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.

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APPROVAL

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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.

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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.

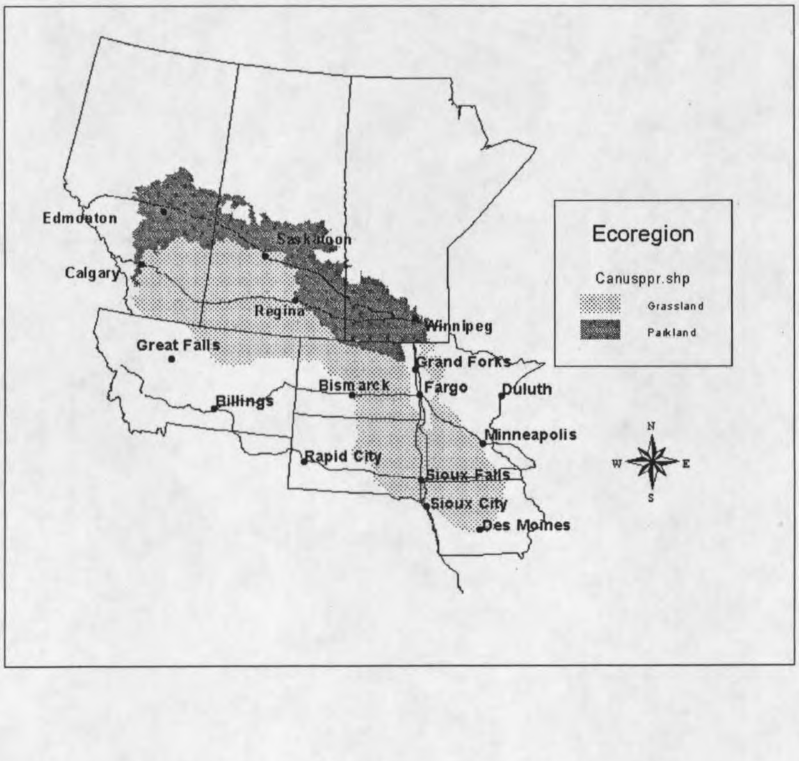
CHAPTER 1.

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.

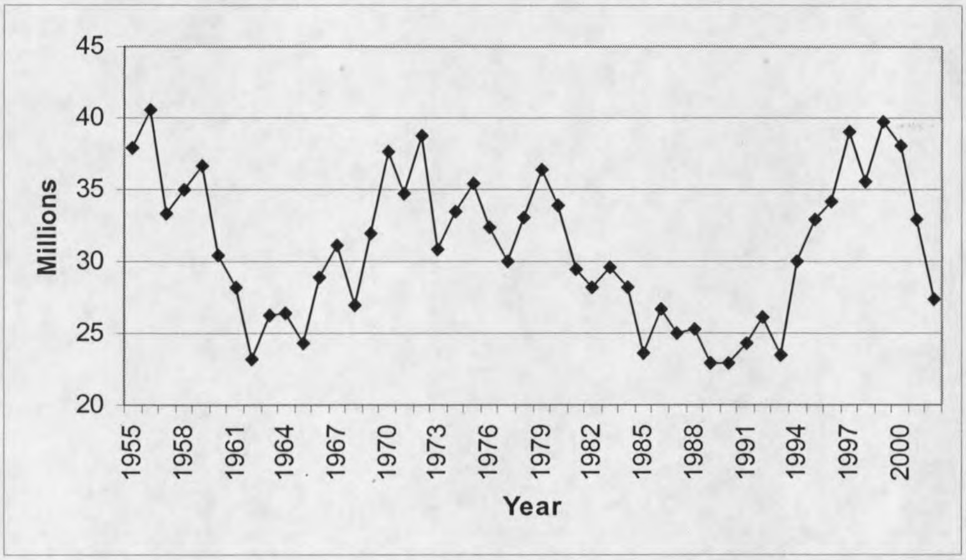
Figure 1.1. Map of Prairie Pothole Region indicating grassland and parkland ecoregions.



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 fragmentation 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.

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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 duck nests. Such discrepancies may occur because artificial duck nests have been shown to generally be poor predictors of hatching rates (Butler and Rotella 1998). Clark and Shutler (1999) documented edge effects in only 2 of 5 species of ducks they studied, and hatching rates were higher near edges for one species (Gadwall, *Anas strepera*) and lower for the other (Blue-winged teal, *Anas discors*). Given the relative paucity of spatial data for nesting ducks and the lack of generality for edge effects in nesting birds (Lahti 2001), especially based on studies of real nests, we asked whether edge effects were apparent in our dataset and cautiously predicted that hatching rates would increase with distance from a habitat edge. Similarly, we predicted that hatching rates would be lower in landscapes that had high densities of habitat edges.

In addition to altering the amount of edge, conversion of natural habitats to crop fields also reduces the sizes of remaining patches of natural vegetation. Duck nests in small patches of remaining cover may experience high rates of predation as has been documented in some studies of other avian taxa (e.g., Clark et al 1999). To date, results of investigations of patch-size effects on duck hatching rates have been inconsistent. Two studies conducted in the Dakotas (Horn 2000, Sovada et al. 2000) found elevated hatching rates in large patches of perennial cover, whereas a Saskatchewan study (Pasitshniak-Arts and Messier 1996) found no relationship between predation rate on artificial duck nests and patch size. Results of previous studies may be inconsistent because of process variation or differences in study design. Further, some studies may have failed to detect important effects due to (1) sampling error associated with modest sample sizes, (2) use of a narrow range of patch sizes (see comments by Clark and Nudds 1991), and/or (3) use of artificial nests, which may not adequately indicate patterns for real nests. Here, we asked whether hatching rate was related to patch size using a large sample of real nests monitored in patches of perennial cover ranging in size from 60 m^2 to nearly 29 km^2 (Table 2.1, 2-habitat classification). We predicted that hatching rates would be positively related to the size of the habitat patch.

Table 2.1. Range of selected spatial covariates for 15 study sites in the parklands of south-central Canada under different habitat classifications

	8-Habitat	4-Habitat	2-Habitat
AREA (ha)[a]	0.0012 - 793	0.0060-2582	.0060-2880
HDIST (m)	0-220	0-389	0-389
SHAPE	1.02-37.15	1.24-26.90	1.24-25.36

[a]Variables are defined in Table 2.3

Because edge effects and patch size effects both may be related to predator foraging activity in the vicinity of habitat edges, a metric that combines these measures may provide more information than either individual metric. For example, a railroad right-of-way may be quite large but consist entirely of habitat that is within a few meters of a habitat edge. As such, we considered a shape index that scales the size of the habitat patch by the length of its perimeter or edge (McGarigal and Marks 1993). Such a ratio has proven useful in predicting habitat patch occupancy rates for a number of grassland bird species (Helzer and Jelinski 1999). We asked whether hatching rate was related to the perimeter-to-area ratio and predicted that hatching rates would decline as the ratio of perimeter-to-area increased.

Predator Activity Centers

Agriculture does not only causes habitat loss and fragmentation. Anthropogenic changes to landscapes also can alter spatial distributions of nest predators. For example, farm activities have added numerous buildings to the parkland environment, which may affect distributions of striped skunks. Skunks, which are important nest predators, use buildings within both active and abandoned farmsteads as winter and maternal dens (Lariviere and Messier 1998, Lariviere et al. 1999). When females have kits, the distance they are able to forage away from their dens may be restricted by their need to return regularly to dens to nurse. Given that buildings may be used as centers of activity, we asked whether nest-predation rate was related to the distance a nest was from a farmstead or building, and predicted that hatching rates would be reduced near farmsteads.

Similarly, we predicted that hatching rates would increase with distance from a wetland. It could be argued that this really is a type of edge effect; however, we expected effects between wetlands and upland habitats to be qualitatively different than edge effects between adjacent upland habitats. Wetlands in the parklands are very productive (Murkin 1989) and hence, are likely to be profitable foraging areas for a number of mammalian predators that also prey on duck eggs. This prediction was supported by evidence of increased foraging activity near wetland margins by both striped skunks and red foxes (Greenwood et al. 1999, Lariviere and Messier 2000, Phillips 2001).

To summarize, our primary focus with this study was to determine if landscape configurations affect hatching rates of ducks in the parklands. In exploring these questions we posed, we also considered the ramifications of (1) using different habitat classification schemes, and (2) observing the system at different scales (see Methods).

Methods

Study Areas

Nest and landscape information was collected at 15 sites throughout the aspen (*Populus tremuloides*) parklands of Manitoba, Saskatchewan, and Alberta, Canada (Figure 2.1) from 1993-1997. In 1993 the Hamiota, MB and Punnichy, SK sites were 78 and 54 km^2, respectively. The remaining 13 sites were 65 km^2. Each site was monitored for 1 year.

The topography at all sites was flat to gently rolling. Dominant agricultural practices included cereal- and oil-seed production and livestock grazing. The study sites attracted large numbers of breeding ducks--typically between 10-50 breeding pairs per km^2. Despite these similarities, the 15 sites encompassed a broad range of landscape conditions, with varying degrees of fragmentation (Table 2.2, Appendix A1).

Figure 2.1. Map showing locations of 15 study sites in the parklands of south-central Canada

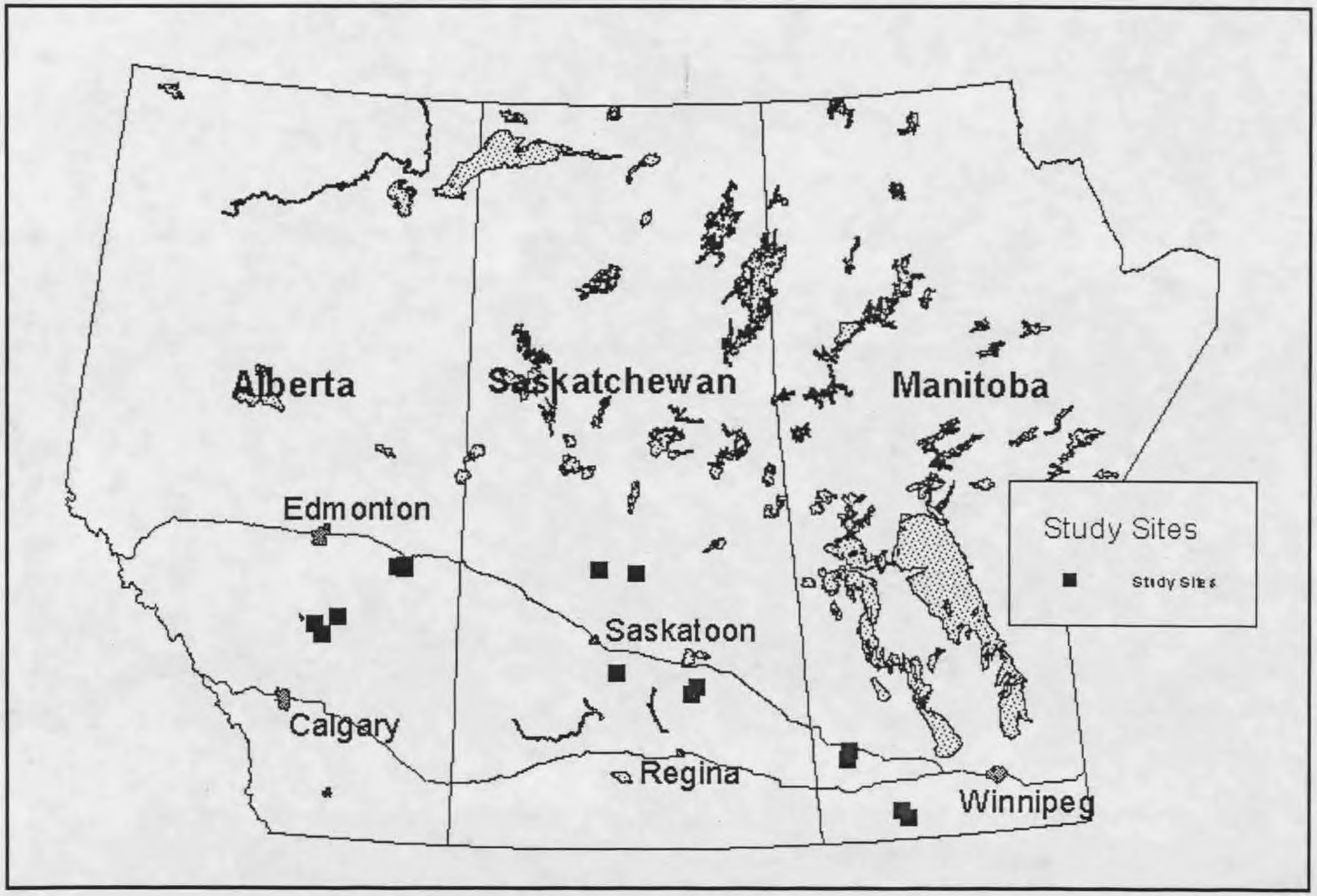


Table 2.2 Locations and habitat compositions for 15 sites studied from 1993-1997 in south-central Canada

					Wetland Density (#/km^2)										
Study Site	Province	Year	Latitude	Longitude	II[a]	III[a]	IV[a]	Total	%Crop	%Hay	%Planted	%Grass	%Trees	%Shrub	%Wetland
Hamiota	MB	1993	50.28	-100.75	0.7	12.6	0.6	13.9	77.5	0.5	0.0	3.0	4.4	3.6	9.1
Punnichy	SK	1993	51.35	-104.38	2.9	21.5	4.2	28.6	64.5	1.1	4.5	9.0	8.3	2.1	9.4
Belmont	MB	1994	49.45	-99.53	6.9	7.8	7.2	21.9	39.8	8.3	0.8	17.2	5.9	8.3	17.4
Davis	SK	1994	53.18	-105.68	1.2	13.4	7.9	22.5	47.2	8.7	2.9	11.3	5.9	6.2	15.3
Erskine	AB	1994	52.35	-112.98	5.3	12.5	6.4	24.2	34.6	6.1	0.0	34.0	4.4	4.2	14.2
Shoal Lake	MB	1995	50.40	-100.67	5.2	17.6	3.1	25.9	40.7	0.8	0.0	8.0	5.1	7.5	36.8
Kutawa	SK	1995	51.45	-104.23	1.0	22.0	4.4	27.4	57.2	2.6	0.0	14.6	6.4	2.8	15.0
Camp Lake	AB	1995	53.17	-111.60	6.0	24.1	7.2	37.3	42.0	2.0	6.4	24.9	6.7	6.1	10.6
Baldur	MB	1996	49.45	-99.37	2.6	3.1	4.2	9.9	29.0	6.0	6.8	16.9	16.2	2.7	20.7
Parkside	SK	1996	53.20	-106.60	0.3	4.9	2.6	7.8	58.3	8.8	0.4	13.1	7.3	0.9	8.5
Pine Lake	AB	1996	52.22	-113.47	4.5	24.3	5.6	34.4	20.3	9.4	0.0	36.0	16.6	3.0	13.0
Willowbrook	SK	1997	51.25	-102.95	6.3	18.3	5.3	29.9	53.2	5.3	2.2	12.2	8.6	5.6	11.3
Allan Hills W.	SK	1997	51.68	-106.12	1.1	9.5	8.7	19.3	51.3	1.3	17.7	10.1	1.5	3.3	13.9
Mixburn	AB	1997	53.17	-111.43	7.4	32.3	17.4	57.1	45.8	5.3	6.2	15.9	3.5	6.5	16.2
Elnora	AB	1997	52.07	-113.30	8.7	22.9	3.0	34.6	9.4	6.7	0.0	43.5	19.8	7.1	11.8

Habitat Classification

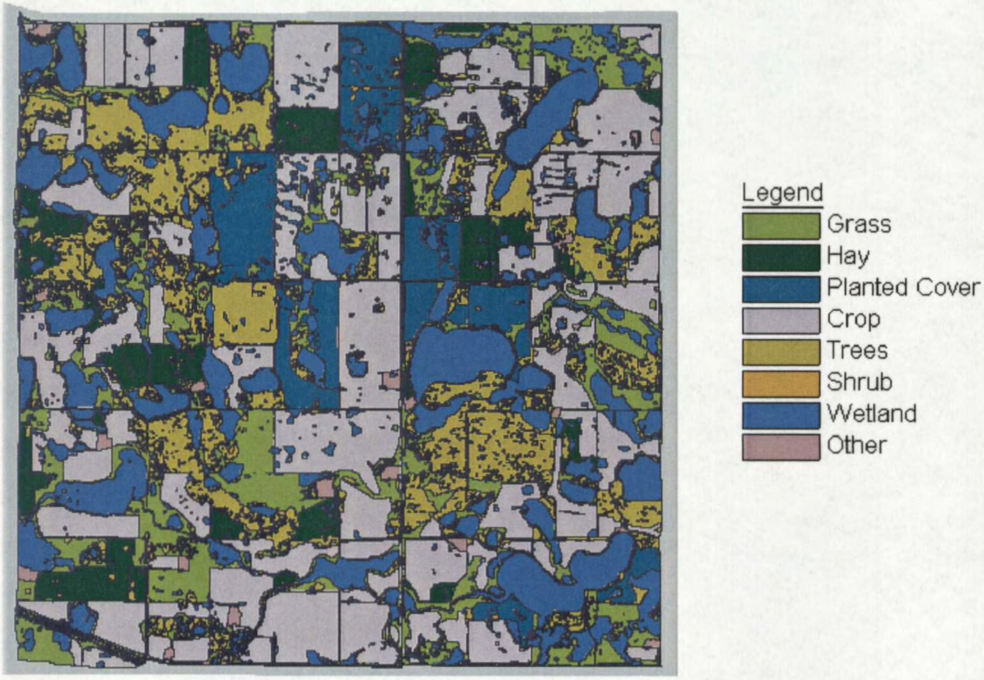
Before we were able to address the questions we posed about the effects of landscape attributes on hatching rates, we needed to consider how to classify habitats. While often not acknowledged in studies that relate landscape measures to population processes, the system of classifying habitats—thereby defining what constitutes a habitat patch—has profound effects on the values of common landscape metrics. An example of these effects is presented graphically in Figure 2.2 and quantitatively in Table 2.1 and Appendix A1. Thus, the answers to questions posed about the effects of spatial attributes may vary dramatically depending on the habitat classification scheme. Further, because we wish to use models resulting from this analysis to guide management actions throughout the aspen parklands, the classification scheme used for habitats has important practical implications; specifically, acquiring data with a more simple classification tends to be less costly and more error free. Thus, we compared model predictions using 3 different habitat classifications: an 8-habitat classification based on a combination of vegetation physiognomy and land use; a 4-habitat classification based on land use; and a 2-habitat classification that separates cropped land from all other potential nest habitat types.

Scale

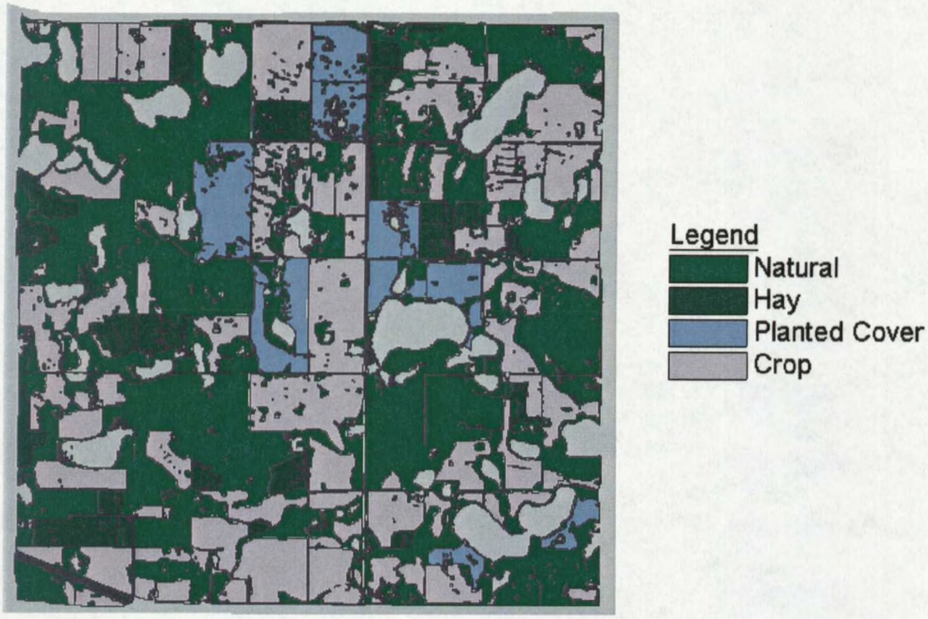
The scale of observation used also affects patterns of landscape structure and thus, is important to consider when studying spatial patterning of a species' vital rates (Wiens 1989). Therefore, researchers must carefully consider what scale is appropriate for collecting data. Several authors have suggested conducting studies at an 'organism-centered' scale that mimics the typical range of movements experienced by the focal species (Wiens 1989, Mac Nally 1999, McGarigal and Cushman 2002). Hence, in addition to considering patch attributes, we also measured habitat attributes at a scale thought to be representative of the home range of nesting mallard females (10.36 km^2, Cowardin et al. 1985).

Figure 2.2. Map of the Baldur, Manitoba study site demonstrating effect of 3 different habitat classification schemes on landscape metrics; (A) 8-habitat, (B) 4-habitat, and (C) 2-habitat.

(A.)



(B.)



(C.)

It also is important to consider the scale at which resulting models are likely to be applied. Ideally, the scale at which we study a system should match the scale at which we wish to apply our results to management decisions (Morrison et al. 1998). In the parklands, most land-use decisions are made at the quarter-section scale (0.65 km^2) both for private landowners and conservation agencies. Therefore, for practical reasons 0.65 km^2 was a logical scale at which to examine impacts of landscape configurations on patterns of hatching rates. Prior to analyzing nesting data at this scale, however, we wanted to confirm that land-use decisions made at this scale resulted in measurable differences in landscape patterning.

A number of statistical techniques have been developed to determine when the numerical behavior of a system changes as the scale of observation changes (Wiens 1989). One method that is increasingly used is lacunarity analysis (Plotnick et al. 1993, Elkie and Rempel 2001), which compares the variance-to-mean ratio of samples to the Poisson expectation over a range of moving-window sizes. By examining a ln-ln plot of lacunarity relative to window size, scales at which habitats are 'clumped' (deviate from random) are detectable (Plotnick et al. 1993). We performed a preliminary lacunarity analysis on a sample of our study sites (Ducks Unlimited Canada, unpublished data) and, thereby, confirmed that patterns in landscape structure were related to the quarter-section scale. Therefore, our confidence that this was a suitable scale for investigation increased and we examined the effects of landscape pattern on hatching rates at the 0.65 km^2 scale.

Finally, there is increasing empirical evidence that fragmentation effects observed at a local scale may be context-specific (i.e., local effects may depend on characteristics of the surrounding landscape; Donovan et al. 1997). Landscape features at multiple scales may simultaneously affect the behavior of the system being observed. For example, characteristics of the vegetation immediately surrounding a nest site may influence whether or not an individual predator detects the nest, but attributes of the surrounding landscape may influence the distributions of nest predators. Phillips (2001) provided evidence that this may occur in prairie landscapes by documenting that the likelihood of red foxes foraging within the center of planted cover fields depended on the total amount of perennial cover in the surrounding landscape. Accordingly, we felt it important to contrast predictive models generated from landscape metrics at a variety of spatial extents.

