bruce McLeod, Graduate Dean ______________________ 1-13-03
Date

STATEMENT OF PERMISSION TO USE

In presenting this dissertation in partial fulfillment of the requirements for a doctoral degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library. I further agree that copying of this dissertation is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for extensive copying or reproduction of this dissertation should be referred to Bell & Howell Information and Learning, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom I have granted "the exclusive right to reproduce and distribute my dissertation in and from microform along with the non-exclusive right to reproduce and distribute my abstract in any format in whole or in part."

Signature ____________________

Date 10 January 03

ACKNOWLEDGEMENTS

Many people had a hand in shaping this research and, as such, deserve much of the credit. All blame, however, for misinterpretations or inaccuracies shall remain mine alone. I would like to begin by thanking the other members of the 'Assessment Team'. Jim Devries, Bob Emery, and Brian Joynt all did some heavy lifting on this project, and I'd like to thank them for their diligence, friendship and encouragement throughout. Llwellyn Armstrong provided invaluable statistical advise—always dispensed with a dose of good humor. In addition to Team members, over 150 field technicians collected the data used for this project, and I'd like to thank each of them for the long hours they toiled, especially, Doug Shaw and Glenn Mack, who led research crews.

My Graduate Committee always was ready to offer sage advise, and for that I offer thanks to Dan Goodman, Andy Hansen, and Bill Quimby. Special thanks needs to go to Mike Anderson for his scientific guidance, his generous logistical and moral support, and persistent encouragement. Jay Rotella, my Graduate Advisor, demonstrated tremendous patience and an unwavering drive for scientific excellence and for that I am grateful. Steve Cherry generously provided additional statistical counsel.

Funding and/or logistical support for this project was provided by Ducks Unlimited Canada, Ducks Unlimited, Inc., the Canadian Wildlife Service, the National Fish and Wildlife Foundation, and the North American Wetlands Conservation Council through the Institute for Wetland and Waterfowl Research.

Finally, I'd like to thank my wife and best friend, Jackie, whose love, support, and boundless patience were constant sources of inspiration.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

ABSTRACT

Habitat fragmentation often has been cited as a cause for reduced reproductive success of grassland-nesting birds, including ducks, though results of many studies have been equivocal. As remotely sensed habitat data become increasingly available, an increased understanding of how habitat configurations affect demographic parameters will allow wildlife managers to make better decisions about habitat preservation and restoration. We used duck (*Anas* spp.) nesting data from 15 65-km^2 study areas ($n \approx 6300$ nests) dispersed throughout the aspen (*Populus tremuloides*) parklands of south-central Canada, to test hypotheses and build models that predict hatching rates and nest-site distributions in relation to landscape features. We constructed separate models using landscape features generated at 3 different spatial extents and using 3 different habitat classification schemes. Generalized linear mixed-modeling techniques were used to model hatching rates, and logistic regression was used to discriminate between nest location and random points. Information-theoretic techniques were used to select the best models. Hatching rates generally increased with habitat patch size, and with distance from habitat edge and nearest wetland though relationships were complex. Several interactions improved the fit of our models. We used life-history theory and models of hatching rates to construct hypotheses about how birds should choose nest sites. The same covariates that were useful for predicting hatching rates also were useful for discriminating between nest sites and random points; however, birds did not always choose the safest habitats as nest locations. Therefore, fitness may not be maximized by nest choice. In each case, models built from landscape features generated at the smallest spatial extent had the greatest discriminatory ability; however, inclusion of variables from >1 spatial extent significantly improved our models. Finally, we demonstrate how our models can be incorporated into spatially explicit decision support tools to help guide management. Based on our results, it is clearly important to consider spatial configurations of habitats when planning habitat management.