Data Collection

Locating and monitoring nests. We searched for nests using vehicle-pulled cable-chain drags, by walking and dragging a rope between 2 observers, or by walking while striking the vegetation with willow switches (Klett et al. 1986). We searched all parcels on which PHJV habitat programs had been implemented and an additional sample of 11-58 randomly selected quarter sections at each site. The number of randomly selected quarter sections that we were able to search depended on (1) the number of PHJV habitat parcels that were on the study site, (2) the number of duck nests we encountered, and (3) the amount of cover that required searching on each quarter section. Within selected quarter sections, we searched all upland habitats except growing crop fields (crop stubble was searched early in the growing season) and tree-covered areas. Three searches, spaced approximately 21 days apart, were performed at each site. Once a nest was located, we revisited it at 7-10 day intervals (until it failed or hatched) to monitor its status and to determine its fate. Only nests laid by ducks from the genus *Anas* and lesser scaup (*Aythya affinis*), the only common upland-nesting ducks in the parkland region, were included in these analyses.

An additional sample of nests was located by tracking 111-137 radio-tagged female mallards at each site. Pre-laying mallards were decoy-trapped (Sharp and Lokemoen 1987, Ringelman 1990) and radio-marked in April. From 1993-1995 we outfitted each female with either an abdominally implanted transmitter (Korschgen et al 1984, Olsen et al. 1992, Rotella et al. 1993) or a transmitter attached to the back with an anchor and suture (Mauser and Jarvis 1991, Paquette et al. 1997). In 1996 and 1997 only abdominally implanted transmitters were used as we became concerned about the utility of using back-mounted transmitters for studying duckling survival (IWWR, unpublished data). Following radio attachment, mallards were released back onto the wetland where they were caught.

We used a vehicle-mounted null-array receiving system to estimate the location of each radiomarked female twice daily between 0600 and 1300 hours, i.e., the hours when they were most likely to be attending their nests (Glouteny et al. 1993). We approached females using handheld antennas when daily telemetry locations placed them near the same spot in nesting cover for 3 consecutive mornings. Prior to 31 May 1994, we intentionally flushed females and then located their nests. To cause less disturbance to females and, hence, reduce nest abandonment, after 31 May 1994 we estimated the female's location using a hand-held antenna and triangulation, recorded the estimated location, and then left the area without flushing the bird. We returned in the afternoon to search for the nest at a time when females typically were away from nests. Subsequently, if a female was absent from her nest for 2 consecutive morning telemetry locations, we returned to the nest to determine its fate. We visited the nests of radio-marked females one more time (when the nest was about 18 days old) to determine the final number of eggs in the clutch. This allowed us to estimate the date on which the nest would hatch.

For all nests, we candled ≥1 egg/nest to estimate its stage of laying/incubation (Weller 1956). To estimate the date that a nest was initiated (IDATE), we assumed that (1) a female laid one egg per day, (2) partial nest predation had not occurred prior to when we found the nest unless there were broken eggshells in the nest bowl, and (3) females did not lay an egg until late morning. IDATEs for nests found during laying were determined by subtracting the number of eggs in the nest from the date on the previous day (if nest found in the morning), or subtracting the number of eggs in the nest from the date the nest was found (if nest found in the afternoon). IDATEs for nests found during incubation were determined by subtracting the number of days incubated and the number of eggs in the nest from the date the nest was found.

On our field forms, we assigned each nest to one of 7 habitat types that corresponded to the dominant vegetation type within a 5-m radius of the nest. Habitat types included grass, hay (grasses and legumes hayed annually), planted cover (a mixture of grasses and legumes planted specifically to provide wildlife habitat), crop, trees (woody vegetation with >30% areal coverage and average height > 6 m), shrub (woody vegetation with >30% areal coverage and average height ≤ 6 m), and emergent wetland vegetation. We also recorded the dominant canopy layer for vegetation within 1 m of the nest bowl. We used a differentially corrected global positioning system to map nest locations. We excluded from analyses all nests that were in the process of hatching or were damaged when they were found, and those where we judged that our activity caused a female to abandon her nest.

Spatial data. To obtain information about the spatial attributes of habitat features for each nest, we digitized habitat information from stereo pairs of 1:5,000 black and white infrared aerial photographs taken during July or August of the year the study site was under investigation. This resolution allowed us to capture each habitat feature ≥10 m in its widest dimension corresponding to our definition of a habitat patch as recorded at nests in the field. Digitized maps were imported into the SPANS geographical information system (GIS; PCI Geomatics, Richmond Hills, Ontario, Canada).

Because we were interested in how robust our predictions were to different habitat classifications, we classified our GIS maps using 3 different schemes. The first classification matched the designations we used in the field to record nest information (i.e., Grass, Hay, Planted Cover, Crop, Trees, Shrub, Wetland; Figure 2.2A). For the second scheme, we again classified hay fields, planted cover fields and crop fields separately but combined the remaining habitats (grass, trees, shrub, and wetland) into a single habitat type that we termed Natural (Figure 2.2B). Finally, we considered a binary habitat-classification scheme that treated habitat as crop versus potential cover (Figure 2.2C). This classification may be appropriate because previous research (Cowardin et al 1985, Greenwood et al 1995) has shown that spring-seeded annual crop fields, though occasionally used as nesting habitat by ducks, are typically used far less than expected by chance; whereas, other habitat types typically are used more or less in proportion to their availability (but see Chapter 2).

Nest locations were imported into the GIS and overlaid onto our digitized maps. As a check of the accuracy of our habitat classification from aerial photographs, we compared the habitat recorded for the nest in the field to the habitat type determined from our most-detailed GIS habitat map. Overall correspondence was good (83–99% correspondence) for all habitats except shrub (52% correspondence). We had difficulty reliably distinguishing areas of low shrub (< 1 m tall; typically *Symphoricarpos occidentalis*) from grass in our aerial photos. Therefore, we defined a new habitat type. If nests were misclassified and had low shrub recorded as the dominant canopy layer, that nest was assigned a habitat type of Grass-Shrub. With the exception of nests in Grass-Shrub, nests whose habitat types did not correspond between field observations and GIS habitat maps were deleted from all further analyses.

For each nest site, we calculated the size and perimeter length of the patch using each of our 3 habitat classifications. From these 2 metrics, we also calculated a shape index (Magarigal & Marks 1994: page C5) that indicated the degree to which a patch deviated from a circular standard. We also calculated linear distances from each nest to the nearest habitat edge, nearest wetland edge, and nearest farm site or building.

To explore the effects of changes in scale on our predictions, we measured landscape attributes on 0.65-km^2 and 10.36-km^2 circular buffers centered on each nest. We calculated the percentage of the area that was cropped, edge density, a mean patch shape index, and mean patch size at each scale (Table 2.3). Because acquiring the fine-resolution habitat data we used was costly, we only obtained habitat data within study-site boundaries. Thus, portions of some circles fell outside the area for which we had habitat information. Nests were deleted from analyses if >50% of the 10.36 km^2 circle fell outside the area for which we had remotely-sensed habitat information. For nests that had partial coverage, we assumed that the habitat configuration for the portion of the circle that was missing was similar to that on the area within the study site.

All procedures used during this research were approved by the University of Saskatchewan's Protocol Review Committee on Animal Care and Supply (Protocol No. 920007)

Data Analysis

We used generalized linear mixed-modeling techniques (GLMM, Breslow and Clayton 1993) to investigate relationships between landscape metrics and hatching rates. A generalized linear model allows the prediction of the dependent variable from a linear combination of predictor variables but does not require that the errors in the dependent variable follow a Gaussian distribution or be continuous. Furthermore, because predictors are related to the dependent variable via link functions, the effect of the predictors on the dependent variable can be nonlinear. The GLMM approach allowed us to incorporate random effects in our analysis, which we felt was important because we were concerned that local uncontrolled and unmeasured conditions at each study area (e.g., weather conditions, predator populations) that were not the focus of our investigation might influence hatching rates. Because study sites were selected randomly from the “population” of available sites, we included study site as a random factor in each model we examined. The nest was treated as the experimental unit, and the response variable was the proportion of days under observation (exposure) that the nest survived (PPNS). If a nest survived until hatch, PPNS = 1 (days survived/exposure = 1). If a nest failed prior to hatch, we first calculated the number of days of exposure. For nests that we only visited periodically (nests not found by radio telemetry), we assigned the midpoint of the interval between visits as the date the nest was destroyed for unsuccessful nests and used this date to calculate exposure. Because our revisit intervals were relatively short (7-10 days) this simplifying assumption should yield relatively unbiased estimates (Johnson 1979). We then calculated the number of days survived as 1 day less than exposure, and PPNS as days survived divided by exposure. Thus, a nest that failed between when we located it and a visit 8 days later had PPNS = 0.75 (3 days survived/4 days of exposure). This method is akin to other likelihood or maximum likelihood methods previously used for estimating hatching rates (Johnson 1979, Bart and Robson 1982) but allows incorporation of continuous covariates as fixed or random effects. Modeling was performed using the GLIMMIX macro in SAS (Littell et al. 1996). Within GLIMMIX, we specified a binomial error distribution with a logit link. Covariance parameters were estimated using restricted maximum likelihood, and appropriate denominator degrees of freedom were approximated using the Satterthwaite procedure (SAS Institute, Inc. 1999).

Table 2.3. Variable definitions and predicted relationships between covariate values and hatching rates

Scale	Variable	Definition	Predicted relationship	
			Linear/SQRT[a]	Quadratic
Nest	HABn[b]	Habitat Type	$\beta_{HAB1} \neq \beta_{HAB2} \neq ,\ldots,$	
	AREAn	Habitat patch size	$\beta_{AREAn} > 0$	
	HDISTn	Distance from nearest habitat patch edge	$\beta_{EDGEDISTn} > 0$	
	SHAPEn	Habitat patch shape index[c]	$\beta_{SHAPEn} < 0$	
	WETDIST	Distance from nearest wetland edge	$\beta_{WETDISTn} > 0$	
	FARMDIST	Distance from nearest farm on study area	$\beta_{FARMDISTn} > 0$	
0.45 km buffer	CROPB1	Percent of the circle comprised of annual crops	$\beta_{CROPB1} < 0$	$\beta_{CROPB1}^2 < 0$
	MEANAREAB1	Mean patch size within circle	$\beta_{MEANAREAB1} > 0$	$\beta_{MEANAREAB1}^2 < 0$
	MEANSHAPB1	Mean shape index for patches within circle	$\beta_{MEANSHAPB1} < 0$	$\beta_{MEANSHAPB1}^2 < 0$
	EDGEDENB1	Total km of edge/area of circle	$\beta_{EDGEDNB1} < 0$	$\beta_{EDGEDNB1}^2 > 0$
1.82 km buffer	CROPB2	Percent of the circle comprised of annual crops	$\beta_{CROPB2} < 0$	$\beta_{CROPB2}^2 < 0$
	MEANAREAB2	Mean patch size within circle	$\beta_{MEANAREAB2} > 0$	$\beta_{MEANAREAB2}^2 < 0$
	MEANSHAPB2	Mean shape index for patches within circle	$\beta_{MEANSHAPB2} < 0$	$\beta_{MEANSHAPB2}^2 < 0$
	EDGEDENB2	Total km of edge/area of circle	$\beta_{EDGEDNB2} < 0$	$\beta_{EDGEDNB2}^2 > 0$

[a] SQRT = Square-root transformed covariates

[b] "n" refers to habitat classification scheme; 8 = 8-habitat, 4 = 4-habitat, 2 = 2-habitat.

[c] Shape Index = patch perimeter/2(π*patch area) (McGarigal and Marks 1994)

We formalized each of our predictions (see Hypotheses and Predictions) as a set of statistical models that we considered *a priori* models for analyzing the effects of landscape features on duck hatching rates. A summary of the predicted effects of individual covariates can be found in Table 2.3, and a list of our *a priori* models can be found in Appendix A2.

We considered alternate forms of those *a priori* models that contained continuous variables. In the first form, all continuous variables were modeled as linear effects (i.e., changing the covariate value affected log odds of PPNS at a constant rate). In the second form all continuous covariates were square-root transformed (hereafter, SQRT), which represented our prediction of a proportionally diminishing effect as the covariate values increase. For example, we believed it possible that hatching rates increased with distance from a wetland and that the strength of this relationship might diminish at some distance. In our *a priori* set, all models were additive (i.e., interactions were not considered). This was done because there was little foundation upon which to build in the literature; the ability to analyze nesting data with continuous covariates is very new. To contrast the effects of different habitat classifications, we examined the same set of *a priori* models for each of our 3 different habitat classification schemes (8-habitat, 4-habitat, 2-habitat).

In a separate analysis of some of these data, a strong seasonal trend in hatching rates was indicated (Ducks Unlimited Canada, unpublished). We, therefore, included the date the nest was initiated (IDATE) in all models to account for these seasonal changes in hatching rates. Because the shape index for a patch was a linear combination of patch area and amount of edge, we did not consider any models that included both shape index and patch size or any models that included shape index and distance from a habitat edge. We did not include an effect for different duck species in our *a priori* models. While acknowledging that there may be subtle differences in nest-guarding behavior among species, we reasoned that (1) most interspecific differences in hatching rates would be adequately accounted for by differences in initiation date and habitat variables, and (2) that effects of differing species compositions among sites would be accounted for in random effects of study site. Also, Greenwood et al. (1995) failed to find interspecific differences in duck hatching rates within the aspen parklands of southern Canada. We did, however, include species as a potential predictor variable in *post hoc* exploratory analyses (see below).

We developed an additional list of 9 *a priori* models (Appendix A2) to evaluate effects of landscape features measured at different scales. Again we did not consider models that combined mean measures of patch shape with mean measures of patch size or edge density. For the comparison of models at various scales we considered 3 different forms. As with the "patch-scale" models above, we examined models with linear and SQRT effects. In this case, however, we also considered models where covariates were included as quadratic terms in addition to their linear counterparts because prior examination of the landscape metrics indicated that some were related to the amount of cropland on the study area, but in a predictably nonlinear fashion (Hargis et al. 1998).

Information theoretic techniques were used to select the most parsimonious model (Burnham and Anderson 1998) from each of our suites of *a priori* models (*n* = 297 total models). Specifically, we used the small-sample form of Akaike's Information Criterion ($\mathrm{AIC_c}$) to evaluate each of our *a priori* models. $\mathrm{AIC_c}$ is calculated as:

$$\mathrm{AIC_c} = -2\log(L(\hat{\theta} \mid y)) + 2K + \frac{2K(K+1)}{n-K-1}$$

where $L(\hat{\theta} \mid y)$ is the likelihood of a specific parameter value θ given the data y, K is the number of parameters in the model, and n is the sample size. The model with the minimum $\mathrm{AIC_c}$ value is generally considered the most parsimonious. Subtraction can be used to rank other models according to their $\mathrm{AIC_c}$ values to examine the 'strength of evidence' for each (i) model in the suite (i.e., $\Delta\mathrm{AIC_c} = \mathrm{AIC}_{\mathrm{c}i} - \mathrm{minAIC_c}$; Burnham and Anderson 2001). As further evidence of the relative support for individual models, we calculated Akaike weights for all models within each suite according to the formula:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta\mathrm{AIC_c})_i}{\sum\exp(-\frac{1}{2}\Delta\mathrm{AIC_c})_s}$$

where s is the suite of models in which the focal model i appears (Burnham and Anderson 1998:124). As evidence of the importance of individual predictors, we calculated average model weights, $\overline{w}_\theta = \frac{\sum w_i}{N_s}$ where N_s = the number of models in a given suite that contain a specific predictor, θ. This is an extension of the method given by Burnham and Anderson (1998: page 178) that accounts for individual covariates appearing in different numbers of *a priori* models.

Because we were concerned about the potential for overdispersion in our data, we examined the estimate of the overdispersion scale parameter for the most saturated models in each of our suites of models (patch-scale, 8-habitat; ; 0.65-km^2, 8-habitat; 10.36-km^2, 8-habitat) estimated by the GLIMMIX macro. The estimated overdispersion scale parameter of the most saturated models in each suite fell within the range 1.89-1.90; therefore, we used the quasi-likelihood form of Akaike's Information Criterion adjusted for sample size (QAIC$_c$, Burnham and Anderson 1998: page 53) to select the most parsimonious model from each set. The formula for QAIC$_c$ has the form:

$$\mathrm{QAIC_c} = -[2\log(L(\hat{\theta}))/\hat{c}] + 2K + \frac{2K(K+1)}{n-K-1},$$

where $L(\hat{\theta})$ is the likelihood, $\hat{c}$ is the variance inflation factor for the most saturated model, K is the number of parameters in the model, and n is the sample size. Our sample sizes likely were large enough that the small sample adjustment was not required, however, as sample sizes increase QAIC$_c$ approaches QAIC, so there effectively was no penalty for using the small sample version. Because estimates of the overdispersion scale were very similar among our model suites, we estimated the variance inflation factor as $(1.895)^{0.5} = 1.38$ for each suite of models, where 1.895 was the mean value observed for the overdispersion parameter.

The variance inflation factor ($\hat{c}$) may be poorly estimated with our type of data because neither the deviance nor Pearson's statistic is distributed as chi-square (McCullagh and Nelder 1989). This may result in an underestimation of variance components and fixed effects (Breslow and Clayton 1993); however, the problem is not severe for binomial trials such as ours with denominators > 1. In simulations, variance components were only moderately underestimated when the number of trials equaled 8

(Breslow and Clayton 1993). With our data, number of trials (exposure days) ranged from 1 - 42 with a median value of 12 ($\bar{x} = 13.7$). Therefore, we do not expect variance components to be severely underestimated. Furthermore, using quasilikelihood allowed us to estimate the magnitude of a random study-site effect, which we feel is an important improvement over previous attempts at modeling hatching rates. Nevertheless, we recognize that model-selection uncertainty (see below) may be increased slightly by using quasilikelihood estimation methods.

We followed our examination of *a priori* models with an exploratory analysis that examined the influence of additional effects including interactions, combinations of forms of covariates (i.e., mix of linear, SQRT, quadratic), and combinations of effects from multiples scales. These models were not considered *a priori* because we were aware of no previous research that simultaneously considered these factors. Hence, we were unable to predict how various spatial factors might interact across scales and habitat classification schemes. For this exploratory phase of the analysis, we sequentially removed fixed effects and interaction terms where confidence intervals included zero; however, we continued to use QAIC_c as our measure of model parsimony. We continued removing covariates, while maintaining model hierarchy, until QAIC_c was minimized.

To evaluate the fit of our best approximating model we plotted the Receiver Operating Characteristic (ROC) curve, which represents a plot of all the sensitivity values (true positive fraction) against all 1-specificity values (false positive fraction). The area under the curve (AUC) provides a measure of model performance. An AUC of 0.5

would indicate no discriminatory ability, whereas, AUC of 1.0 would indicate perfect discrimination (SAS Institute 1995, Pearce and Ferrier 2000).

Results

In this section, we first give a general overview of the dataset, then examine how using different habitat classifications and measuring landscape attributes at different scales affected predictions in our a priori model sets. Finally, we examine the support in our a priori models for our various hypotheses and review results of exploratory analyses of models with greater complexity. To keep the length of the results section reasonable, in the next sections we typically present only coefficient estimates and standard errors for the best approximating models.

We found and successfully monitored 6,311 nests on 15 sites. Sites varied widely in their compositions and the degree to which natural habitats had been converted to agricultural uses. Crop fields comprised from 9-78% of study sites (Table 2.2). Wetland densities ranged from 7.8-57.1 per km^2, while comprising 8.5-36.8% of each site (Table 2.2).

Each site provided 74 to 1,823 ($\bar{x} = 420.1, \mathrm{SE} = 113.3$) nests. The majority of nests were laid by mallards (47%), blue-winged teal (21%), gadwalls (11%), and northern shovelers (*Anas clypeata*, 11%). Covariate values varied widely among nests (Table 2.4). Therefore, these sites provided a good opportunity to address the questions we posed. Correlation among covariates was generally low (Table 2.5), so multicolliniarity should not be a problem; however, edge density and mean area at the aggregated scales were strongly negatively related to each other.

Comparison of habitat classification schemes

For models with linear covariates only, the best 8-habitat and 4-habitat models had similar $QAIC_c$ values (Table 2.6, Figure 2.3) and, therefore, should be viewed as potential competitors. In contrast, models within the 2-habitat model set using linear covariates performed poorly, with the best model receiving essentially no support when compared to the best 8-habitat model ($\Delta QAIC_c > 17$; Table 2.6, Figure 2.3).

When considering models with SQRT covariates, again 8-habitat and 4-habitat models performed similarly and had similar $QAIC_c$ values to those for the 8-habitat and 4-habitat linear models. As with the set of models with linear covariates, 2-habitat models with SQRT covariates performed poorly ($\Delta QAIC_c > 18$; Table 2.6, Figure 2.3). Thus, we did not consider models built with the 2-habitat classification in any further analyses.

Comparison of scales

Although models using the 4-habitat classification performed similarly to the *a priori* models using the 8-habitat classification, we used the 8-habitat classification as a benchmark for our comparison of model performance at various scales because 8-habitat models received slightly greater support regardless of whether we considered models with linear or SQRT covariates (Table 2.6). All models built from covariates collected within circular buffers performed poorly when compared to models collected at the patch scale ($\Delta QAIC_c$ >18; Tables 2.6, 2.7, Figure 2.4). Within the 10.36-km^2 model set, the model with EDGEDENS$^{0.5}$ as the only spatial covariate was marginally superior to the model without any spatial covariates ($\Delta QAIC_c = 0.44$).

Spatial Habitat Features – Support for hypotheses

Our best models included covariates measured at the patch scale and used either the 8- or 4-habitat classification scheme. Therefore, we considered the evidence provided from these suites of models for evaluation of our hypotheses about the effects of spatial habitat features on hatching rates.

The basic habitat models used in the past were improved by the inclusion of spatially explicit covariates. Our hypothesis that hatching rate increases with distance from a habitat edge was supported, and there was some indication that the edge effect was non-linear. For our 8-habitat classification, models including distance from a habitat edge (HDIST) were selected as the most parsimonious regardless of whether the linear or SQRT form was used (Table 2.6).

Similarly, all but one model in the best set ($\Delta QAIC_c < 2$) included spatial features when using the 4-habitat classification; however, the model with the lowest $QAIC_c$ value ($\Delta QAIC_c = 0.15$) included just IDATE and habitat type. There was little evidence from our *a priori* models to support the hypothesis that patch size (AREA) was an important predictor of hatching rates for either our 8- or 4-habitat classifications. With models built using the 4-habitat classification there is some evidence that a shape index (SHAPE) improves predictions (Figure 2.5). However, the direction of this trend is opposite to our prediction (i.e., hatching rates increase for patches with a high ratio of edge to area).

Table 2.4. Sample sizes and ranges of individual covariates by habitat type

	Habitat type							
	Crop	Hay	Planted Cover	Grass	Grass-Shrub	Shrub	Trees	Wetland
No. of nests	86	485	2521	1476	101	383	551	708
Covariate								
IDATE (Julian)	111-191	109-187	105-196	107-192	112-186	104-187	105-182	105-192
AREA8 (ha)	1.2-252.0	0.2-90	0.4-529.9	<0.01-793	0.02-296	<0.01-107	<0.01-57	<0.01-119
HDIST8 (m)	1-176	0-120	0-220	0-95	0-23	0-56	0-61	0-128
SHAPE	1.4-8.4	1.1-6.5	1.3-12.7	1.1-37.2	1.1-19.6	1.0-16.4	1.0-7.5	1.0-13.4
WETDIST (m)	1-223	0-390	0-338	0-367	1-358	0-348	0-524	0
FARMDIST (m)	60-2575	25-2437	3-2175	1-3828	2-2115	2-3231	2-3122	2-3241
CROPB1 (%)	28-93	0-81	0-65	0-90	0-91	0-88	0-94	0-89
CROPB2 (%)	11-74	0-79	18-80	0-92	4-73	3-80	0-83	0-88
EDGEDENB1 (km/km^2)	26.8-106.6	26.9-126.1	26.3-120.5	28.0-171.5	23.9-112.9	32.0-171.5	22.3-161.5	29.5-159.4
EDGEDENB2 (km/km^2)	29.7-94.0	33.4-107.9	35.7-100.7	24.7-110.7	37.4-92.1	35.1-109.8	29.8-112.5	31.1-111-9
MEANAREAB1 (ha)	0.3-1.5	0.2-1.9	0.2-2.0	0.1-2.2	0.2-2.2	0.1-2.1	0.1-2.7	0.1-1.9
MEANAREAB2 (ha)	0.3-1.8	0.3-1.6	0.3-1.4	0.3-2.5	0.3-1.4	0.3-1.7	0.2-1.8	0.3-2.2
MEANSHAPB1	1.6-2.3	1.6-2.2	1.5-2.4	1.4-2.7	1.6-2.2	1.5-2.2	1.5-2.3	1.5-2.6
MEANSHAPB2	1.6-1.9	1.6-2.0	1.6-2.1	1.6-2.0	1.6-2.0	1.6-2.0	1.6-2.0	1.6-2.0

Table 2.5. Pearson correlation coefficients among covariates at 15 sites in south-central Canada

	AREA8	HDIST8	SHAPE8	WETDIST	FARMDIST	MEANAREAB1	EDGEDENB1	MEANSHAPB1	CROPB1	MEANAREAB2	EDGEDENB2	MEANSHAPB2	CROPB2
AREA8	1.00	0.36	0.70	0.21	-0.05	0.11	-0.16	0.35	-0.31	0.09	-0.10	0.49	-0.24
HDIST8		1.00	0.12	0.54	0.06	0.24	-0.30	0.16	-0.29	0.20	-0.18	0.36	-0.01
SHAPE8			1.00	0.08	-0.03	0.00	0.00	0.21	-0.18	-0.02	0.03	0.26	-0.20
WETDIST				1.00	-0.04	0.32	-0.28	0.16	-0.08	0.28	-0.24	0.25	0.01
FARMDIST					1.00	-0.01	-0.00	-0.09	-0.03	-0.12	-0.06	-0.21	0.08
MEANAREAB1						1.00	-0.80	0.40	0.15	0.73[a]	-0.66	0.40	0.16
EDGEDENB1							1.00	-0.13	-0.22	-0.67	0.71	-0.36	-0.24
MEANSHAPB1								1.00	-0.00	0.32	-0.25	0.59	0.02
CROPB1									1.00	0.15	-0.23	-0.14	0.57
MEANAREAB2										1.00	-0.89	0.53	0.29
EDGEDENB2											1.00	-0.39	-0.40
MEANSHAPB2												1.00	0.10
CROPB2													1.00

[a] Never occurred simultaneously with other covariates in shaded cells in any model

Table 2.6. Ranking of hypothesized models of hatching rates of duck nests at 15 sites in south-central Canada. Rankings are based on the quasi-likelihood form of Akaike's Information Criteria. Model suites are for covariates measured at the patch scale and compares models using 8- or 4- or 2-habitat classifications and either linear or square-root transformed forms of continuous covariates. Only models within 2 $QAIC_c$ values of the most parsimonious model in each suite are presented.

Hypothesized model[a]	$QAIC_c$	K	$\Delta QAIC_{ci}$	w_i[b]
8-Habitat, linear form				
N8) $H_{(HAB8+HDIST8)}$	6367.24	11	0	1
N1) $H_{(HAB8)}$	6365.41	10	0.16	0.92
N25) $H_{(HAB8+HDIST+WDIST)}$	6368.92	12	1.68	0.43
N24) $H_{(HAB8+HDIST+FDIST)}$	6368.94	12	1.70	0.43
N20) $H_{(HAB8 +HDIST+AREA)}$	6369.12	12	1.88	0.39
N10) $H_{(HAB8+FDIST)}$	6369.18	11	1.94	0.38
8-Habitat, SQRT				
N8) $H_{(HAB8+HDIST8)}$	6364.78	11	0	1
N20) $H_{(HAB +HDIST+AREA)}$	6366.15	12	1.37	0.50
N24) $H_{(HAB+HDIST+FDIST)}$	6366.45	12	1.68	0.43
N25) $H_{(HAB+HDIST+WDIST)}$	6366.53	12	1.75	0.42
4-Habitat, Linear form				
N1) $H_{(HAB4)}$	6368.35	6	0	1
N7) $H_{(HAB+AREA)}$	6368.50	7	0.15	0.93
N9) $H_{(HAB+SHAPE)}$	6368.71	7	0.36	0.83
N10) $H_{(HAB+FDIST)}$	6370.02	7	1.75	0.42
N21) $H_{(HAB+AREA+SHAPE)}$	6370.23	8	1.88	0.39
N8) $H_{(HAB4+HDIST4)}$	6370.27	7	1.92	0.38
N22) $H_{(HAB+AREA+FDIST)}$	6370.27	8	1.92	0.38
N11) $H_{(HAB+WDIST)}$	6370.29	7	1.94	0.38
N20) $H_{(HAB+AREA+HDIST)}$	6370.30	8	1.95	0.38
4-Habitat, SQRT				
N1) $H_{(HAB4)}$	6368.35	6	0	1
N9) $H_{(HAB+SHAPE)}$	6369.01	7	0.66	0.72
N10) $H_{(HAB+FDIST)}$	6369.71	7	1.36	0.51
N7) $H_{(HAB+AREA)}$	6369.71	7	1.36	0.51
2-Habitat, Linear form				
N4) $H_{(SHAPE)}$	6384.36	4	0	1
N12) $H_{(AREA+HDIST)}$	6384.78	5	0.4	0.81
N3) $H_{(HDIST)}$	6385.04	4	0.69	0.71
N2) $H_{(AREA)}$	6385.30	4	0.94	0.62
N18) $H_{(SHAPE+WDIST)}$	6385.74	5	1.39	0.50
N9) $H_{(HAB+SHAPE)}$	6386.13	5	1.78	0.41
N17) $H_{(SHAPE+FDIST)}$	6388.24	5	1.89	0.38

Hypothesized model[a]	QAIC$_c$	K	ΔQAIC$_{ci}$	w_i[b]
2-Habitat, SQRT				
N12) $H_{(AREA+HDIST)}$	6383.47	5	0	1
N3) $H_{(HDIST)}$	6383.52	4	0.05	0.97
N4) $H_{(SHAPE)}$	6384.10	4	0.64	0.73
N16) $H_{(HDIST+WDIST)}$	6384.54	5	1.07	0.59
N18) $H_{(SHAPE+WDIST)}$	6384.56	5	1.08	0.58
N30) $H_{(AREA+HDIST+WDIST)}$	6384.74	6	1.28	0.53
N2) $H_{(AREA)}$	6384.90	4	1.43	0.49
N8) $H_{(HAB+HDIST)}$	6384.91	5	1.44	0.49
N29) $H_{(AREA+HDIST+FDIST)}$	6385.07	6	1.60	0.45
N20) $H_{(HAB+AREA+HDIST)}$	6385.07	6	1.61	0.45
N15) $H_{(HDIST+FDIST)}$	6385.12	5	1.65	0.44
N14) $H_{(AREA+WDIST)}$	6385.34	5	1.88	0.39

[a] All models include a random effect for study area, and an effect for IDATE.

[b] w_i = QAIC$_c$ weight for an individual model divided by the QAIC$_c$ weight for the best approximating model from that suite of models. $w_i = \frac{\exp(-\frac{1}{2}\Delta \mathrm{QAIC}_c)_i}{\sum \exp(-\frac{1}{2}\Delta \mathrm{QAIC}_c)_s}$, where s is the suite of models in which the focal model i appears (Burnham and Anderson 1998:124).

Figure 2.3. Comparison of minimum QAIC$_c$ values for suites of models using different habitat classification schemes and different forms of continuous covariates.

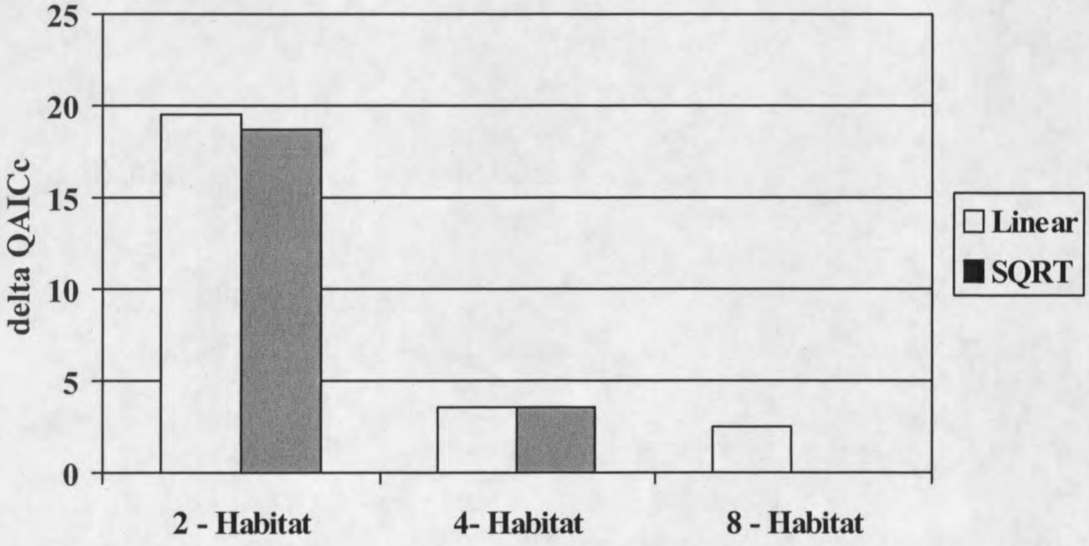


Table 2.7. Ranking of hypothesized models of hatching rates of duck nests at 15 sites in south-central Canada. Rankings are based on the quasi-likelihood form of Akaike's Information Criteria. Model suites are for covariates measured within 0.65- or 10.36-km^2 circles centered on nest locations and either linear or square-root transformed forms of continuous covariates. Only models within 2 $QAIC_c$ values of the most parsimonious model in each suite are presented.

Hypothesized model[a]	$QAIC_c$	K	$\Delta QAIC_{ci}$	w_i/w_*
0.65 km^2, linear form				
$B_1$1) $H_{(\mathrm{CROP})}$	6385.66	4	0	1
Sar Idate	6386.70	3	1.03	0.60
$B_1$5) $H_{(\mathrm{CROP+MEANAREA})}$	6386.73	5	1.08	0.58
$B_1$2) $H_{(\mathrm{MEANAREA})}$	6386.87	4	1.21	0.55
$B_1$7) $H_{(\mathrm{CROP+MEANSHAP})}$	6387.57	5	1.91	0.38
$B_1$6) $H_{(\mathrm{CROP+EDGEDENS})}$	6387.62	5	1.96	0.38
0.65 km^2, SQRT				
Sar Idate*	6386.70	3	0	1
$B_1$2) $H_{(\mathrm{MEANAREA}^{0.5})}$	6387.40	4	0.70	0.70
$B_1$3) $H_{(\mathrm{EDGEDENS}^{0.5})}$	6387.93	4	1.23	0.54
$B_1$1) $H_{(\mathrm{CROP}^{0.5})}$	6388.13	4	1.43	0.49
$B_1$4) $H_{(\mathrm{MEANSHAP}^{0.5})}$	6388.55	4	1.853	0.40
0.65 km^2, quadratic				
$B_1$1) $H_{(\mathrm{CROP+CROP}^2)}$	6383.03	5	0	1
$B_1$6) $H_{(\mathrm{CROP+CROP}^2\mathrm{+EDGEDENS+EDGEDENS}^2)}$	6384.53	7	1.50	0.47
10.36 km^2, linear form				
$B_2$3) $H_{(\mathrm{EDGEDENS})}$	6386.57	4	0	1
$B_2$1) $H_{(\mathrm{CROP})}$	6387.07	4	0.50	0.78
$B_2$2) $H_{(\mathrm{MEANAREA})}$	6387.88	4	1.31	0.52
$B_2$4) $H_{(\mathrm{MEANSHAP})}$	6388.21	4	1.63	0.44
$B_2$6) $H_{(\mathrm{CROP+EDGEDENS})}$	6388.24	5	1.67	0.43
$B_2$8) $H_{(\mathrm{MEANAREA+EDGEDENS})}$	6388.31	5	1.74	0.42
10.36 km^2, SQRT				
$B_2$3) $H_{(\mathrm{EDGEDENS}^{0.5})}$	6387.42	4	0	1
$B_2$1) $H_{(\mathrm{CROP}^{0.5})}$	6387.83	4	0.40	0.81
$B_2$2) $H_{(\mathrm{MEANAREA}^{0.5})}$	6388.44	4	1.02	0.60
$B_2$4) $H_{(\mathrm{MEANSHAP}^{0.5})}$	6388.74	4	1.32	0.52
$B_2$8) $H_{(\mathrm{MEANAREA}^{0.5}\mathrm{+EDGEDENS}^{0.5})}$	6389.04	5	1.62	0.45
$B_2$6) $H_{(\mathrm{CROP}^{0.5}\mathrm{+EDGEDENS}^{0.5})}$	6389.17	5	1.75	0.42
10.36 km^2, quadratic				
$B_2$3) $H_{(\mathrm{EDGEDENS+EDGEDENS}^2)}$	6387.31	5	0	1
$B_2$1) $H_{(\mathrm{CROP+CROP}^2)}$	6388.12	5	0.67	0.67
$B_2$4) $H_{(\mathrm{MEANSHAP+MEANSHAP}^2)}$	6389.29	5	1.99	0.37

[a] All models include a random effect for study area, and an effect for IDATE.

Figure 2.4 Comparison of minimum QAIC$_c$ scores for suites of models using landscape metrics measured at different scales and using different forms of continuous covariates

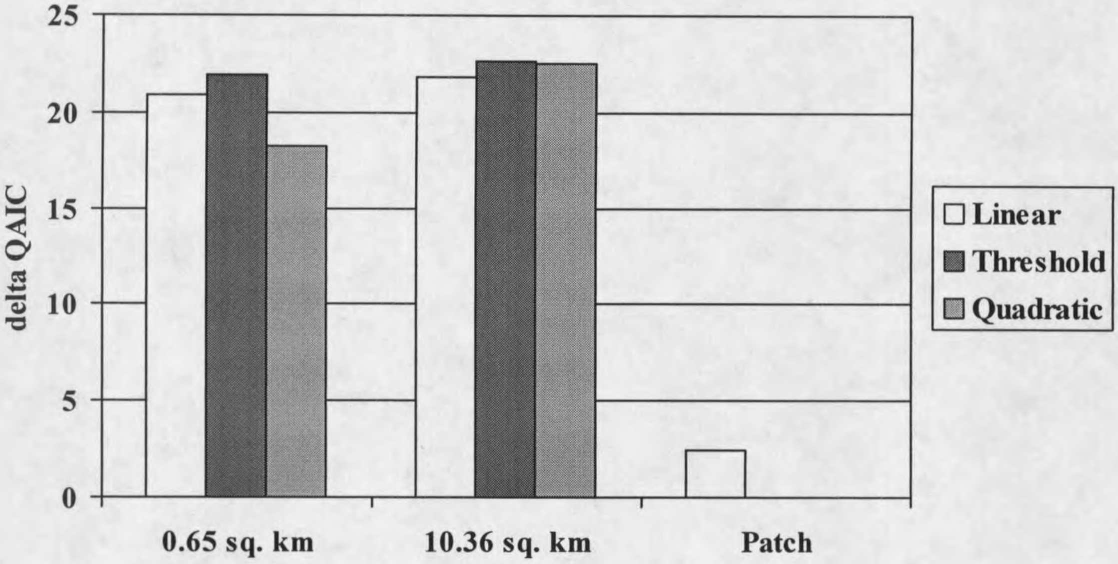
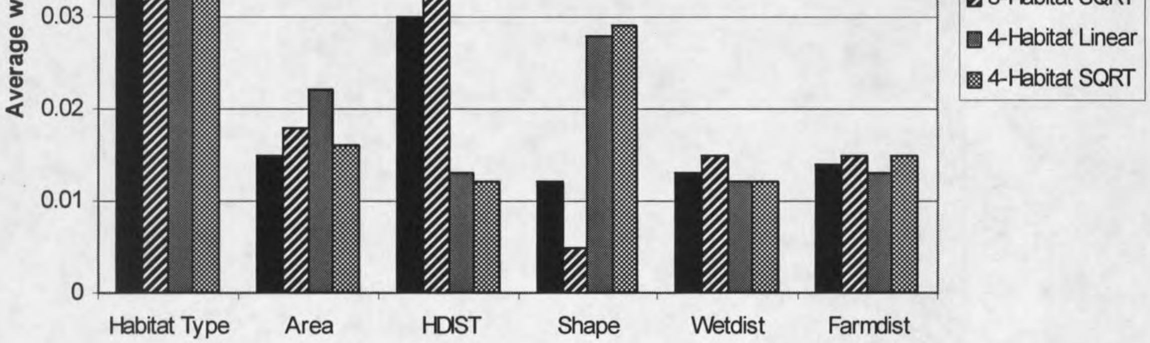


Figure 2.5. Average QAIC$_c$ weights for covariates in hypothesized models usinging different habitat classification schemes and different forms of continuous covariates.



Predator Activity Centers

Our *a priori* models provide little support for our hypotheses that nests in close proximity to farm sites or wetlands are susceptible to elevated rates of predation (Figure 2.5). Despite the fact that WETDIST and FARMDIST appear in several models with $\Delta QAIC_c < 2$ (Table 2.6), the average weight for these predictors (Figure 2.5) is relatively low.

Model-Selection Uncertainty

Within each of our model sets there were a number of models with $\Delta QAIC_c$ values ≤ 2 (Table 2.6, 2.8), which may be plausible alternatives to the best approximating models. In most cases, however, models with similar $QAIC_c$ values shared many of the same covariates. The relative value of individual covariates is reflected in (Figure 2.5). From this we can see that despite much model uncertainty, habitat type consistently was an important predictor of hatching rates. Results regarding spatial covariates were more variable. Despite the fact that best models using the 8-habitat classification had similar $QAIC_c$ scores as the best 4-habitat models, the important covariates beyond habitat type were different in the best 8- and 4-habitat models. The distance a nest was from a habitat edge was the most important spatial covariate for the 8-habitat classification, while the shape index was the most important spatial covariate for the 4-habitat classification.

Exploratory analysis

Finally, our exploratory analysis of an additional set of 35 models that included covariates from the best 4-habitat and 8-habitat models, multiple scales, multiple covariate forms, selected 2-way interactions, and potential species effects yielded a model that was far superior to any of our *a priori* candidate models ($\Delta QAIC_c > 60$). Our selected model was considerably more complicated than any of our hypothesized models with several interactions contributing substantially to the predictive capability of the model, thus providing an excellent opportunity to increase our understanding about how the interplay of spatial factors shape patterns of hatching rates. Although we arrived at this model through exploratory analysis, we believe it to be the model that best describes patterns of hatching rates because it has a far lower $QAIC_c$ score and the interactions seem biologically plausible (Table 2.8). As such, we will describe this model in more detail. Because it is the result of exploratory analyses, readers may want to use caution in applying this model.

The best model included effects of initiation date (IDATE), habitat type (HAB8), patch size (AREA8), distance to a habitat edge ($HDIST8^{0.5}$), distance to a wetland edge ($WETDIST^{0.5}$), and interactions between initiation date and habitat type (IDATE*HAB8*), patch size and distance to a habitat edge ($AREA8*HDIST8^{0.5}$), initiation date and patch size (IDATE*AREA8), initiation date and distance to a wetland ($IDATE* WETDIST^{0.5}$), and distance to a habitat edge and distance to a wetland ($HDIST8^{0.5}*WETDIST^{0.5}$). The only variable retained from a scale larger than patch-level was edge density within the 0.65 km^2 circle around the nest. Edge density as both a linear effect (EDGEDENSB1) and as a quadratic ($EDGEDENSB1^{0.5}$) improved the model (Table 2.9). For this model AUC = 0.70 (Figure 2.6). In other words, a randomly selected pair of nests, one successful and the other unsuccessful, will be classified correctly by this model in 70% of instances.

Closer examination of the model reveals a complex relationship between hatching rates, habitat type, size of the habitat patch, and initiation date (Figure 2.7). As expected, nests laid late in the nesting season in hay fields suffered high mortality—mostly due to the haying operation (Figure 2.7B). Similarly, nests laid in crop fields early in the season were vulnerable to destruction by tillage activities (Figure. 2.7C). For most habitats, hatching rates tended to be somewhat higher in larger habitat patches than in small patches regardless of initiation dates. Notable exceptions , however, occurred in the habitat types dominated by perennial graminoids (Grass and Planted Cover). In both of these habitats, hatching rates were highest in large patches early in the season; however, there was a strong interaction whereby late in the season small patches were substantially safer than large patches (Figure 2.7D, F). The seasonal decline in hatching rate in the smallest patches of Grass and Planted Cover was less severe.

The effect of distance from a habitat edge was more pronounced for distance from wetland edges than for other types of habitat edges (Figure 2.8), but again, because wetlands represent one type of habitat edge, it is not possible to be near a wetland edge and far from a habitat edge. Thus, our inference space is restricted to half the normal surface. Model performance was improved by including a single covariate, $\text{EDGEDEN}_{\text{B1}}$, from the 0.65 km^2 buffer scale as both a linear and quadratic effect (Figure 2.9).

As with the *a priori* models, several similarly structured models were close competitors; a number of models had similar QAIC_c values. The model with the second lowest QAIC_c, was identical to the best approximating model with the exceptions that the linear form of HDIST replaced the SQRT-form. The third best model ($\Delta\text{QAIC}_c = 0.54$)

was identical to the best model except for the exclusion of the AREA8*HDIST$^{0.5}$ interaction. The fourth best model ($\Delta QAIC_c = 0.62$) was identical to the best model except that AREA8$^{0.5}$ replaced AREA.

Discussion

Previous studies, due to analytical constraints, have been unable to examine the effects of spatial factors on waterfowl hatching rates in the detail we have here. Landscape features do appear to influence duck hatching rates in the aspen parklands. However, the relationships are complex, and some of the effects are subtle.