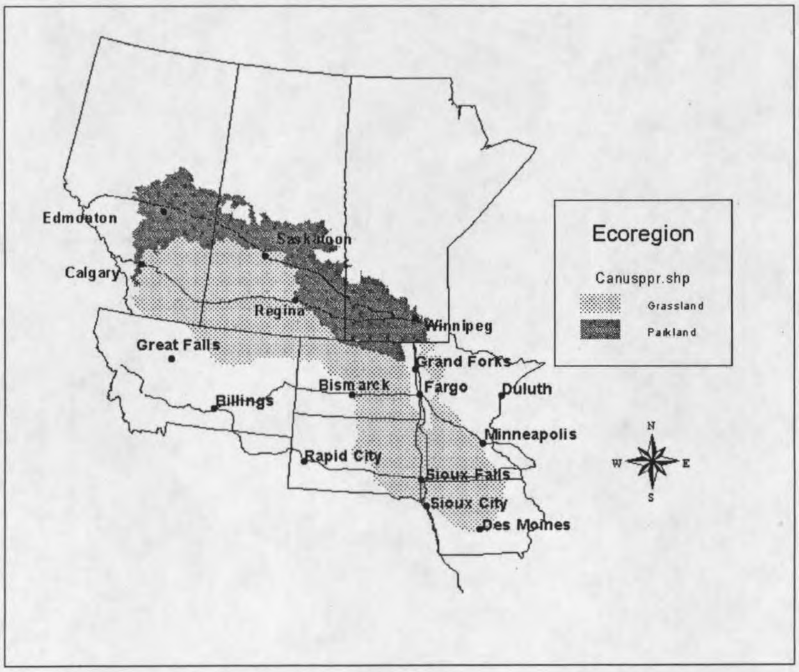
CHAPTER 1.

INTRODUCTION TO DISSERTATION

The Prairie Pothole Region (PPR) of southcentral Canada and the northcentral United States encompasses an area of 768,000 km^2 and historically has been the most productive area for breeding ducks on the continent (Batt et al. 1989). Melting subterranean ice, stranded as the Wisconsin glacier retreated northward, resulted in thousands of depressions (potholes) that fill to varying degrees, depending on annual climatic conditions with either groundwater or precipitation runoff (Kantrud et al. 1989, Pielou 1991). Because these potholes typically are shallow and overlay fertile glacial drift, they warm quickly in spring and provide a flush of aquatic invertebrates rich in proteins, lipids, and calcium needed by breeding ducks for egg production (Batt et al. 1989, Krapu and Duebbert 1989).

Uplands in the PPR historically ranged from the tallgrass prairie in Iowa to the fescue grasslands of southeastern Alberta. Forming the northern extent of the PPR is an area of transition between grassland and boreal forest referred to as the aspen (*Populus tremuloides*) parklands (Figure 1.1). Major forces shaping the ecology of the region prior to settlement included grazing by herbivores (especially bison [*Bison bison*]), fire, and periodic drought. Since the 1870's, however, grazing and fire have largely been replaced by agricultural activities. Fire, while still present in the parklands, most often occurs as small, low-intensity burns designed to control weeds along crop field margins. These low-intensity fires typically are insufficient to kill woody vegetation. As a result, woody species (especially aspen) have expanded within the parklands, potentially increasing perch and nesting sites for a number of avian species including known predators of ducks (e.g., red-tailed hawk [*Buteo jamaicensis*], great horned owl [*Bubo virginianus*]) or duck eggs (e.g., American crow [*Corvus brachyrhynchos*]). Large ungulates (cattle) still graze portions of the region, but several studies have documented that grazing by cattle is qualitatively different than grazing by bison; one of the most significant differences is that cattle tend to concentrate grazing around wetlands to a much greater extent than do bison (Hamilton 1996, Biondini et al. 1999, Knapp et al 1999). By far, the largest impact on upland vegetation, however, has been the conversion of native vegetation to annual crop fields. As little as 20 percent of native parkland vegetation remains (Sugden and Beyersbergen 1984, Turner et al. 1987), mostly in small fragments along wetland edges, road and railroad rights-of way, fencelines or in isolated patches.

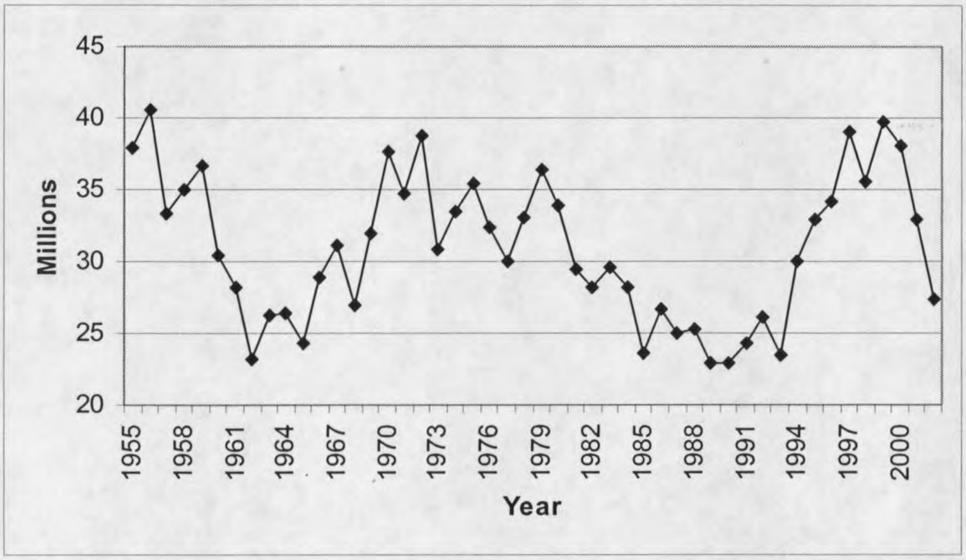
Figure 1.1. Map of Prairie Pothole Region indicating grassland and parkland ecoregions.