We found some evidence that hatching rates were related to distance from a habitat edge. Results of other studies of ducks (Pasitschniak-Arts and Messier 1995, Pasitschniak-Arts et al. 1998) and other bird species (Paton 1994, Lahti 2001) have been equivocal. Factors that may lead to such variable results include differences in (1) the scale at which measurements were taken, (2) predator species compostion, (3) dominant landuse, or (4) biogeographical region (Chalfoun et al. 2002). Our results indicated strong interactions; these interactions may partially explain the variable results seen in previous studies. Horn (2000) found edge effects to be dependent on landscape context. In contrast, we found no evidence for an interaction between landscape metrics generated at either of our aggregated scales (0.65 km^2 or 10.36 km^2 buffers) and distance from edge. We did, however, find an interaction between distance to the nearest wetland and distances from other types of edges, with the edge effect being more pronounced for wetland edges than for other types of habitat edges. A strong effect of distance from a wetland edge is consistent with documented foraging behavior by striped skunks. Several authors have documented that skunks preferentially select wetland habitats for foraging (Greenwood et al. 1999, LaRiviere and Messier 2000, Phillips 2001). This result is in contrast to two previous studies (Horn 2000, Pasitschniak-Arts et al. 1998) that failed to detect a relationship between duck hatching rates and proximity to wetlands. These inconsistencies highlight the need to more formally link predator foraging behavior and patterns of avian nest predation (Chalfoun et al. 2002) by studying these aspects simultaneously.

Hatching rates generally were positively related to patch size, although this varied substantially with the type of habitat patch and seasonally. Most striking was the interaction between patch size and initiation date for planted cover and grass—both habitats dominated by perennial grasses. In both habitats, early in the nesting season large patches had higher hatching rates than small patches, but in both habitats, hatching rates decline sharply during the nesting season for large patches, while remaining relatively constant (Grass) or declining gradually (Planted Cover) for small patches. This interaction has important implications because (1) planted cover is a managed habitat, (2) nest success is highest in large patches of planted cover early in the season, (3) early-hatched nests result in the greatest recruitment to breeding populations (Anderson et al. 2001, Blums et al. 2002), and (4) planted cover is attractive to nesting birds early in the season. Although a clear explanation for this pattern eludes us, we suspect that it relates to seasonal changes in predator foraging patterns. For example, Lariviere and Messier (1997) documented increased foraging activity of adult female skunks later in the nesting season, however, they did not document an increased focus on planted cover or grassland habitats (Lariviere and Messier 2000). Unfortunately, little other research is available about seasonal changes in foraging activities of common nest predators.

Sovada et al. (2000) examined duck hatching rates in the north-central states and found an effect of patch size in 1 of 6 patch size comparisons they considered. They also found an interaction between patch size and date; however, the pattern was opposite to the one we observed. During one year of their study, hatching rates increased for large patches of planted cover as the season progressed, while hatching rates in small patches decreased. The presence of these interactions may explain the inconsistent results seen in earlier studies. Future studies should consider complex models with interactions as we have here; important patterns may be masked in models that consider only main effects.

The habitat classification scheme affected the fit of our *a priori* models. Models using the 4- and 8-habitat classification schemes performed substantially better than the 2-habitat classification. The best 4-habitat and 8-habitat *a priori* models had similar $QAIC_c$ values, however, exploratory models built on the 8-habitat classification were superior to their 4-habitat counterparts. In practical terms, then, we would recommend that detailed habitat information be collected and used if possible. Nevertheless, a 4-habitat classification scheme based on land uses may be adequate if more detailed information is unavailable or too costly to acquire. Also, the 4-habitat classification as we have defined it, may be reasonable given the preponderance (at least in Prairie Canada) of remotely-sensed habitat information generated by agricultural interests, in which accuracy is often good for agricultural land uses (crop and hay) but more subject to classification errors for other habitat types.

We believe that using a GLMM approach represents a substantial advance in the analysis of nesting data. The inclusion of study area as a random effect markedly improved our models. A model containing the same covariates as our best approximating model, but without the study area effect, had a $\Delta QAIC_c > 140$. This implies (1) partitioning the effect of a given study area is important for estimating other effects, (2) there may be a scale larger than the ones we examined that might yield useful models, and (3) there is much variation that remains unexplained by spatial covariates (e.g., predator populations, alternate prey).

Spatial patterns of hatching rates were sensitive to the scale at which landscape attributes were measured. Attributes of the habitat patch in which the nest was located related to the likelihood of that nest hatching much better than did aggregated attributes collected within either a radii of 0.45 or 1.82 km of the nest. Models at the 2 aggregated scales performed similarly though the covariates that best related to hatching rates differed. Because the most important covariates differed at different scales, managers should be cautious about applying models to management problems at a different scale than that at which the data originally used to construct the model were collected. Similarly, researchers must be careful to clearly specify the scale at which studies were conducted.

Table 2.8. Ranking of exploratory models of hatching rates of duck nests at 15 sites in south-central Canada. Rankings are based on the quasi-likelihood form of Akaike's Information Criteria. Only models within 2 $QAIC_c$ values of the most parsimonious model are presented

Exploratory model		$QAIC_c$	K	$\Delta QAIC_{ci}$	w_i/w_*
H*(IDATE + HAB8 + AREA + HDIST$^{0.5}$ + WDIST$^{0.5}$ + IDATE*HAB8 + IDATE*AREA + IDATE*WDIST$^{0.5}$ + AREA*HDIST$^{0.5}$ + HDIST$^{0.5}$*WDIST$^{0.5}$)		6304.41	26	0	1
H(IDATE + HAB8 + AREA + HDIST + WDIST$^{0.5}$ + IDATE*HAB8 + IDATE*AREA + IDATE*WDIST$^{0.5}$ + AREA*HDIST + HDIST*WDIST$^{0.5}$)	Replace SQRT form of HDIST with linear form	6304.70	26	0.28	0.87
H(IDATE + HAB8 + AREA + HDIST$^{0.5}$ + WDIST$^{0.5}$ + IDATE*HAB8 + IDATE*AREA + IDATE*WDIST$^{0.5}$ + HDIST$^{0.5}$*WDIST$^{0.5}$)	Remove HDIST$^{0.5}$*AREA interaction	6304.96	25	0.54	0.76
H(IDATE + HAB8 + AREA$^{0.5}$ + HDIST$^{0.5}$ + WDIST$^{0.5}$ + IDATE*HAB8 + IDATE*AREA$^{0.5}$ + IDATE*WDIST$^{0.5}$ + HDIST$^{0.5}$*WDIST$^{0.5}$)	Replace linear form of AREA with SQRT form	6305.04	26	0.62	0.73
H(IDATE + HAB8 + WDIST$^{0.5}$ + IDATE*HAB8 + IDATE*AREA$^{0.5}$ + IDATE*WDIST$^{0.5}$ + HDIST$^{0.5}$*WDIST$^{0.5}$)	Remove HDIST$^{0.5}$*AREA$^{0.5}$ interaction	6305.31	25	0.89	0.64
H(IDATE + HAB8 + AREA$^{0.5}$ + HDIST$^{0.5}$ + WDIST$^{0.5}$ + IDATE*HAB8 + IDATE*AREA$^{0.5}$ + IDATE*WDIST$^{0.5}$ + HDIST$^{0.5}$*WDIST$^{0.5}$)	Replace HDIST$^{0.5}$*AREA$^{0.5}$ interaction; add CROP	6306.18	27	1.76	0.41

Table 2.9. Coefficient estimates, standard errors (SE) and 95% confidence intervals (C.I.) for best approximating model of duck nest hatching rates in south-central Canada

Effect	Estimate	SE (C.I.)
Intercept	0.8211	0.7576 (-0.6638, 2.3060)
$HAB_{(CROP)}$	-2.4063	1.2629 (-4.8816, 0.0690)
$HAB_{(GRASS)}$	0.3713	0.7266 (-1.053, 1.7954)
$HAB_{(GRSSH)}$	-2.6960	1.6910 (-6.0104, 0.6184)
$HAB_{(HAY)}$	5.1734	1.2882 (2.6485, 7.6983)
$HAB_{(PCOV)}$	2.0596	0.7551 (0.5796, 3.5396)
$HAB_{(SHRUB)}$	0.8203	0.8744 (-0.8935, 2.5341)
$HAB_{(WETL)}$	0.7730	0.8468 (-0.8867, 2.4327)
$HAB_{(WOOD)}$	0	.
IDATE	0.0080	0.0050 (-0.0018, 0.0178)
AREA	0.2558	0.1587 (-0.0553, 0.5669)
$HDIST^{0.5}$	0.0559	0.0222 (0.0124, 0.0994)
$WDIST^{0.5}$	0.1270	0.0689 (0.0080, 0.2620)
$IDATE*HAB_{(CROP)}$	0.0158	0.0085 (-0.0009, 0.0325)
$IDATE*HAB_{(GRASS)}$	-0.0014	0.0051 (-0.0114, 0.0086)
$IDATE*HAB_{(GRSSH)}$	0.0205	0.0117 (-0.0024, 0.0434)
$IDATE*HAB_{(HAY)}$	-0.0313	0.0083 (-0.0476, -0.0150)
$IDATE*HAB_{(PCOV)}$	-0.0112	0.0053 (-0.0216, -0.0008)
$IDATE*HAB_{(SHRUB)}$	-0.0084	0.0062 (-0.0207, 0.0037)
$IDATE*HAB_{(WETL)}$	-0.0053	0.0062 (-0.0175, 0.0069)
$IDATE*HAB_{(WOOD)}$	0	.
$AREA*HDIST^{0.5}$	0.0082	0.0058 (-0.0032, 0.0196)
IDATE*AREA	-0.0022	0.0010 (-0.0042, -0.0002)
$IDATE*WDIST^{0.5}$	-0.0007	0.0005 (-0.0017, 0.0003)
$HDIST^{0.5}*WDIST^{0.5}$	-0.0053	0.0024 (-0.0100, -0.0006)
EDGEDEN	0.0117	0.0058 (0.0003, 0.0231)
$EDGEDEN^2$	-0.0001	<0.0001 (-0.0002, 0.0000)

Figure 2.6. Receiver operator characteristic (ROC) curve for best approximating model of duck hatching rates.

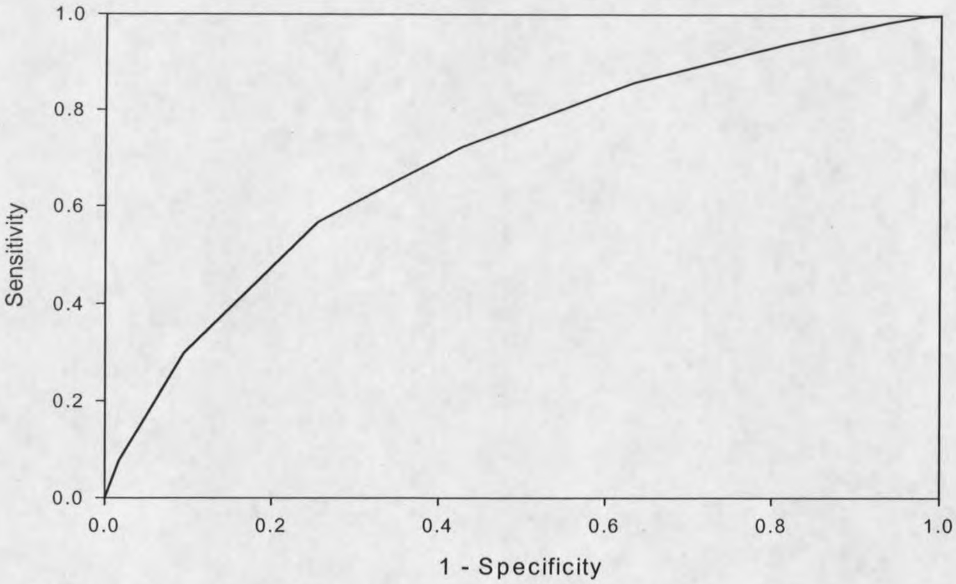
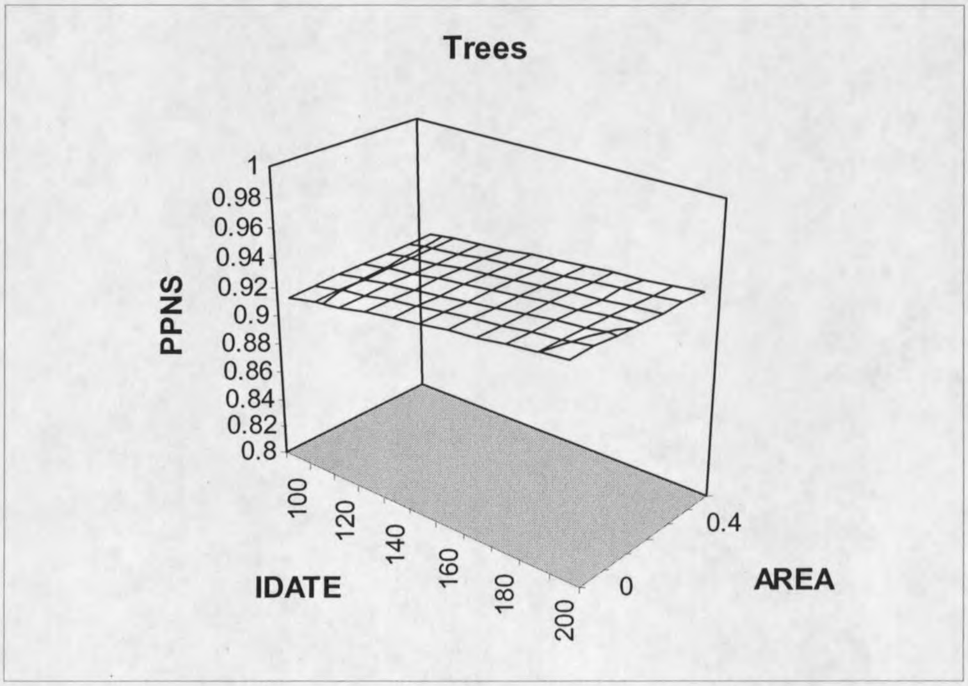
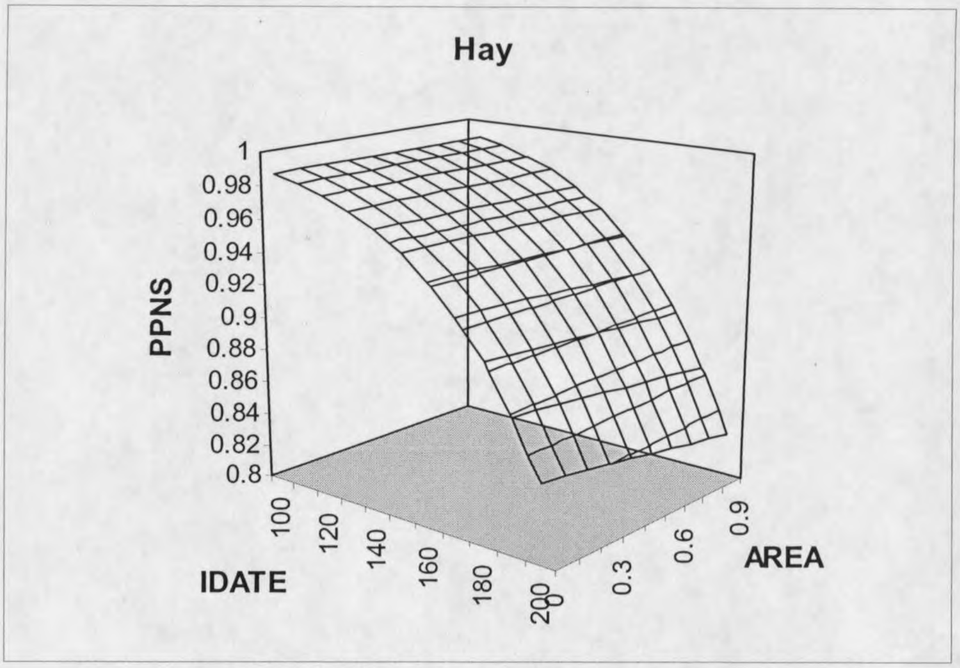
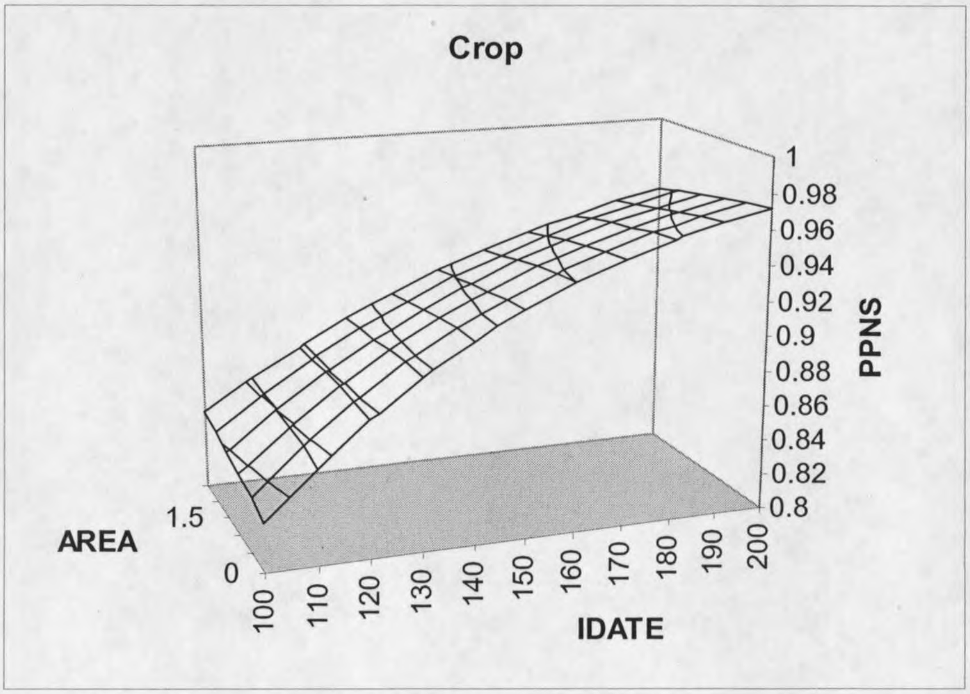
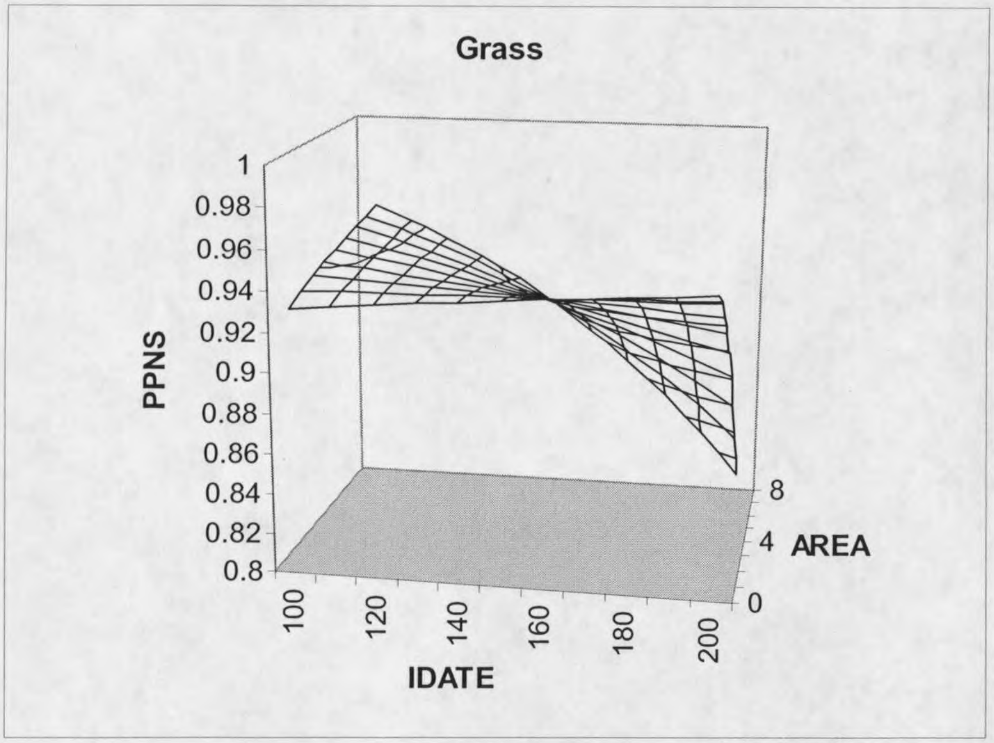


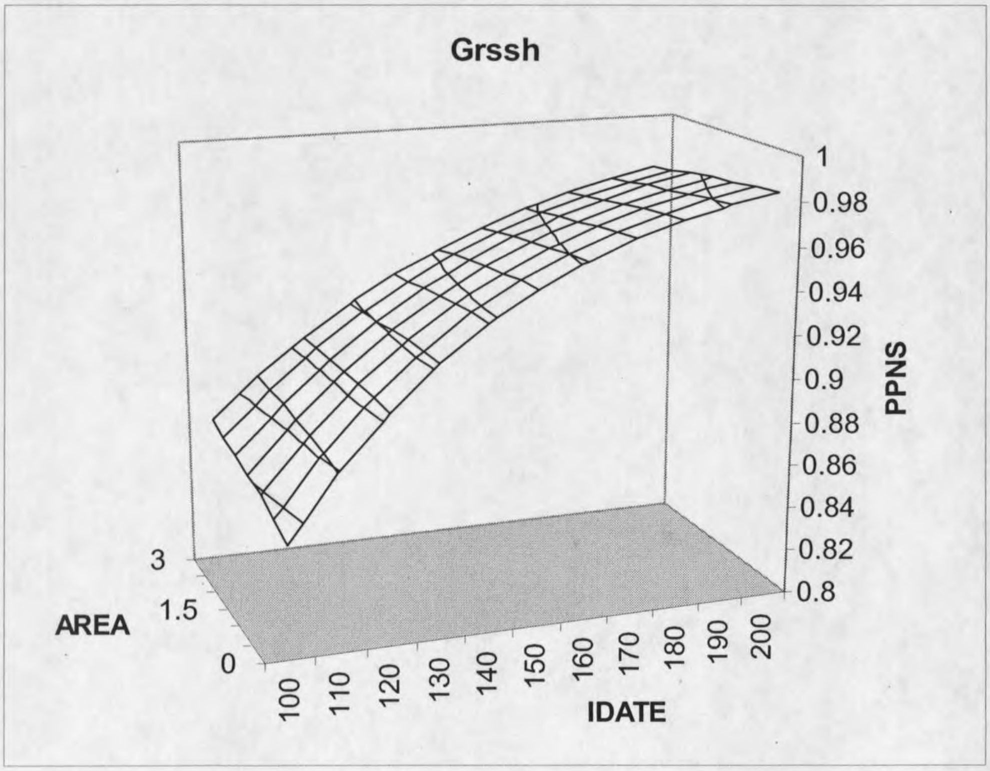
Figure 2.7. Response surface of daily survival rate of nests (PPNS) for AREA*IDATE interaction by habitat type. PPNS^{34}= proportion of nests expected to hatch. Range of AREA axis varies to represent the range of patch sizes for each habitat type

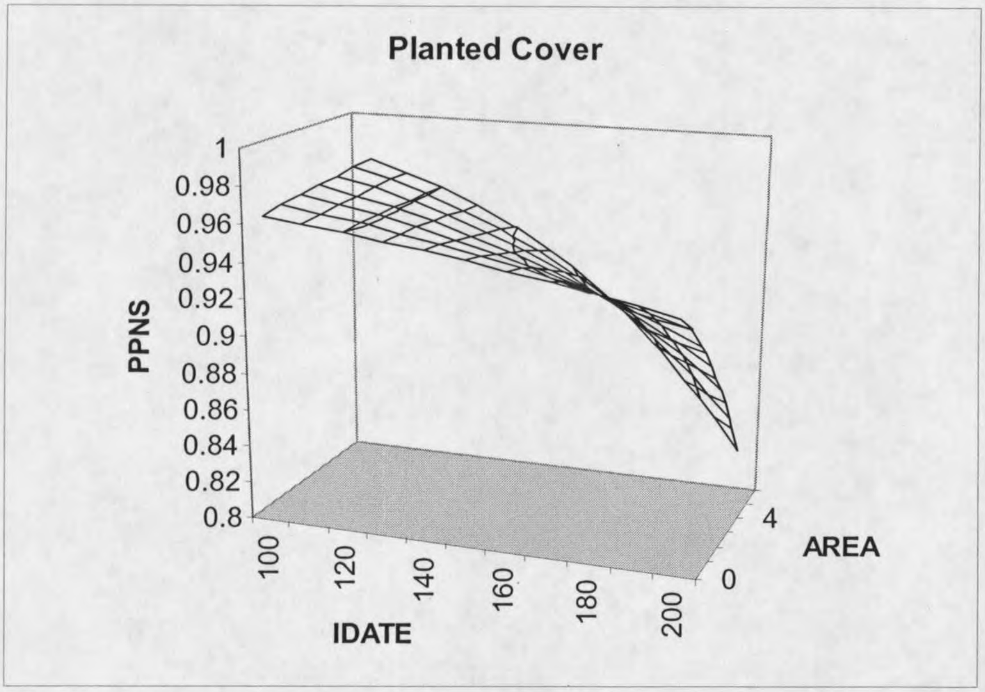


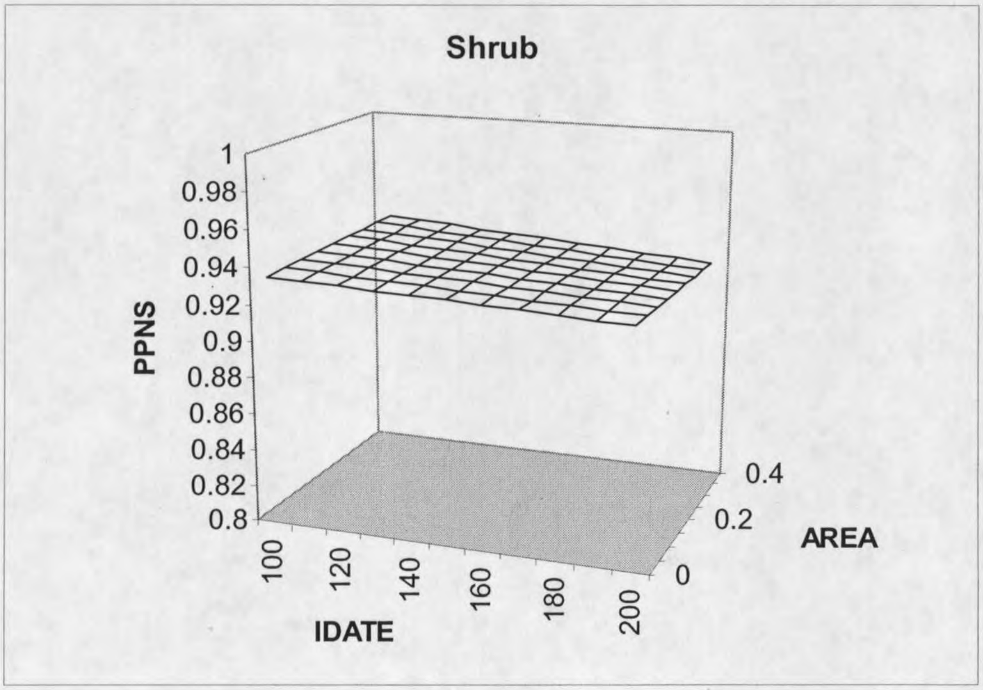

Hay
PPNS
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
IDATE
100
120
140
160
180
200
AREA
0
0.3
0.6
0.9


Crop
PPNS
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
AREA
1.5
0
IDATE
100
110
120
130
140
150
160
170
180
190
200


Grass
PPNS
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
100
120
140
160
180
200
IDATE
8
4
0
AREA


Grssh
PPNS
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
AREA
3
1.5
0
100
110
120
130
140
150
160
170
180
190
200
IDATE


Planted Cover
PPNS
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
100
120
140
160
180
200
IDATE
0
4
AREA


Shrub
PPNS
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
0.8
100
120
140
160
180
200
IDATE
0
0.2
0.4
AREA

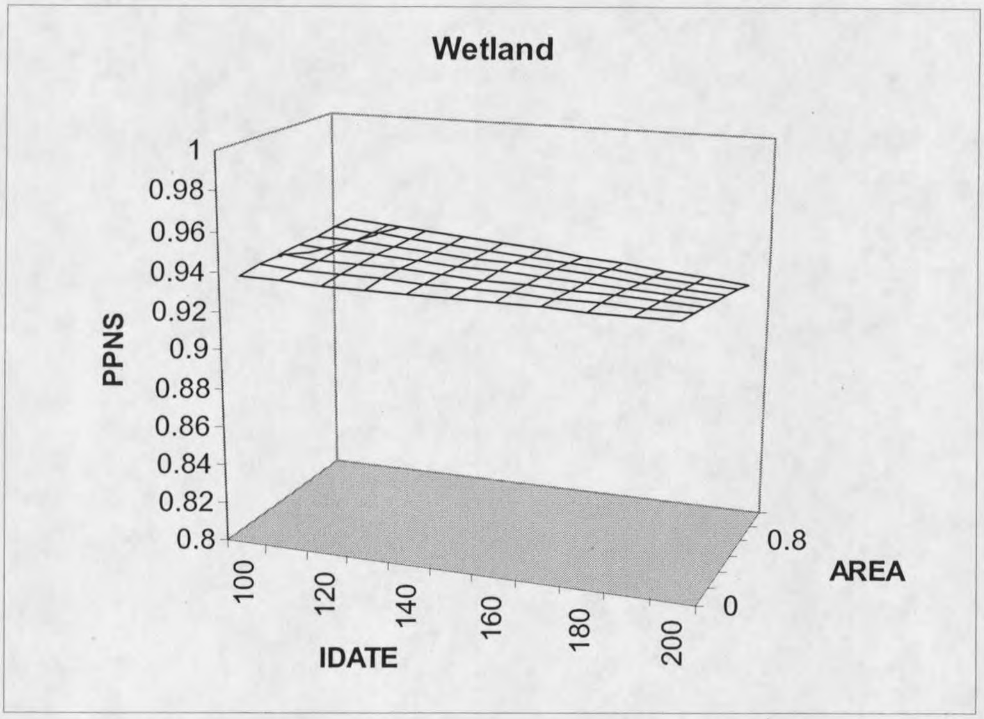


Figure 2.8. Surface representing interaction between HDIST and WDIST

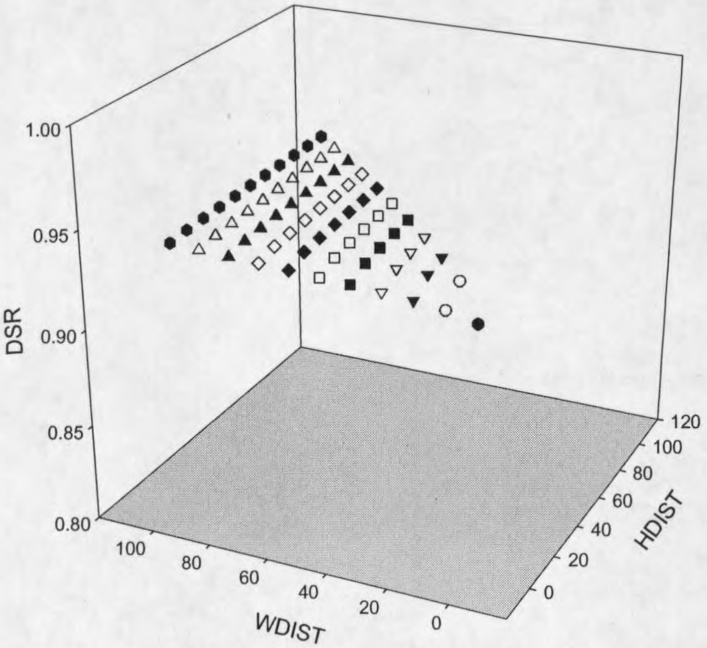
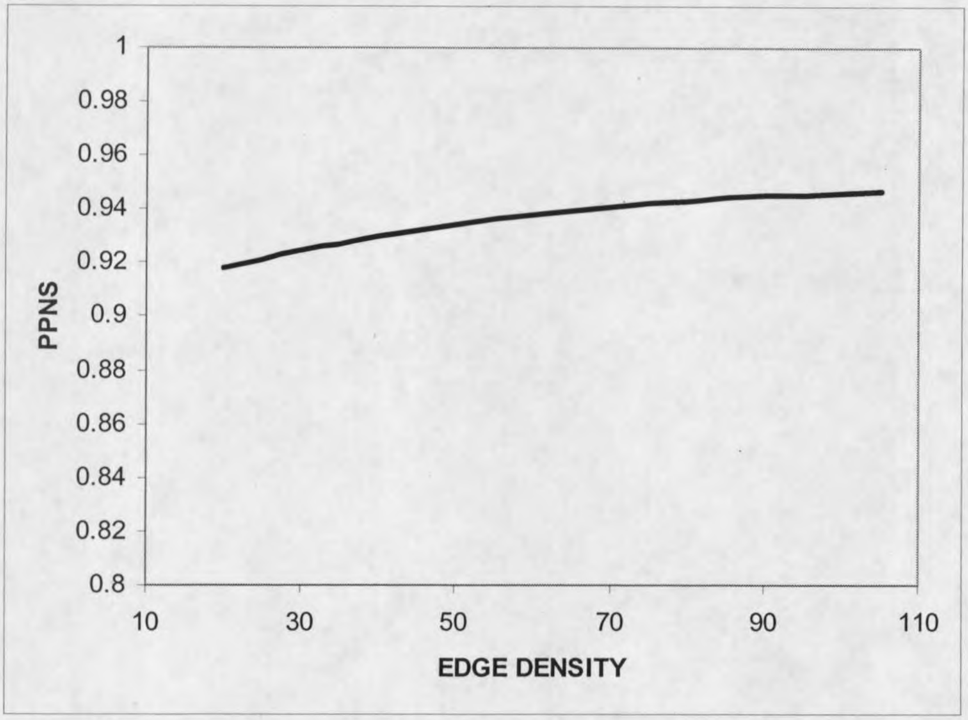


Figure 2.9. Relation between daily survival rate (PPNS) and edge density measured within a 0.65-km^2 circle centered on the nest.



In this study, the selection of appropriate scales at which to investigate patterns of hatching rates was complicated by the complexity of the study system, i.e., we were attempting to model patterns of hatching rates for a number of duck species, and the process in which we were most interested—nest predation—is mediated through a variety of predator species. There may be other scales that would yield models with improved precision. Chalfoun et al. (2002) found that fragmentation effects were most commonly detected at the landscape scale. This is in contrast with our results where the best models included mostly covariates measured at the patch scale. Nevertheless, inclusion of covariates from multiple scales ultimately improved our final model.

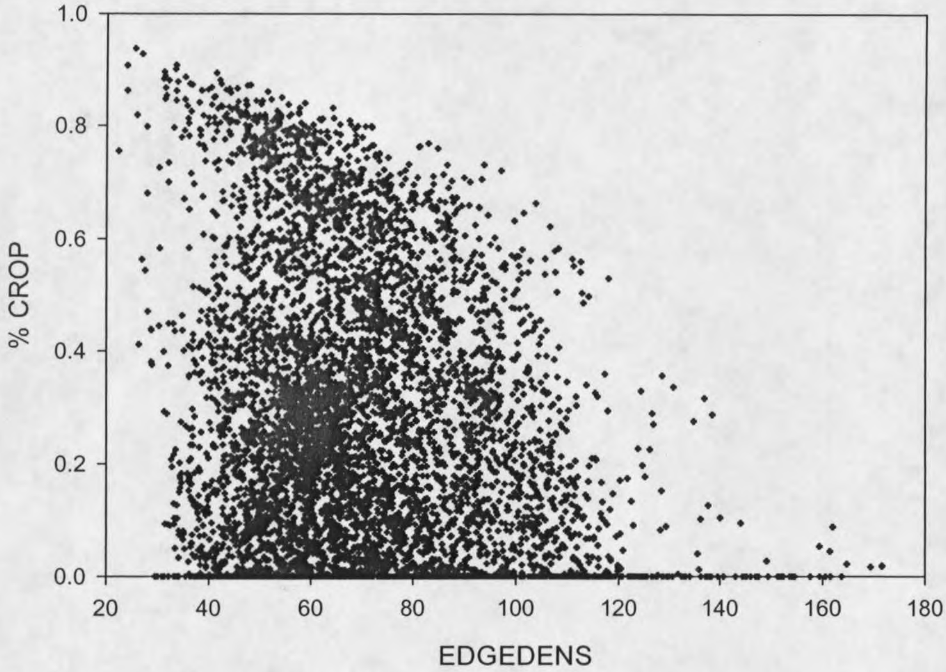
The amount of annual crop is conspicuously absent from our best approximating models. It's absence is notable because a negative relationship between the amount of cropland and hatching rates is the main conceptual model guiding many management efforts to improve duck hatching rates in the prairie pothole region. Greenwood et al. (1995) also failed to find a significant relationship between the percentage of cropland and hatching rates on parkland habitats for species other than northern pintails (*Anas acuta*). In contrast, they and several other authors have detected a difference between the percentage of cropland and duck hatching rates in prairie regions (Greenwood et al. 1995, Horn 2000, Reynolds et al. 2001). This apparent difference between parkland and prairie may be related to a more complex predator community (more avian nest predators) in the parklands but merits future study.

The only factor that improved our predictions of hatching rates from the aggregated scales we examined was edge density collected within 0.45 km of the nest. Hatching rates increased with the total amount of edge within 0.45 km of the nest (Figure 2.9). This effect was in the opposite direction than we predicted and seemingly incongruous with the fact that, at the patch scale, hatching rates increased with distance from a habitat edge. To better understand this relationship, and the absence of percentage crop in our models, we plotted EDGEDENS against % CROP (Figure 2.10). From this plot it becomes apparent that the 2 factors are not entirely independent. In this landscape as natural areas are converted to annual crops, the total amount of edge declines. Thus, there may be an effect of cropland that is masked in our data. Future studies should carefully consider how anthropogenic changes to the landscape might affect values of landscape metrics.

Overall, hatching rates were related to a number of landscape attributes. Planners and mangers should consider the spatial configuration of habitat features when attempting to model or affect duck hatching rates. These analyses, for the first time, allowed the exploration of how landscape features measured at individual nests affect hatching rates and demonstrate the extremely complex dynamics that drive reproductive success of parkland-nesting ducks. Because the dynamics are clearly complicated, complex models are needed to make advancements in our understanding. Recent analytical advancements allow this.

Despite these complexities, certain situations result in high hatching rates. Early in the season, hay fields and large patches of planted cover had high hatching rates. Similarly, nests away from habitat edges, especially wetland edges, also experienced relatively low predation rates. It is not clear, however, what mechanisms are driving these patterns. We know that predators are the prime agents of nest loss. Thus, knowledge of predator foraging patterns and the role of alternate prey items will be crucial to improving our understanding. However, these are difficult topics to study. Also needed are more studies that investigate the effects of spatial habitat configurations on duck nesting. We had little to build on for our *a priori* models. Finally, future studies will demonstrate the most rapid advances in knowledge if they simultaneously measure spatial and temporal factors that affect hatching rates.

Figure 2.10. Relationship between the proportion of crop fields and habitat edge density measured within 0.65-km^2 circles centered on nests



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CHAPTER 3.

MALLARD NEST-SITE SELECTION IN AN ALTERED ENVIRONMENT: PREDICTIONS AND PATTERNS

Introduction

An animal's reproductive success and survival depends critically on the choices it makes when selecting habitat for breeding. We expect, then, that habitat choice should be adaptive and that individuals should, either instinctively or through learning select those habitats where they are able to produce more progeny, survive better, or both (e.g., Fretwell and Lucas 1970, Rosenzweig 1981). If individuals experience variation in survival or reproduction among habitats and if there are proximate habitat cues that allow individuals to discern which habitats are likely to yield the highest individual fitness, we expect selection to develop (Misenhelter and Rotenberry 2000, Rolstad et al. 2000).

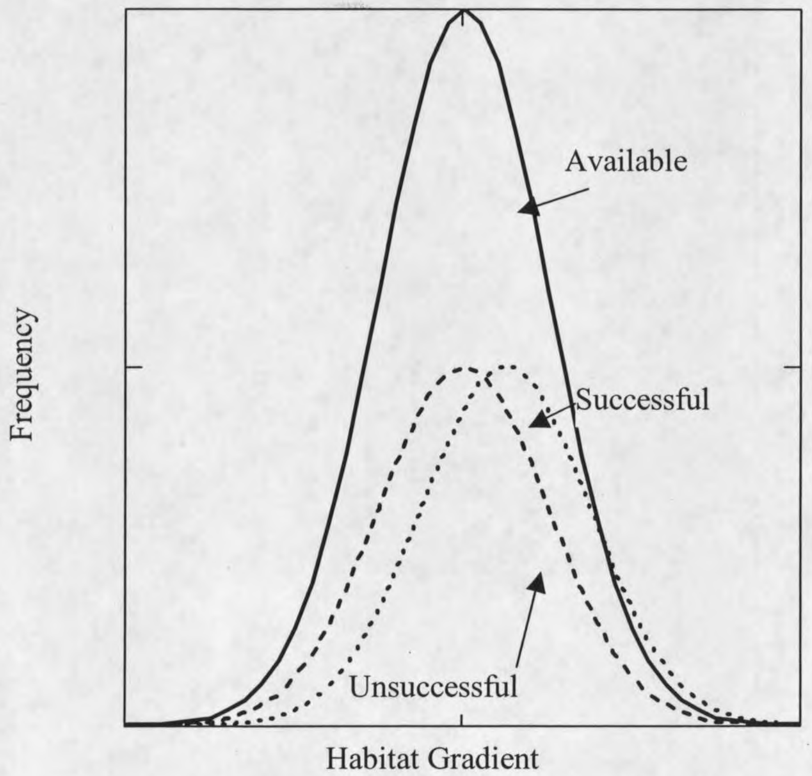
For birds, and especially for ground-nesting birds, the choice of a nest site likely has important consequences for both the chances of the individual's reproductive success and survival. For example, Badyaev (1995) identified several habitat characteristics that, when selected as nest sites, led to higher reproductive success of turkeys (*Meleagris gallopavo*). Similarly, Clark et al. (1999) identified a number of spatially explicit habitat features that resulted in high hatching rates for ring-necked pheasants (*Phasianus colchicus*).

Many researchers have attempted to better understand how patterns of nest-site selection differ from random placement (e.g., Ramsey et al 1994, Ripple et al. 1997, Pribil 1998). If nest-site selection has been subject to natural selection, we would expect those habitats selected most commonly to yield higher reproductive success, to confer higher female survival, or to provide both when compared to those habitats used less frequently (e.g., Orians and Wittenberger 1991).

Although observed nest distributions have led some to infer that habitat-specific variation in nest success has generated habitat preferences, rarely have observed patterns been cast as specific predictions about the fitness consequences of nest-site selection and more rarely have these predictions been tested (Clark and Shutler 1999). A complicating factor is that observed patterns may result from short-term spatial variation in predation pressure, which we expect to be more variable than longer-term evolutionary pressures (Clark and Shutler 1999). This lack of formal predictions and tests has hindered the development of generalities about the evolutionary ramifications of nest-site selection and may lead to erroneous conclusions (Jones 2001, Morrison 2001). Clark and Shutler (1999) examined patterns of nest-site selection and provided a theoretical framework from which to base predictions about how selection patterns should vary with different selection pressures. They concluded that mallards chose nest sites in a manner consistent with directional natural selection (Figure 3.1), although the relationship was not particularly strong. Furthermore, they encouraged researchers to "first measure natural selection pressure (consequences of choosing a nest site) and then predict and test for adaptive responses in habitat use." Accordingly, we used the results from our analysis of hatching rates (Chapter 2) as *a priori* predictions of nest-site selection.

Ducks provide an excellent opportunity to study nest-site selection theory – they show much individual variation in the characteristics of nest sites used, it is relatively easy to acquire large sample sizes of nests, and we have documented evidence of habitat-specific differences in success. Further, hatching rates of nests are the most important determinant of mid-continent mallard population dynamics (Hoekman et al. 2002). Thus, we expect strong selection for safer sites.

Figure 3.1. Hypothetical model of habitat selection representing conditions needed for directional selection (adapted from Clark and Shutler 1999).



However, the situation is complicated by anthropogenic habitat alteration. Several authors have reported evidence that hatching rates have declined due to habitat alteration (Clark and Nudds 1991, Beauchamp et al. 1996). In terms of nest-site selection processes, this pattern of decline might be explained in 2 ways: (1) either the historic range of variability along habitat gradients that previously characterized "safe" sites in which to locate nests has been altered by changes to the landscape (i.e., fewer "safe" sites in the landscape), or (2) selection patterns that developed through evolutionary time no longer result in the safest sites being selected for nests sites as a result of anthropogenic changes to the landscape and predator populations (i.e., selection has become decoupled from suitability; Misenhelter and Rotenberry 2000) and these changes have occurred too rapidly for natural selection to result in optimal nest-site choices. Therefore, though we expect nest sites to be selected in a manner that maximizes fitness, we recognize that there may be alternative explanations for observed patterns.

In summary, our primary objective was to examine whether current patterns of mallard nest-site selection conform to the prediction that habitat choices should maximize fitness. We did this by testing whether observed relationships between spatially explicit habitat features and hatching rates resulted in adaptive choices of nest sites. This research was conducted using a large sample of nests from radio-marked female mallards collected throughout the aspen parklands of south-central Canada at 15 sites that varied widely in their habitat configurations. In doing so, we examined a number of hypotheses related to the scale of observation and how habitats were classified.

Hypotheses and Predictions

To generate hypotheses about how mallards may select nest sites, we reviewed the literature, and in accordance with the recommendations of Clark and Shutler (1999), we constructed specific hypotheses based on the patterns of hatching rates we observed in Chapter 2. Below, we provide details for 3 key features of habitat: different habitat classification schemes, the scale of measurement, and specific spatial characteristics.