These changes to the landscape and human persecution also have engendered shifts in the community of mammalian predators (Sargeant et al. 1993). Gray wolves (*Canis lupus*) have largely been extirpated throughout the region, while other mammalian predators have greatly expanded (e.g., red foxes [*Vulpes vulpes*], raccoon [*Procyon lotor*]). Many of the predators that have increased are efficient predators of ducks or duck eggs (Johnson et al. 1989).

Duck populations are strongly influenced by hatching rates of nests (Johnson et al. 1987, Hoekman et al. 2002). Simultaneous changes to the configuration of habitats and predator populations have led several authors to hypothesize that the loss and fragmenation of natural parkland habitats has resulted in reduced reproductive success of many upland-nesting duck species (Clark and Nudds 1991, Beauchamp et al. 1996).. In 1985, continental duck populations had declined substantially from levels seen in the previous decade (Figure 1.2). As a result, the governments of the United States and Canada endorsed the strategy of habitat restoration and protection contained within the North American Waterfowl Management Plan (NAWMP; Mexico became a signatory to the agreement in 1994). To accomplish NAWMP goals a number of partnerships (joint ventures) among conservation organizations, government agencies, corporations, and individuals were formed. The largest of these joint ventures is the Prairie Habitat Joint Venture (PHJV), which targets the prairie pothole region of southern Canada. A variety of habitat programs have been sponsored by the PHJV, including programs that replace annual crop fields with mixtures of legumes and grasses and programs that provide financial incentives to landowners to modify agricultural practices to benefit wildlife (e.g., rest-rotational grazing systems). Most habitat programs were designed to address the main tenet that the reduction and fragmentation of upland habitats has resulted in depressed hatching rates of ducks. Because parkland habitats are less susceptible to drought than more southern grassland regions of the PPR, most PHJV habitat programs were delivered within the parklands—plan implementers reasoned that benefits would accrue more rapidly where wetlands, and therefore, duck populations were more stable.

Figure 1.2 Continental duck populations as estimated by the May Breeding Waterfowl and Habitat Survey (U.S. Fish and Wildlife Service 2002)



Following a framework of adaptive resource management (ARM, Walters and Holling 1990), the PHJV Assessment project evaluated the effectiveness of PHJV habitat programs by measuring a number of duck population vital rates. Two, however, are key to understanding whether PHJV habitat programs are meeting their objectives: (1) for PHJV habitat programs to be successful, they must provide habitat for nesting ducks that is safer than surrounding habitats, and (2) they must be attractive to nesting ducks, otherwise, even if they are relatively safe, birds will not select them as nesting habitat.

This study, done as part of the PHJV Assessment, directly addresses these key uncertainties. The data available, due to their broad spatial and temporal extent, provide an outstanding opportunity to test a number of hypotheses about how landscape features affect nesting ducks—the locations of their nests, and probability of hatching. The results provide valuable new information about how the spatial patterning of habitats affect waterfowl production, which is interesting from both evolutionary and landscape ecology perspectives while providing practical guidance to land mangers.

Dissertation organization

Chapter 2 evaluates a variety of competing hypotheses about how landscape features affect hatching rates of duck nests. Chapter 3 builds on patterns observed in Chapter 2, by hypothesizing that high predation rates on nests has provided directional selective pressure on ducks to choose safe nest sites. We used patterns in hatching rates observed in Chapter 2 to predict which factors would affect mallard nest locations. Chapter 4 encapsulates the findings of the previous chapters and demonstrates how models of nest-site selection and hatching rates can be incorporated into a spatially explicit decision support tool for projecting the effects of habitat manipulations or continued loss and fragmentation of habitats on duck production. Recurring themes throughout the dissertation are the effects that different habitat classification schemes and scales of observation have on the selection of appropriate models and, hence, the inferences that are drawn from them. Because this study was conducted as a portion of the PHJV Assessment, many people contributed to this effort. Accordingly, the text throughout is written in third person in anticipation of a number of coauthors in submitted journal articles.