Habitat classification

One complication with habitat-selection studies is defining what comprises habitat. Mallards nest in a number of different vegetation types (Cowardin et al. 1985, Greenwood et al. 1995), and most of the predators that prey on duck eggs also are habitat generalists. Furthermore, the values of many of the commonly used landscape metrics depend critically on how habitats are defined (Chapter 2). Thus, using a habitat classification system that matches how the organisms being studied perceive their environment becomes critical. Because these fundamental uncertainties exist, we felt it would be valuable to consider a number of alternatives and determine which was best supported by the data. Therefore, we examined 3 different habitat classification schemes. The performance of models of hatching rates based on an 8-habitat classification was similar to those using a 4-habitat classification, whereas, models of hatching rates built using a 2-habitat classification performed poorly (Chapter 2). Therefore, our *a priori* expectation was that models built with more detailed habitat classifications would predict nest-site selection better than models built with more general classifications.

Scale

Many of the same uncertainties described for habitat classification apply to the scale of observation. It is crucial that observations of natural systems are recorded at scales relevant to the organisms being studied (Kotliar and Wiens 1990, Levins 1992). Several studies have examined mallard nest-site-selection at the microhabitat scale (Joyce 2001, Glouteny 1997). Habitat selection, however, may be a hierarchical process. Johnson (1980) described 4 nested scales of habitat selection and others have documented scale-dependent patterns of nest-site selection in bird species (e.g., Cowardin et al. 1985, Orians and Wittenberger 1991, Badyaev 1995, Clark et al. 1999, Misenhelter and Rotenberry 2000). Choice of a home range may ultimately constrain which habitats are available for nest sites. Models of hatching rates built using attributes estimated from the patch containing the nest performed better than models using attributes estimated from 0.65 or 10.36 km^2 circular buffers surrounding individual nests (Chapter 2). Therefore, we similarly predicted that models of nest-site selection using patch-scale attributes would discriminate between nest sites and random points better than models using attributes estimated from circular buffers. However, including covariates collected at more than one scale ultimately improved the fit of our models of hatching rates (Chapter 2). Therefore, we predicted that covariates from multiple scales may improve the predictions of our models of nest-site selection.

Spatial Attributes

There have been few previous studies of spatial features and how they affect nest-site selection. Thus, it was difficult to establish hypotheses/predictions. However, we did find that the spatial arrangement of habitat features impacted hatching rates of duck nests (Chapter 2) and used that information along with results for other avian species in other landscape types to develop predictions. Habitat edges have the potential to influence predator foraging movements (Lariviere and Messier 2000, Chalfoun et al. 2002), and there is some evidence that hatching rates near habitat edges may be reduced (Lahti 2001, Chapter 2). Therefore, we predicted that mallards would select nest sites away from edges.

Wetland edges may be qualitatively different than other types of edges. Several species that prey on duck nests have been documented to forage preferentially in wetland fringes (Greenwood et al 1999, LaRiviere and Messier 2000, Phillips 2001). Consistent with this evidence, hatching rates were lower for nests near wetlands, and edge effects for wetlands were distinct from those of upland habitats. We predicted, therefore, that mallards would favor nest sites away from wetland edges. Further, we predicted that the relationship would begin to plateau as distance from wetlands increased, because the negative effect on hatching rates of nests near wetlands diminished with distance (i.e., nonlinear response).

Hatching rates on our study sites tended to be higher in large patches of habitat than in smaller patches (Chapter 2). Consequently, we expected mallards to select large habitat patches more often than small patches. Conversely, there was little evidence that a shape index (McGarigal and Marks 1993) that combined measures of patch area and perimeter was related to hatching rates; therefore, we did not expect a shape index to be a strong predictor of nest-site selection.

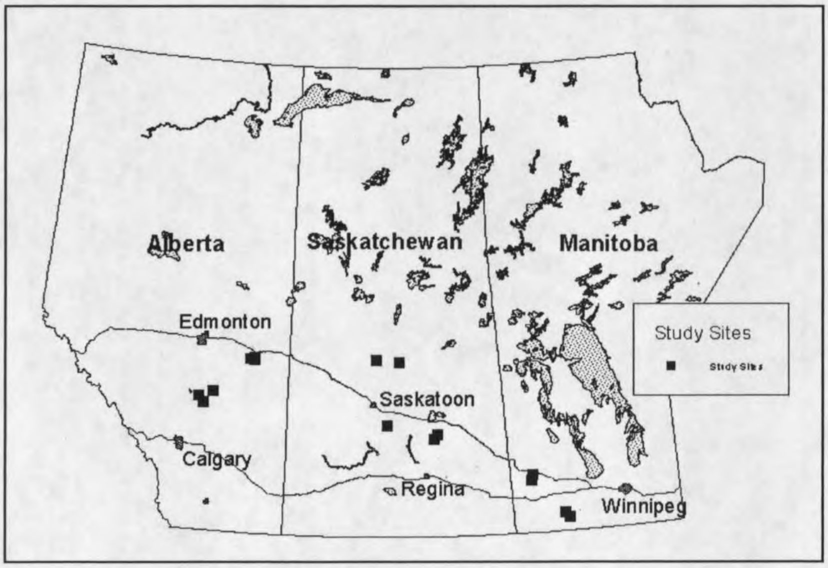
Methods

Study Areas

We collected mallard nest information at 15 sites throughout the aspen (*Populus tremuloides*) parklands of Manitoba, Saskatchewan, and Alberta, Canada (Figure 3.2) from 1993-1997. In 1993, the Hamiota, MB and Punnichy, SK sites were 78 and 54 km^2, respectively. Each of the remaining sites was 65 km^2.

The topography at all sites was flat to gently rolling. At all sites, agriculture was a dominant land use with cereal- and oil-seed production and livestock grazing being most prominent. Despite these similarities, the 15 sites varied widely in their landscape compositions and the degree to which remaining natural habitats were fragmented (Table 3.1). Mallard populations ranged from 2.3 to 13.8 breeding pairs per km^2.

Figure 3.2. Map showing locations of the 15 study sites in the Parkland region of south-central Canada.



Data Collection

Locating and monitoring nests. We located mallard nests by tracking 111-137 radio-tagged female mallards at each site. Pre-laying mallards were decoy-trapped (Sharp and Lokemoen 1987, Ringelman 1990) and radio-marked in April. From 1993-1995, each female was outfitted with a transmitter that was either abdominally implanted (Korschgen et al 1984, Olsen et al. 1992, Rotella et al. 1993) or back-mounted with an anchor-and-suture attachment (Mauser and Jarvis 1991, Paquette et al. 1997). In 1996 and 1997 only abdominally implanted transmitters were used as we became concerned about the utility of using back-mounted transmitters for studying duckling survival (IWWR, unpublished data). We released birds back onto the wetland where they were caught following radio attachment.

We used a null-array vehicle-mounted receiving system to estimate the location of each radiomarked female twice daily between 0600 and 1300 hours, i.e., when they were most likely to be attending their nests (Glouteny et al. 1993). When daily telemetry locations placed a female near the same place in nesting cover for 3 consecutive mornings, we used a handheld antenna to closely approach the female. Prior to 31 May 1994, we intentionally flushed females and then located their nests. To cause less disturbance to females and, hence, reduce nest abandonment, after 31 May 1994 we estimated the female's location using a hand-held antenna and triangulation, recorded the estimated location, and then left the area without flushing the bird. We returned in the afternoon to search for the nests at a time when females typically were away from nests. Subsequently, if a female was absent from her nest for 2 consecutive morning telemetry locations, we returned to the nest to determine its fate. We candled eggs in all nests when they were located to determine their stage of laying/incubation (Weller 1956). If a nest was destroyed or abandoned, we continued to track the bird to identify renesting attempts. Radio-tracking continued until the bird emigrated from the study area, was killed, or until 15 July.

We assigned each nest to 1 of 7 habitat types that corresponded to the dominant vegetation type within a 5 m radius of the nests. Habitat types included grass, hay, planted cover (a mixture of grasses and legumes planted specifically as wildlife habitat), crop fields, trees (woody vegetation with >30% areal coverage and an average height > 6 m), shrub (woody vegetation with >30% areal coverage and an average height ≤ 6 m tall), and emergent wetland vegetation.

Spatial habitat data. We digitized habitat information from stereo pairs of 1:5000 black and white infrared aerial photographs taken during July or August of the year the study site was under investigation. This resolution allowed us to capture each habitat feature ≥10 m in its widest dimension. This corresponded to our definition of a habitat patch as recorded at nests in the field. Digitized maps were imported into the SPANS geographical information system (GIS; PCI Geomatics, Richmond Hills, Ontario, Canada). We used a differentially corrected global positioning system to map nest locations. Nest locations were imported into the GIS and overlain onto digitized habitat maps. Nest locations that did not correspond between field observations and GIS habitat maps were deleted from all further analyses (see Chapter 2 for additional details).

Table 3.1. Locations and habitat compositions for 15 sites studied from 1993-1997 is south-central Canada.

					Wetland Density (#/km^2)										
Study Site	Province	Year	Latitude	Longitude	II[a]	III[a]	IV[a]	Total	%Crop	%Hay	%Planted	%Grass	%Trees	%Shrub	%Wetland
Hamiota	MB	1993	50.28	-100.75	0.7	12.6	0.6	13.9	77.5	0.5	0.0	3.0	4.4	3.6	9.1
Punnichy	SK	1993	51.35	-104.38	2.9	21.5	4.2	28.6	64.5	1.1	4.5	9.0	8.3	2.1	9.4
Belmont	MB	1994	49.45	-99.53	6.9	7.8	7.2	21.9	39.8	8.3	0.8	17.2	5.9	8.3	17.4
Davis	SK	1994	53.18	-105.68	1.2	13.4	7.9	22.5	47.2	8.7	2.9	11.3	5.9	6.2	15.3
Erskine	AB	1994	52.35	-112.98	5.3	12.5	6.4	24.2	34.6	6.1	0.0	34.0	4.4	4.2	14.2
Shoal Lake	MB	1995	50.40	-100.67	5.2	17.6	3.1	25.9	40.7	0.8	0.0	8.0	5.1	7.5	36.8
Kutawa	SK	1995	51.45	-104.23	1.0	22.0	4.4	27.4	57.2	2.6	0.0	14.6	6.4	2.8	15.0
Camp Lake	AB	1995	53.17	-111.60	6.0	24.1	7.2	37.3	42.0	2.0	6.4	24.9	6.7	6.1	10.6
Baldur	MB	1996	49.45	-99.37	2.6	3.1	4.2	9.9	29.0	6.0	6.8	16.9	16.2	2.7	20.7
Parkside	SK	1996	53.20	-106.60	0.3	4.9	2.6	7.8	58.3	8.8	0.4	13.1	7.3	0.9	8.5
Pine Lake	AB	1996	52.22	-113.47	4.5	24.3	5.6	34.4	20.3	9.4	0.0	36.0	16.6	3.0	13.0
Willowbrook	SK	1997	51.25	-102.95	6.3	18.3	5.3	29.9	53.2	5.3	2.2	12.2	8.6	5.6	11.3
Allan Hills W.	SK	1997	51.68	-106.12	1.1	9.5	8.7	19.3	51.3	1.3	17.7	10.1	1.5	3.3	13.9
Mixburn	AB	1997	53.17	-111.43	7.4	32.3	17.4	57.1	45.8	5.3	6.2	15.9	3.5	6.5	16.2
Elnora	AB	1997	52.07	-113.30	8.7	22.9	3.0	34.6	9.4	6.7	0.0	43.5	19.8	7.1	11.8

[a] Represents wetland permanence class according to Stewart and Kantrud (1971); II=temporary wetlands, III=Seasonal, IV=Semipermanent

We compared attributes of nest sites to a sample of 499 randomly-generated points for each site. Mallards occasionally select annual cropland as nesting habitat, but far less than expected by chance (Cowardin et al. 1985, Greenwood et al. 1995). Despite comprising, on average, 48 % of our study areas, only ~3 % of mallard nests were located in annual crop fields. Thus, we restricted our sample of random points to habitat types other than annual cropland. We felt comparisons of nests sites to a purely random sample of points (48% of which could be expected to fall in crop fields that have substantially different spatial attributes) would be uninformative because crop fields have very different spatial attributes than other habitat types. Nests in annual crop fields are not discussed further. For each nest and random point, the attributes we generated from GIS maps included habitat type, patch size, and a shape index (Magarigal & Marks 1994: page C5) that combines estimates of patch size and the perimeter of the patch to indicate the degree with which a patch deviates from a circular standard. We also calculated linear distances between the nest and (1) the nearest habitat edge and (2) the nearest wetland edge. Definitions of habitat covariates can be found in (Table 3.2).

Given our interests in different habitat classification schemes, we classified our map 3 different ways and measured landscape metrics for each. The most general classification had 6 habitats after we dropped crop. The next most general classification had 3 habitats; for this classification, we again classified hay fields and planted cover fields separately, but combined the remaining habitats (grass, trees, shrub, and wetland) into a single habitat type that we termed Natural. Finally, our simplest habitat classification used 2 classes: (1) crop fields or (2) an aggregate of all other vegetation types (i.e., grass, hay fields, DNC fields, trees, shrubs, wetlands). Thus, this scheme consisted of habitat patches embedded in a matrix of seldom-used crop. For each of these classifications, WDIST remained the same.

To determine whether there were scale-dependent patterns of nest-site selection, in addition to considering the attributes of the habitat patch containing the nest or random point we also measured landscape attributes within 0.65-km^2 and 10.36-km^2 circular buffers centered on the nest or random point. The 10.36-km^2 (4 mi.^{2}) scale corresponds to the scale of much previous research and is thought to approximate the home range of a mallard in some prairie landscapes (Cowardin et al. 1985). The 0.65-km^2 scale corresponds to 0.25 mi^2 or the size of a legal quarter-section. Landowners and conservation agencies within the prairie pothole region typically make land-use decisions at the quarter- section scale; therefore, many of the spatial attributes of the landscape demonstrate measurable differences at this scale (See Chapter 2 for additional details).

Within each circle (both scales), we calculated the percentage of the area that was cropped, edge density, a mean patch shape index, and mean patch size (Table 3.2). Because each study area was a fixed size and because acquiring the fine-resolution habitat data we used is costly, we did not obtain data for all portions of circles for nests near the edges of the study area. Nests and random points were deleted from analyses if >50% of the 10.36 km^2 circle fell outside the area for which we had remotely sensed habitat information. For nests that had partial coverage, we assumed that the habitat configuration for the portion of the circle that was missing was similar to the area within the study area.

Table 3.2. Variable definitions and predicted relationships between covariate values and nest-site selection functions.

Scale	Variable	Definition	Predicted relationship	
			Linear/SQRT	Quadratic
Nest	HABn[a]	Habitat Type	$\beta_1 \neq \beta_2 \neq ,\ldots,$	
	AREAn	Habitat patch size	$\beta_{AREAn} > 0$	
	HDISTn	Distance from nearest habitat patch edge	$\beta_{EDGEDISTn} > 0$	
	SHAPEn	Habitat patch shape index[b]	$\beta_{SHAPEn} < 0$	
	WETDIST	Distance from nearest wetland edge	$\beta_{WETDISTn} > 0$	
$0.65\ km^2$	CROPB1	Percent of the circle comprised of annual crops	$\beta_{CROPB1} < 0$	$\beta_{CROPB1}^2 < 0$
	MEANAREAB1	Mean patch size within circle	$\beta_{MEANAREAB1} > 0$	$\beta_{MEANAREAB1}^2 < 0$
	MEANSHAPB1	Mean shape index for patches within circle	$\beta_{MEANSHAPB1} < 0$	$\beta_{MEANSHAPB1}^2 < 0$
	EDGEDENB1	Total km of edge/area of circle	$\beta_{EDGEDNB1} < 0$	$\beta_{EDGEDNB1}^2 > 0$
$10.36\ km^2$	CROPB2	Percent of the circle comprised of annual crops	$\beta_{CROPB2} < 0$	$\beta_{CROPB2}^2 < 0$
	MEANAREAB2	Mean patch size within circle	$\beta_{MEANAREAB2} > 0$	$\beta_{MEANAREAB2}^2 < 0$
	MEANSHAPB2	Mean shape index for patches within circle	$\beta_{MEANSHAPB2} < 0$	$\beta_{MEANSHAPB2}^2 < 0$
	EDGEDENB2	Total km of edge/area of circle	$\beta_{EDGEDNB2} < 0$	$\beta_{EDGEDNB2}^2 > 0$

[a] "n" refers to habitat classifications scheme; 6 = 6-habitat, 3 = 3-habitat.

All procedures used during this research were approved by the University of Saskatchewan's Protocol Review Committee on Animal Care and Supply (Protocol No. 920007).

Data Analysis

We used logistic regression to evaluate potential differences in landscape attributes between nest sites and random points. Modeling was performed using PROC LOGISTIC (SAS Institute 1999). We examined the correlation among potential covariates before beginning our modeling exercise to avoid the possibility of models with severe multicolliniarity.

To test whether or not birds selected sites that maximized their fitness, we created an *a priori* model list of competing models that were based upon the results of our analysis of hatching rates and the literature (see Hypotheses and Predictions section above). These competing models represent various combinations of our predictions about spatial features, habitat classification schemes, and the scale of measurement. The predicted effects of individual covariates are summarized in Table 3.2, and a list of the *a priori* models we considered can be found in Appendix A3.

Because in some instances square-root (SQRT) transformed covariate values fit our models of hatching rates better than linear covariates, we considered 2 alternate forms of our *a priori* models containing continuous variables. First, we modeled all continuous variables as linear effects. In a second suite of models, all continuous covariates were SQRT transformed prior to model fitting, which represented our prediction of a proportionally diminishing effect as covariate values increased. In our *a priori* set, all models were additive (i.e., interactions were not considered). We examined the same set of *a priori* models for each of our 3 different habitat classification schemes (6-habitat, 3-habitat, 1-habitat). Study area was included in all the models we considered to account for otherwise uncontrolled variation. Because the shape index we calculated for patches was a linear combination of patch area and amount of edge, we did not consider any models that included both shape index and patch size or any models that included shape index and distance from a habitat edge.

We developed an additional list of 9 *a priori* models (Appendix A3) to evaluate effects of landscape features measured at different scales on nest-site selection. Again we did not consider models that combined mean measures of patch shape with mean measures of patch size or edge density. For the comparison of models at various scales, we considered 3 different forms. As with the patch-scale models above, we examined models with both linear and SQRT effects. In this case, however, we also considered models where covariates were included as quadratic terms because prior examination of the landscape metrics indicated that some were related to the amount of cropland on the study area but in a predictably nonlinear fashion (Hargis et al. 1998).

We used information theoretic techniques to select the most parsimonious model (Burnham and Anderson 1998) from each of our suites of *a priori* models ($n = 150$ total models). Specifically, we used the small sample form of Akaike's Information Criterion ($\mathrm{AIC_c}$) to evaluate each of our *a priori* models. $\mathrm{AIC_c}$ is calculated as:

$$\mathrm{AIC_c} = -2\log(L(\hat{\theta} \mid y)) + 2K + \frac{2K(K+1)}{n-K-1}$$

where $L(\hat{\theta} \mid y)$ is the likelihood of a specific parameter value θ given the data y, K is the number of parameters in the model, and n is the sample size. We considered the model with the minimum AIC$_c$ value as the most parsimonious and used subtraction to rank other models according to their AIC$_c$ values to examine the 'strength of evidence' for each (i.e., $\Delta\text{AIC}_c = \text{AIC}_{ci} - \text{minAIC}_c$; Burnham and Anderson 2001). As further evidence of the relative support for individual models, we calculated Akaike weights for all models within each suite according to the formula:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta\text{AIC}_c)_i}{\sum \exp(-\frac{1}{2}\Delta\text{AIC}_c)_s}$$

where s is the suite of models in which the focal model i appears (Burnham and Anderson 1998:124). As evidence of the importance of individual predictors, we calculated average model weights, $\overline{w}_\theta = \frac{\sum w_i}{N_s}$ where N_s = the number of models in a given suite that contain a specific predictor, θ. This is an extension of the method given by Burnham and Anderson (1998: page 178) that accounts for individual covariates appearing in different numbers of *a priori* models.

We followed our examination of *a priori* models with an exploratory analysis that examined the influence of including additional effects including interactions, combinations of forms of covariates (i.e., mix of linear, SQRT, quadratic), and combinations of effects from multiples scales.

To further evaluate the fit of our final selected model we plotted the Receiver Operating Characteristic (ROC) curve. An ROC curve represents a plot of all the sensitivity values (true positive fraction) against all 1-specificity values (false positive fraction). The area under the curve (AUC) provides a measure of model performance (SAS Institute 1995, Pearce and Ferrier 2000).

Results

We used 1,710 mallard nests and 6,880 random points to model the selection function that describes mallard nests distributions. Birds had a wide range of available habitat configurations from which to choose nest sites (Tables 3.1, 3.3); therefore, we were well positioned to examine questions about the influences of landscape configurations, scale, and habitat classification schemes (see Hypotheses and Predictions).

Correlations generally were low among covariates (Table 3.4), except for where the same variable was measured at both the 0.65- and 10.36 km^2-scales. None of our models simultaneously considered models from both aggregated scales (e.g., EDGEDENB1 and EDGEDENB2); therefore multicolliniarity should not have confounded our models.

Table 3.3. Mean, standard error (SE) and range of covariates for nest and random points.

Covariate	Nest (n = 1,710)		Random Point (n = 6,880)	
Patch-Scale 6-Habitat	Mean (SE)	Range	Mean (SE)	Range
AREA6 (ha)	25.7 (2.2)	>0.1-793.2	49.3 (1.4)	>0.1-793.2
HDIST6 (m)	13 (0.4)	0-139	19 (0.3)	0-210
SHAPE6[a]	3.8 (0.09)	1.02-37.15	4.9 (0.07)	1.02-37.15
WETDIST (m)	40 (1.3)	0-524	53 (0.7)	0-581
Patch-Scale 3-Habitat				
AREA3 (ha)	448.1 (14.9)	>0.1-2581.7	466.8 (7.6)	>0.1-2581.7
HDIST3 (m)	34 (1.1)	0-389	57 (0.7)	0-427
SHAPE3[a]	11.1 (0.17)	1.12-26.90	10.5 (0.08)	1.19-26.90
Patch-Scale 1-Habitat	Mean (SE)	Range	Mean (SE)	Range
AREA1 (ha)	646.7 (17.6)	>0.1-2879.8	689.1 (9.1)	>0.1-2879.8
HDIST1 (m)	42.3 (1.24)	0-389	69.4 (0.86)	0-427
SHAPE1[a]	11.0 (0.14)	1.12-25.35	10.9 (0.07)	1.21-25.36
0.65 km^2 6-habitat				
MEANAREAB1 (ha)	0.5 (0.006)	0.1-2.7	0.6 (0.004)	0.1-5.1
EDGEDENB1 (km/km^2)	74.7 (0.6)	22.3-163.7	69.7 (0.3)	15.5-171.6
MEANSHAPB1	1.8 (0.003)	1.5-2.6	1.8 (0.001)	1.4-2.7
CROPB1 (%)	35 (0.6)	0-94	30 (0.3)	0-96
10.36 km^2 6-habitat				
MEANAREAB2 (ha)	0.7 (0.006)	0.3-2.2	0.7 (0.003)	0.3-2.8
EDGEDENB2 (km/km^2)	64.2 (0.4)	29.8-112.5	62.2 (0.2)	24.0-113.6
MEANSHAPB2	1.8 (.002)	1.6-2.1	1.8 (0.001)	1.6-2.1
CROPB2 (%)	40 (0.5)	0-89	41 (0.2)	0-91

Model selection

A large sample of nests allowed us to support models with a large number of parameters, and a number of spatial features helped explain patterns of nest-site selection. Within our a priori model sets, the best-supported models included habitat type, patch size, distance to a habitat edge, and distance to the nearest wetland. These variables were selected regardless of the habitat classification used or the form (linear vs. SQRT) of the continuous covariates we used to model these effects. However, there was some model-selection uncertainty. We describe our evaluation of our specific hypotheses, and provide parameter estimates below.