Literature Cited

Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. Pages 204-227 *in* A. Van Der Valk, editor. Northern prairie wetlands. Iowa State University Press, Ames, Iowa.

Beauchamp, W. D., R. R. Koford, T. D. Nudds, R. G. Clark, and D. H. Johnson. 1996. Long term declines in nest success of prairie ducks. Journal of Wildlife Management. 60:247-257.

Biondini, M. E., A. A. Steuter, and R. G. Hamilton. 1999. Bison use of fire-managed prairies. Journal of Range Management 52:454-461.

Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. Wildlife Society Bulletin 19:534-543.

Hamilton, R. G. 1996. Using fire and bison to restore a functional tallgrass prairie landscape. Transactions of the North American Wildlife and Natural Resources conference 61:208-214.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analysis of the life cycle of mid-continent mallards. Journal of Wildlife Management 66:883-900.

Johnson, D. H., A. B. Sargeant, and R.J. Greenwood. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. Canadian Journal of Zoology 67:291-297.

Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish and Wildlife Service, Biological Report 85.

Krapu, G. L., and H. F. Duebbert. 1989. Prairie wetlands: characteristics, importance to waterfowl, and status. Pages 811-828 *in* R. R. Sharitz and J. W. Gibbons, eds. Freshwater wetlands and wildlife. U.S. Dept. of Energy Symposium Series 61.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. Bioscience 49:39-50.

Pielou, E. C. 1991. After the ice age: the return of life to glaciated North America. University of Chicago Press, Chicago, Illinois. 366pp.

Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and T. L. Shaffer. 1993. Distribution and abundance of predators that affect duck production—prairie pothole region. U.S. Fish and Wildlife Service Resource Publication 194.

Sugden, L. G., and G. W. Beyersbergen. 1984. Farming intensity on waterfowl breeding grounds in Saskatchewan parklands. Wildlife Society Bulletin 12:22-26.

Turner, B. C., G. S. Hochbaum, F. D. Caswell, and D. J. Nieman. 1987. Agricultural impacts on wetland habitats on the Canadian Prairies, 1981-1985. Transactions of the North American Wildlife and Natural Resources Conference 52:206-215.

U.S. Fish and Wildlife Service. 2002. Waterfowl population status, 2002. U.S. Department of the Interior, Washington, D.C. 51pp.

Walters, C. J., and C. S. Holling. 1990. Large-scale mangement experiments and learning by doing. Ecology 71:2060-2068.

CHAPTER 2.

SPATIAL FACTORS AFFECTING DUCK HATCHING RATES: EFFECTS OF FRAGMENTATION, HABITAT CLASSIFICATION AND SCALE

Introduction

The glaciated prairie-pothole region of south-central Canada has historically been the most productive area for nesting ducks in North America. However, large-scale expansion of agriculture has substantially altered natural vegetation types and disturbance regimes. Since settlement by (primarily) European immigrants began in the late 1870's, as much as 80% of the pre-settlement prairie has been converted to agricultural uses in Canada (Samson and Knopf 1994), while conversion in the aspen (*Populus tremuloides)* parklands that form the transition between prairie and boreal forest has been even more extensive (Sugden and Beyersbergen 1984, Turner et al. 1987). Concurrently, the compositions and abundances of predator populations have changed substantially (Sargeant et al. 1993). Predators that previously were widespread and common throughout the region such as gray wolves (*Canis lupus)* have declined or been eliminated, while populations of other predators such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and raccoons (*Procyon lotor*) have benefited from anthropogenic changes to the landscape (Sargeant et al. 1993). Each of the predator species that have profited from increased agriculture commonly preys on ducks or duck eggs.

Parkland-nesting ducks generally have short life spans. Life-history theory predicts that the population dynamics of short-lived species will be sensitive to changes in reproductive success (Lebreton and Clobert 1991, Stearns 1992, Sæther and Bakke 2000). This is consistent with the observation that the dynamics of mid-continent duck populations are strongly influenced by the hatching rates of nests (Cowardin et al. 1985, Johnson et al. 1987, Hoekman et al. 2002). Therefore, if the profound changes to the landscapes and predator populations that have occurred indeed reduce reproductive fecundity, then they are likely to have strong negative impacts on duck populations.

Several authors have suggested that habitat loss and fragmentation have resulted in duck nests being concentrated in typically small or linear patches of remaining natural covers (Clark and Nudds 1991, Beauchamp et al. 1996a, 1996b). The medium-sized mammalian nest predators that now dominate the predator community may search remnant patches of habitat efficiently. Thus, knowledge of the coincident changes to the predator community and habitat configurations leads to the prediction that mortality of duck nests has increased.

In contrast, emerging theory from the field of landscape ecology predicts that duck hatching rates may be relatively insensitive to habitat fragmentation in the parklands because duck species have high fecundity, are highly mobile and abundant, are migratory, and will nest both near habitat edges and in the interior of habitat patches. These are all autecological traits that have been suggested as leading to low vulnerability to fragmentation (Andren 1994, Noss and Csuti 1994, Bender et al. 1998, Davies et al.

2000). Furthermore, the most likely consequences of fragmentation on hatching rates of ducks would be those related to edge effects that result from increased foraging by predators near habitat edges.

In recent years, studies of other avian taxa have demonstrated that explicitly including information about the spatial arrangement of habitat features can improve predictive models of hatching rates (Andren 1995, Donovan et al. 1997, Clark et al. 1999). However, few attempts have been made to include spatial features in models of waterfowl hatching rates. Most studies of factors that affect hatching rates have ignored spatial variability or considered it a nuisance factor to be partitioned from datasets. The results of studies that have included spatial factors have been somewhat equivocal (Greenwood 1995, Pasitschniak-Arts and Messier 1995, 1996, Pasitschniak-Arts et al. 1998, Horn 2000, Sovada et al. 2000, Reynolds et al. 2001). Greenwood et al. (1995), studying duck hatching rates in southcentral Canada, found an inverse linear relationship between hatching rates and the amount of cropland on prairie sites. On parkland sites, however, the same relationship was apparent for only 1 of 5 species. Similarly, Miller (2000) found the amount of cropped land to be an important predictor of mallard (*Anas platyrhynchos*) production in 4 of 5 Canadian prairie strata, but only 2 of the 9 parkland strata he examined. Thus, questions remain about the degree to which landscape configurations affect duck reproductive success in the parklands.

Information about the relationships between landscape features and hatching rates are useful for advancing basic knowledge about system functions and also important to applied science. Because hatching rates are important to the population dynamics of mid-continent duck populations, conservation agencies working under the auspices of the North American Waterfowl Management Plan's Prairie Habitat Joint Venture (PHJV; Anonymous 1986, 1994) attempt to bolster hatching rates by preserving remaining natural habitats, restoring habitats that have been converted to agricultural uses, and providing incentives to landowners to adopt wildlife-friendly agriculture practices. These efforts have largely concentrated on parkland areas; however, uncertainty remains about whether this effort will be sufficient to increase duck production. If hatching rates are not closely related to landscape configurations, other management options may be required. A clearer understanding of the relationships between landscape attributes and hatching rates will allow managers to make better decisions about habitat expenditures.

To improve our understanding of how landscape attributes affect duck productivity, we designed a broad-scale, multi-year study that measured hatching rates of upland-nesting ducks across a wide range of conditions. The objectives of our study were to (1) determine which factors were most important for predicting hatching rates of upland-nesting ducks, and (2) evaluate how sensitive predictive models of hatching rates models were to changes in (a) habitat classification, and (b) spatial scale. This study was conducted as a portion of the PHJV Assessment Program designed to evaluate the effectiveness of PHJV habitat initiatives.

Hypotheses and Predictions

To expand on existing knowledge, we sought answers to a series of questions about how the spatial arrangement of habitat features affects duck hatching rates using a large sample (>6,000) of nests collected over a wide geographic range. In the following sections, we (1) review the pertinent literature, (2) present each question that we posed, and (3) outline our specific predictions regarding answers to these questions.

Spatial Habitat Features

Researchers have suggested that a number of spatial landscape attributes affect the hatching rates of bird nests. One of the most commonly investigated spatial features is the distance from a nest to a habitat edge or discontinuity in vegetation types (Lahti 2001). Habitat edges are thought to negatively impact nesting birds in a number of ways (Fagan et al. 1999). Nest predation rates may be higher near edges because prey populations and, therefore, predator foraging activities are concentrated there (Chalfoun et al. 2002). Also, edges may be dangerous simply because predators may use them as travel corridors (Andren 1995, Fagan 1999, Lahti 2001) and incidentally find nests located near edges more frequently than those farther away.

Empirical evidence for edge effects on hatching rates of prairie-nesting waterfowl has been equivocal. Pasitshniak-Arts and Messier (1995, 1996) documented increased predation near habitat edges using artificial duck nests but found no edge effect (Pasitshniak-Arts et al. 1998) in an experiment using a limited sample (n = 199) of real