Comparison of habitat classification schemes

Our hypothesis that more detailed habitat classifications would yield better models was supported (Table 3.5). The 6-habitat models performed much better (ΔAIC >194) than the 3-habitat models, which, in turn, performed better (ΔAIC >12) than the models that combined all vegetation types (except annual crop) into a single habitat category (Figure 3.3A). For each of the habitat classification schemes, models using SQRT-transformed forms of continuous covariates performed better (ΔAIC >102) than their counterparts using linear forms of covariates. The most saturated model in each of our suites of additive "patch-scale" models (i.e., those containing effects for habitat type [6- and 3-habitat classifications], patch size, distance from a habitat edge and distance from the nearest wetland), received the most support (ΔAIC 0.06-24.90) from the data regardless of habitat classification or the form of the continuous covariates (Table 3.5).

Table 3.4 Pearson correlation coefficients among covariates at 15 sites in south-central Canada

	AREA6	HDIST6	SHAPE6	WETDIST	MEANAREAB1	EDGEDENB1	MEANSHAPB1	CROPB1	MEANAREAB2	EDGEDENB2	MEANSHAPB2	CROPB2
AREA6	1.000	0.23	0.72	0.05	-0.04	0.00	-0.06	-0.29	-0.11	0.13	-0.01	-0.29
HDIST6		1.00	0.02	0.42	0.19	-0.24	-0.01	-0.25	0.09	-0.17	0.07	-0.10
SHAPE6			1.00	-0.01	-0.16	0.20	-0.08	-0.22	-0.22	0.29	-0.10	-0.28
WETDIST				1.00	0.24	-0.19	0.09	-0.11	0.21	-0.17	0.11	-0.04
MEANAREAB1					1.00	-0.75	0.30	0.26	0.70[a]	-0.63	0.30	0.32
EDGEDENB1						1.00	-0.01	-0.35	-0.63	0.72	-0.21	-0.36
MEANSHAPB1							1.00	0.14	0.30	-0.01	0.62	0.22
CROPB1								1.00	0.34	-0.39	0.17	0.73
MEANAREAB2									1.00	-0.87	0.48	0.49
EDGEDENB2										1.00	-0.34	-0.57
MEANSHAPB2											1.00	0.30
CROPB2												1.00

[a] Never occurred simultaneously with other covariates in shaded cells in any model.

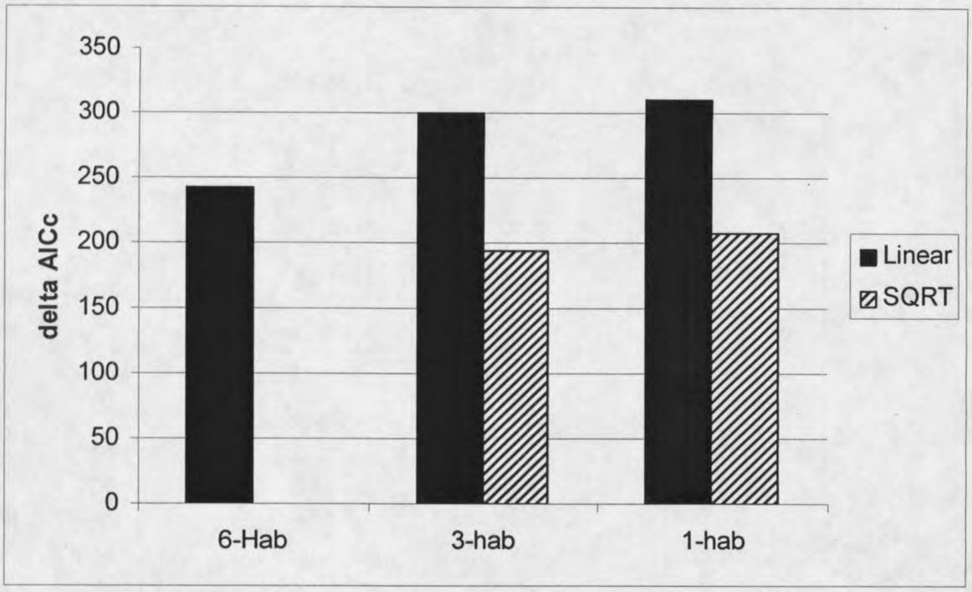
Table 3.5. Ranking of hypothesized models of mallard nest-site selection at 15 sites in south-central Canada. Rankings are based on Akaike's Information Criteria. Model suites are for covariates measured at the patch scale and compares models using 6- or 3- or 1-habitat classifications and either linear or square-root transformed forms of continuous covariates. Only models within 10 AIC values of the best model in each suite are presented

Hypothesized model	AIC	K	ΔAIC_i	w_i/w_*[a]
<u>6-habitat, linear form</u>				
N20) $H_{(HAB+AREA+HDIST+WDIST)}$	8088.40	23	0	1
<u>6-habitat, SQRT</u>				
N20) $H_{(HAB+AREA^{0.5}+HDIST^{0.5}+WDIST^{0.5})}$	7846.52	23	0	1
N16) $H_{(HAB+AREA^{0.5}+WDIST^{0.5})}$	7846.66	22	0.14	0.93
<u>3-Habitat, Linear form</u>				
N20) $H_{(HAB+AREA+HDIST+WDIST)}$	8146.27	20	0	1
N17) $H_{(HAB+HDIST+WDIST)}$	8150.85	19	4.57	0.10
<u>3-Habitat, SQRT</u>				
N20) $H_{(HAB+AREA^{0.5}+HDIST^{0.5}+WDIST^{0.5})}$	8040.80	20	0	1
N17) $H_{(HAB+HDIST^{0.5}+WDIST^{0.5})}$	8042.62	19	1.82	0.40
<u>1-Habitat, Linear form</u>				
N19) $H_{(AREA+HDIST+WDIST)}$	8156.60	18	0	1
N12) $H_{(HDIST+WDIST)}$	8162.30	17	5.71	0.06
<u>1-Habitat, SQRT</u>				
N19) $H_{(AREA^{0.5}+HDIST^{0.5}+WDIST^{0.5})}$	8053.78	18	0	1
N12) $H_{(HDIST^{0.5}+WDIST^{0.5})}$	8054.72	17	0.94	0.62

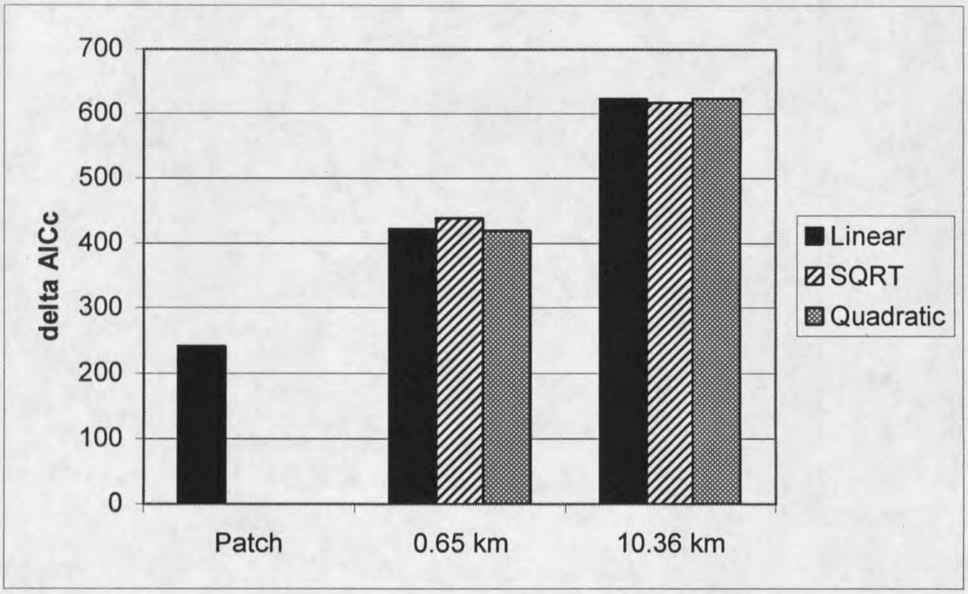
[a] w_i = AIC_c weight for an individual model divided by the AIC_c weight for the best approximating model from that suite of models. $w_i = \frac{\exp(-\frac{1}{2}\Delta QAIC_c)_i}{\sum \exp(-\frac{1}{2}\Delta QAIC_c)_s}$, where s is the suite of models in which the focal model i appears (Burnham and Anderson 1998:124).

Figure 3.3. Relative performance (ΔAIC_c values) for different suites of models: (A) patch-scale 6-hab vs. 3-hab vs. 1-hab, (B) patch scale vs. 0.65 km^2 vs. 10.36 km^2.

A.



B.



Within our best *a priori* model (N20 – SQRT, Appendix A3), the selection function was highest for planted cover, followed by trees. Estimates for the remaining habitats were similar (Table 3.6).

Table 3.6. Odds ratios for selection function for different habitats

Habitat Type	Odds Ratio[a]	Confidence Interval
Grass	0.434	0.364-0.517
Hay	0.480	0.370-0.621
Planted Cover	1.928	1.467-2.533
Shrub	0.600	0.493-0.730
Trees	1	
Wetland	0.479	0.400-0.575

[a] The odds of selecting each habitat type relative to selecting Trees. For example, mallards were nearly twice as likely to select Planted Cover as they were to select Trees. In contrast, they were only about half as likely to select Wetland as they were to select Trees.

Comparison of scales

In general, models generated using landscape variables collected within 0.65 km^2 and 10.36 km^2 circles centered on nests and random points performed poorly (ΔAIC >419) when compared to our best *a priori* "patch-scale" model (Tables 3.5, 3.7; Figure 3.3B). Thus our *a priori* prediction was supported. Within the 0.65-km^2 model set, models with SQRT covariates performed worse (ΔAIC >16) than models with either linear or linear plus quadratic terms. Within the 10.36-km^2 model set, models that included terms for % Crop and EDGEDEN were the most parsimonious (ΔAIC 0.05-0.52) regardless of the form of the covariates. Nevertheless, models constructed using information from this scale performed even worse than the models generated from covariates at the 0.65 km^2 scale (ΔAIC > 197 when compared to the best 0.65 km^2 model.)

Spatial Habitat Features

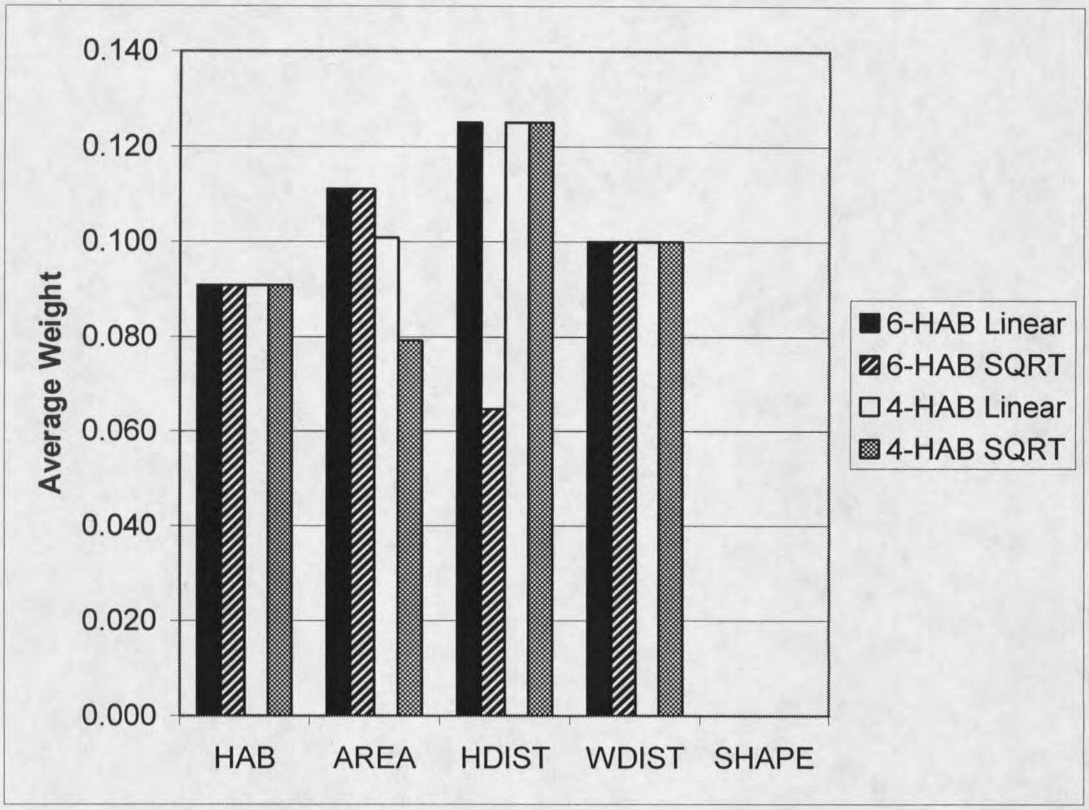
Opposite to our prediction, large habitat patches were selected for nests sites less than small habitat patches. Also contrary to our prediction, mallards tended to nest close to wetlands, despite the fact that nest predation rates were high there (Chapter 2). Our hypothesis that birds should choose to nest away from habitat edges was supported somewhat by our *a priori* models; however, confidence intervals for this effect included zero ($\beta_{\mathrm{HDIST}}{}^{0.5} = -0.0261$, S.E. = 0.018). There was little evidence that SHAPE was a useful covariate for predicting the likelihood of a given habitat patch being selected as a nest site (Figure 3.4).

Our best supported *a priori* model used the 6-habitat classification, and SQRT-transformed covariates measures at the patch scale. Planted cover was the most-selected habitat type (Table 3.5), and mallards tended to select small habitat patches (Table 5; $\beta_{\mathrm{AREA}}{}^{0.5} = -0.9391$, S.E. = 0.1006) close to wetlands ($\beta_{\mathrm{WDIST}}{}^{0.5} = -0.1335$, S.E. = 0.0108). Models that included or excluded distance to a habitat edge were ranked similarly (ΔAIC < 1; Table 5).

Table 3.7. Ranking of hypothesized models of mallard nest-site selection at 15 sites in south-central Canada. Rankings are based on Akaike's Information Criteria. Model suites are for covariates measured within 0.65- or 10.36-km^2 circles centered on nest locations and either linear or square-root transformed forms of continuous covariates. Only models within 10 AIC values of the best model in each suite are presented

Hypothesized model	AIC$_c$	K	ΔAIC$_{ci}$	w_i/w_*
<u>0.65 km^2, linear form</u>				
$B_1$6) $H_{(\mathrm{CROP + EDGEDEN})}$	8267.88	17	0	1
$B_1$9) $H_{(\mathrm{CROP + MEANAREA + EDGEDEN})}$	8269.55	18	1.67	0.43
<u>0.65 km^2, SQRT</u>				
$B_1$6) $H_{(\mathrm{CROP}^{0.5} + \mathrm{EDGEDEN}^{0.5})}$	8284.64	17	0	1
$B_1$9) $H_{(\mathrm{CROP}^{0.5} + \mathrm{MEANAREA}^{0.5} + \mathrm{EDGEDEN}^{0.5})}$	8285.88	17	1.24	0.54
<u>0.65 km^2, quadratic</u>				
$B_1$9) $H_{(\mathrm{CROP} + \mathrm{CROP}^2 + \mathrm{MEANAREA} + \mathrm{MEANAREA}^2 + \mathrm{EDGEDEN} + \mathrm{EDGEDEN}^2)}$	8266.03	21	0	1
$B_1$6) $H_{(\mathrm{CROP} + \mathrm{CROP}^2 + \mathrm{EDGEDEN} + \mathrm{EDGEDEN}^2)}$	8268.14	19	2.11	0.35
<u>10.36 km^2, linear form</u>				
$B_2$6) $H_{(\mathrm{CROP + EDGEDEN})}$	8469.63	17	0	1
$B_2$9) $H_{(\mathrm{CROP + MEANAREA + EDGEDEN})}$	8470.92	18	1.29	0.52
$B_2$5) $H_{(\mathrm{CROP + MEANAREA})}$	8475.68	17	6.05	0.05
<u>10.36 km^2, SQRT</u>				
$B_2$6) $H_{(\mathrm{CROP}^{0.5} + \mathrm{EDGEDEN}^{0.5})}$	8463.87	17	0	1
$B_2$9) $H_{(\mathrm{CROP}^{0.5} + \mathrm{MEANAREA}^{0.5} + \mathrm{EDGEDEN}^{0.5})}$	8465.85	18	1.98	0.37
$B_2$5) $H_{(\mathrm{CROP}^{0.5} + \mathrm{MEANAREA}^{0.5})}$	8473.15	17	9.28	0.01
<u>10.36 km^2, quadratic</u>				
$B_2$6) $H_{(\mathrm{CROP} + \mathrm{CROP}^2 + \mathrm{EDGEDEN} + \mathrm{EDGEDEN}^2)}$	8469.76	19	0	1
$B_1$9) $H_{(\mathrm{CROP} + \mathrm{CROP}^2 + \mathrm{MEANAREA} + \mathrm{MEANAREA}^2 + \mathrm{EDGEDEN} + \mathrm{EDGEDEN}^2)}$	8471.13	21	1.37	0.051
$B_2$5) $H_{(\mathrm{CROP} + \mathrm{CROP}^2 + \mathrm{MEANAREA} + \mathrm{MEANAREA}^2)}$	8478.02	19	8.26	0.02

Figure 3.4. Average AIC$_c$ weights for covariates in hypothesized models using different habitat classification schemes and different forms of continuous covariates



Exploratory analysis

Our exploratory analysis examined 15 additional models. These models included covariates from multiple scales, selected 2-way interactions, and multiple covariate forms. Our best exploratory model was far superior to any of our *a priori* models (ΔAIC > 358) but also was considerably more complicated. This might have been expected, because in each of our *a priori* model sets the most saturated model was the one with the lowest AIC value. A number of 2-way interactions and the inclusion of covariates from more than one spatial scale substantially improved the predictive ability of our model. Although we arrived at this model through exploratory analysis, we believe it to be the model that best describes patterns of nest-site selection for mallards. This model has a much lower AIC score and, while complicated, the interactions seem biologically plausible (Table 3.8). We, therefore, will describe this model in more detail. Because it is the result of exploratory analyses, readers may want to use caution in applying this model and more research should be conducted to either verify or refute the patterns we observed.

The best model included effects for habitat type, patch size, distance from a habitat edge, distance from the nearest wetland, and the amount of annual crops and the density of habitat edges within a 0.65 km^2 circle surrounding either the nest site or the random point (Table 3.9). Interactions between habitat type and patch size, habitat type and distance from a habitat edge, distance from a wetland edge and both patch size and distance from other types of habitat edges improved our model. Finally there was an interaction between the amount of crop and habitat type.

Table 3.8. Ranking of exploratory models of mallard nest-site selection at 15 sites in south-central Canada. Rankings are based on Akaike's Information Criteria. Only models within 10 AIC_c values of the most parsimonious model are presented.

Exploratory model		AIC	K	ΔAIC_i	w_i/w_*
$H^*_{(SAR + HAB6 + AREA^{0.5} + HDIST + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST + AREA^{0.5}*WDIST^{0.5} + HDIST*WDIST^{0.5} + CROP + EDGEDEN + HAB6*CROP)}$		7488.22	42	0	1
$H_{(SAR + HAB6 + AREA^{0.5} + HDIST^{0.5} + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST^{0.5} + AREA^{0.5}*WDIST^{0.5} + HDIST^{0.5}*WDIST^{0.5} + CROP + EDGEDEN + HAB6*CROP)}$	Replace linear form of HDIST with SQRT form	7488.82	42	0.61	0.74
$H_{(SAR + HAB6 + AREA^{0.5} + HDIST^{0.5} + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST^{0.5} + HDIST^{0.5}*WDIST^{0.5} + CROP + EDGEDEN + HAB6*CROP)}$	Remove $AREA^{0.5}*WDIST^{0.5}$ interaction	7489.36	41	1.15	0.56
$H_{(SAR + HAB6 + AREA^{0.5} + HDIST^{0.5} + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST^{0.5} + AREA^{0.5}*WDIST^{0.5} + HDIST^{0.5}*WDIST^{0.5} + CROP + EDGEDEN + HAB6*CROP + EDGEDEN^2)}$	Replace $AREA^{0.5}*WDIST^{0.5}$ interaction; add $EDGEDEN^2$	7489.63	43	1.42	0.49
$H_{(SAR + HAB6 + AREA^{0.5} + HDIST^{0.5} + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST^{0.5} + AREA^{0.5}*WDIST^{0.5} + HDIST^{0.5}*WDIST^{0.5} + CROP + EDGEDEN + HAB6*CROP + EDGEDEN^2 + HAB6*EDGEDEN)}$	Add HAB6*EDGEDEN interaction	7492.84	48	4.62	0.10
$H_{(SAR + HAB6 + AREA^{0.5} + HDIST^{0.5} + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST^{0.5} + AREA^{0.5}*WDIST^{0.5} + HDIST^{0.5}*WDIST^{0.5} + CROP + EDGEDEN + MEANAREA + HAB6*CROP + EDGEDEN^2 + MEANAREA^2 + HAB6*EDGEDEN)}$	Add MEANAREA and $MEANAREA^2$	7495.18	50	6.96	0.03
$H_{(SAR + HAB6 + AREA^{0.5} + HDIST^{0.5} + WDIST^{0.5} + HAB6*AREA^{0.5} + HAB6*HDIST^{0.5} + AREA^{0.5}*WDIST^{0.5} + HDIST^{0.5}*WDIST^{0.5} + CROP + EDGEDEN + MEANAREA + HAB6*CROP + EDGEDEN^2 + MEANAREA^2 + HAB6*EDGEDEN + HAB6*MEANAREA)}$	Add HAB6*MEANAREA interaction	7497.96	55	9.46	0.01

Table 3.9. Coefficient estimates, standard errors (SE) and 95% confidence intervals (C.I.) for best approximating model of mallard nest-site selection in south-central Canada. Estimates

Effect	Estimate[a]	SE (95% C.I.)
Intercept	**[b]	--
$HAB_{(GRASS)}$	-0.7109	0.1753 (-1.054, -0.3673)
$HAB_{(HAY)}$	0.2837	0.3576 (-0.4172, 0.9846)
$HAB_{(PCOV)}$	-0.9905	0.2630 (-1.5060, -0.4750)
$HAB_{(SHRUB)}$	0.4932	0.1643 (0.1712, 0.8152)
$HAB_{(WETL)}$	-0.0400	0.1526 (-0.3391, 0.2591)
$HAB_{(WOOD)}$	0	.
$AREA^{0.5}$	-1.7502	0.2128 (-2.1673, -1.3331)
HDIST	0.0344	0.0064 (0.0219, 0.0469)
$WDIST^{0.5}$	-0.0941	0.0125 (-0.1186, -0.0696)
$AREA^{0.5}*HAB_{(GRASS)}$	1.0329	0.2594 (0.5245, 1.5413)
$AREA^{0.5}*HAB_{(HAY)}$	-1.4772	0.6729 (-2.7961, -0.1583)
$AREA^{0.5}*HAB_{(PCOV)}$	2.2835	0.2502 (1.7931, 2.7739)
$AREA^{0.5}*HAB_{(SHRUB)}$	-0.3062	0.5975 (-1.4773, 0.8649)
$AREA^{0.5}*HAB_{(WETL)}$	0.4115	0.3840 (-0.3411, 1.1641)
$AREA^{0.5}*HAB_{(WOOD)}$	0	.
$HDIST*HAB_{(GRASS)}$	-0.0411	0.0072 (-0.0552, -0.0270)
$HDIST*HAB_{(HAY)}$	0.0190	0.0056 (0.0080, 0.0300)
$HDIST*HAB_{(PCOV)}$	0.0248	0.0049 (0.0152, 0.0344)
$HDIST*HAB_{(SHRUB)}$	-0.0086	0.0132 (-0.0345, 0.0173)
$HDIST*HAB_{(WETL)}$	0.0015	0.0061 (-0.0105, 0.0135)
$HDIST*HAB_{(WOOD)}$	0	.
$HDIST*WDIST^{0.5}$	-0.0044	0.0007 (-0.0058, -0.0030)
CROP	1.1012	0.2037 (0.7019, 1.5005)
EDGEDEN	0.0080	0.0019 (0.0043, 0.0117)
$CROP*HAB_{(GRASS)}$	1.6159	0.2903 (1.0469, 2.1849)
$CROP*HAB_{(HAY)}$	-0.1304	0.5631 (-1.2341, 0.9733)
$CROP*HAB_{(PCOV)}$	0.8149	0.5884 (-0.3384, 1.9682)
$CROP*HAB_{(SHRUB)}$	-1.0933	0.3127 (-1.7062, -0.4804)
$CROP*HAB_{(WETL)}$	-0.5490	3.127 (-1.0472, -0.0508)
$CROP*HAB_{(WOOD)}$	0	.

[a] Estimate reflects the probability that a point is a nest site.

[b] Estimate of intercept unspecified because we retrospectively assigned the number of random points

Our best approximating model reveals a complex relationship between habitat type, patch size and distance from a habitat edge and the amount of crop in the surrounding area. In general, mallards tended to select grass as a nesting site less than expected relative to its availability as a habitat type (Figure 3.5), and when they did select this habitat type they tended to select small patches in association with annual crop fields (Figure 3.6, 3.7A). Possibly related to their predilection to nest in smaller patches, mallards also tended to nest near habitat edges when they selected grass as the habitat type for their nests (Figure 3.7A). Mallard nesting in hay fields, shrub, wetland, or wood again tended to select small habitat patches, but nested nearer the center of these habitat types away from habitat edges (Figure 3.7B-F). The likelihood of selecting a certain habitat type depended on the amount of crop in the surrounding area. Grass and planted cover were substantially more likely to be selected if the surrounding area had much annual crop (Figure 3.8).

Figure 3.5. Comparison of proportion of nests and random points within each habitat type.

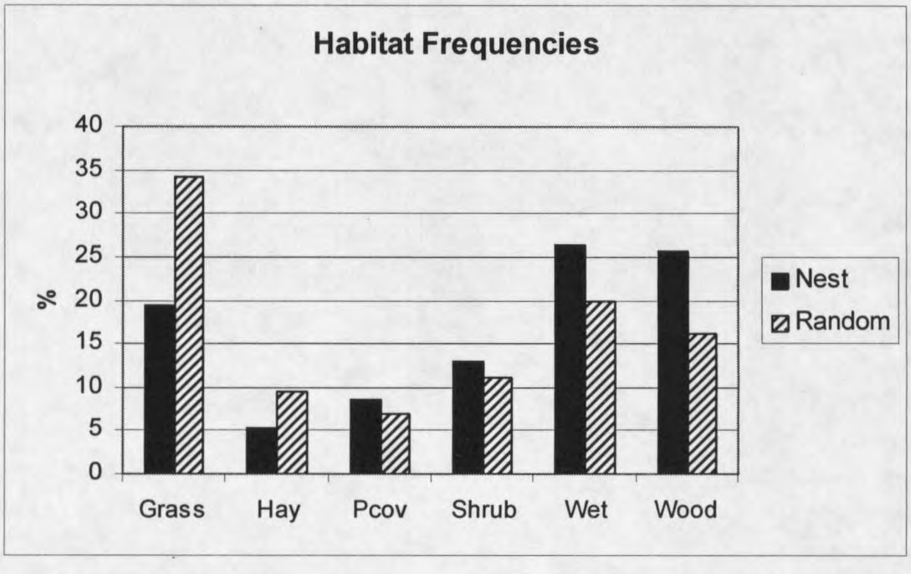


Figure 3.6. Proportion of 0.65-km^2 circle centered on nest-sites and random points comprised of crop fields

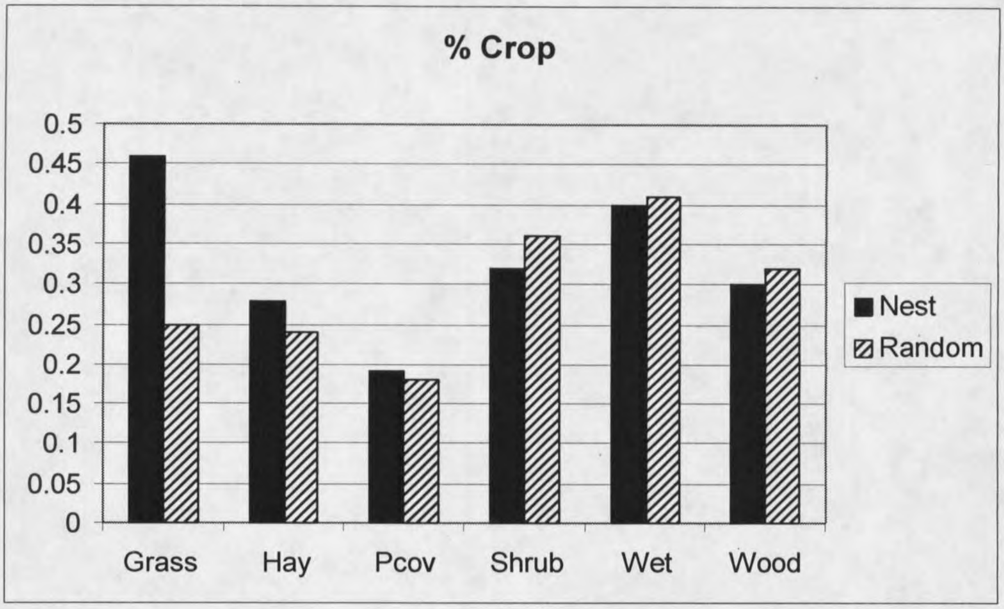
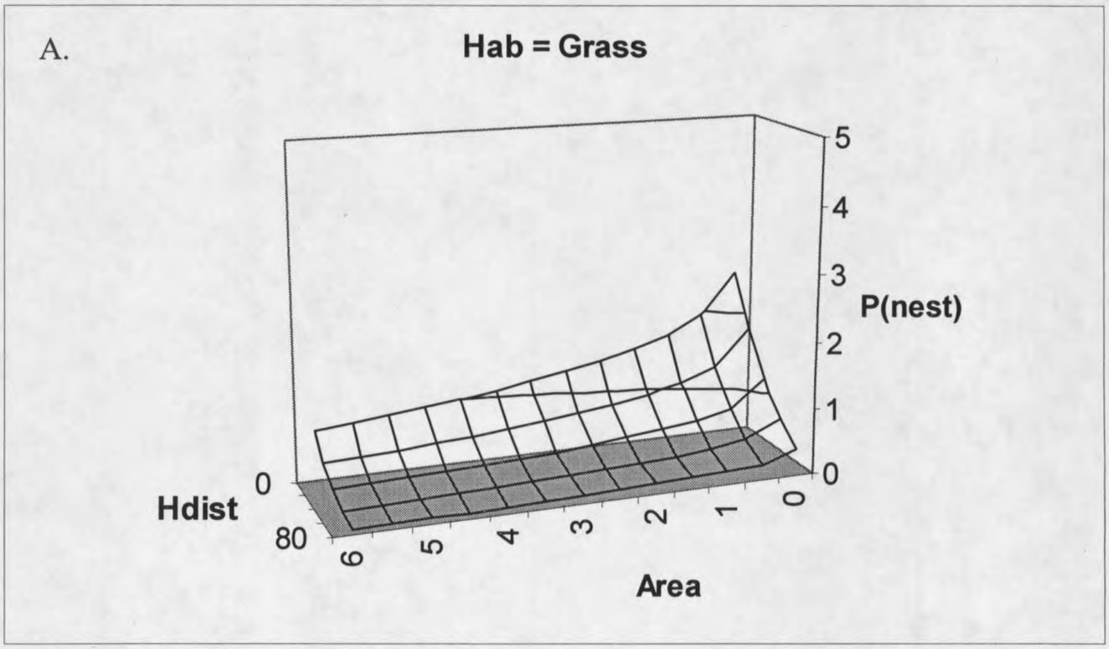
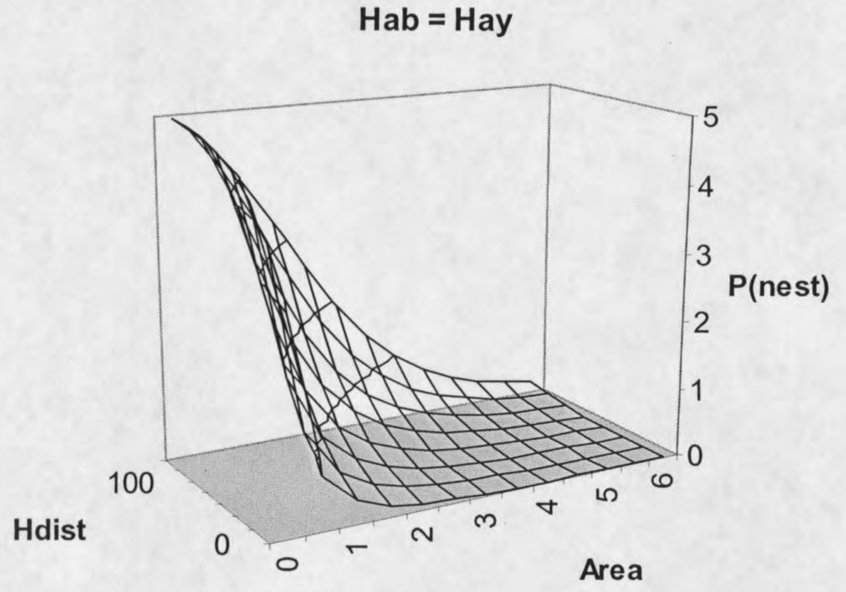


Figure 3.7. Response surface of the odds that a point is a nest vs. a random point in relation to the distance from a habitat edge (HDIST) and patch size (AREA) by habitat type.

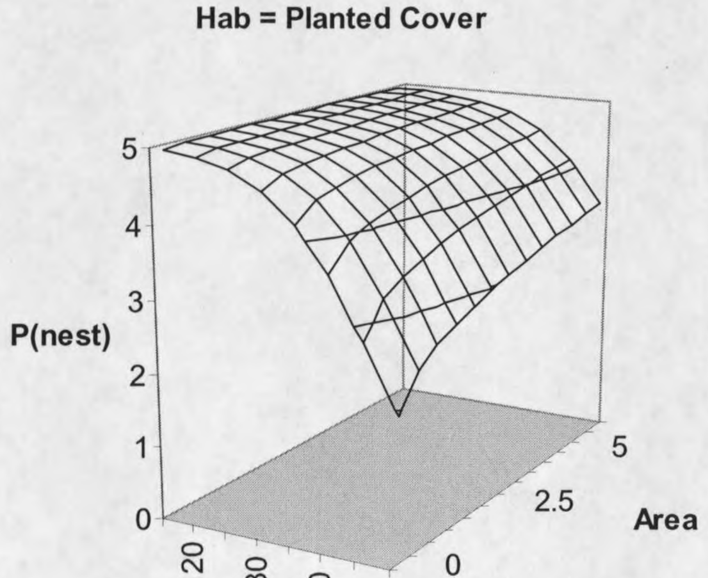
A.

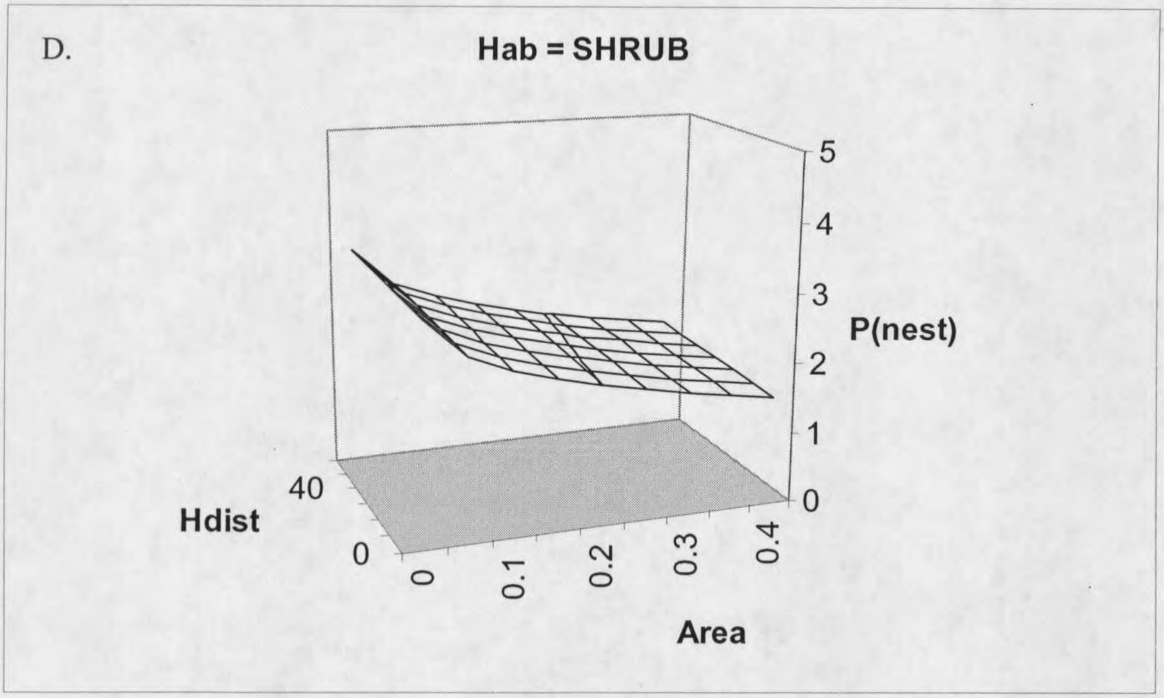


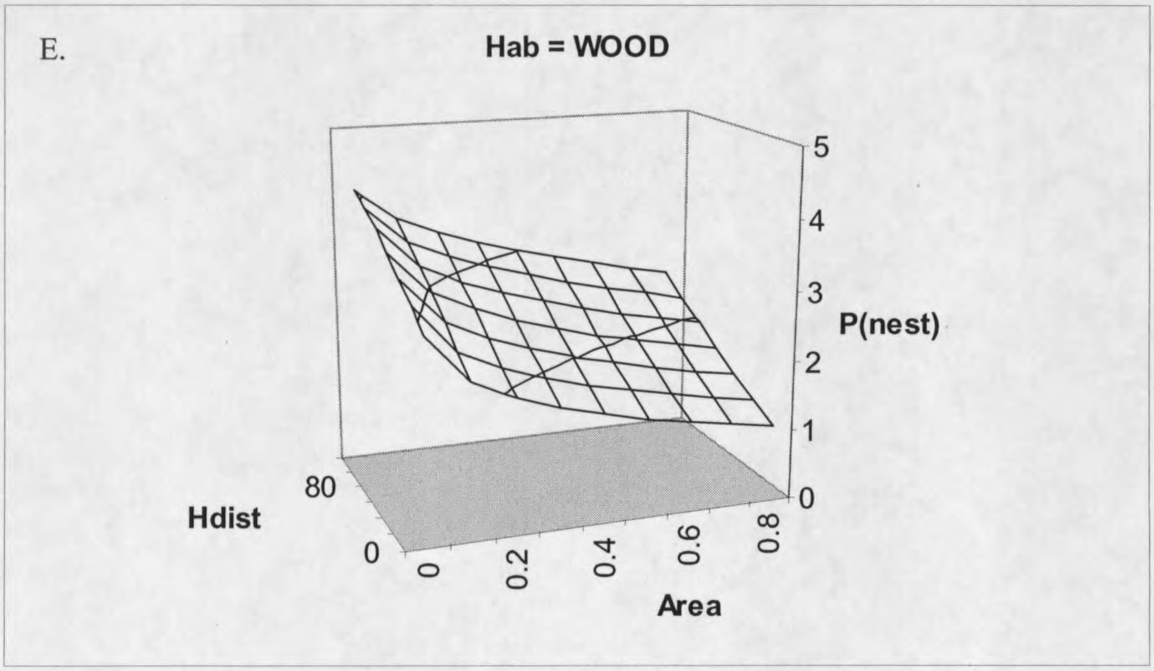
B.


Hab = Hay
5
4
3
2
1
0
P(nest)
100
Hdist
0
0
1
2
3
4
5
6
Area

C.


Hab = Planted Cover
5
4
3
2
1
0
P(nest)
120
80
40
0
Hdist
0
2.5
5
Area


D.
Hab = SHRUB
5
4
3
2
1
0
P(nest)
40
Hdist
0
0
0.1
0.2
0.3
0.4
Area


E.
Hab = WOOD
5
4
3
2
1
0
P(nest)
80
Hdist
0
0
0.2
0.4
0.6
0.8
Area

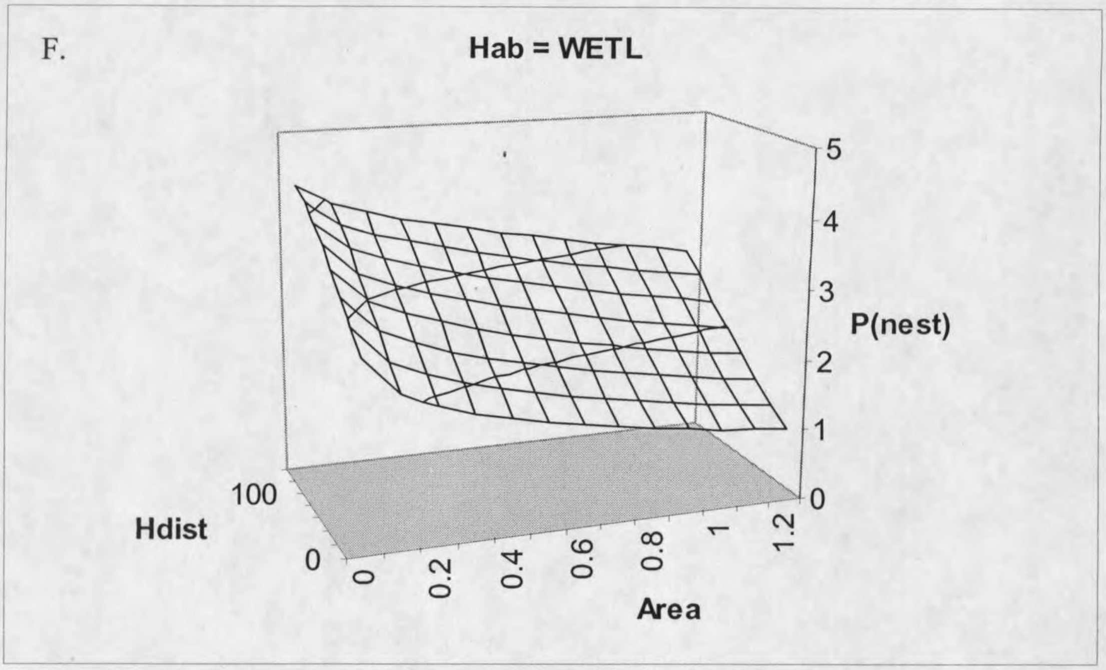
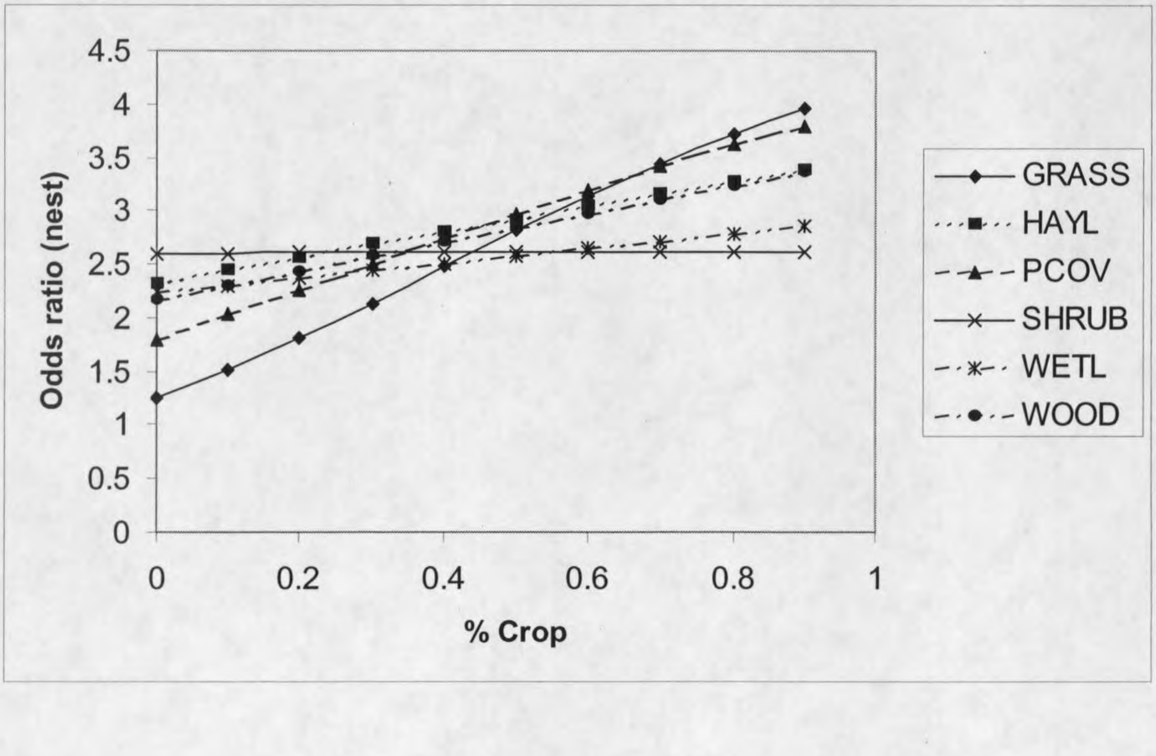


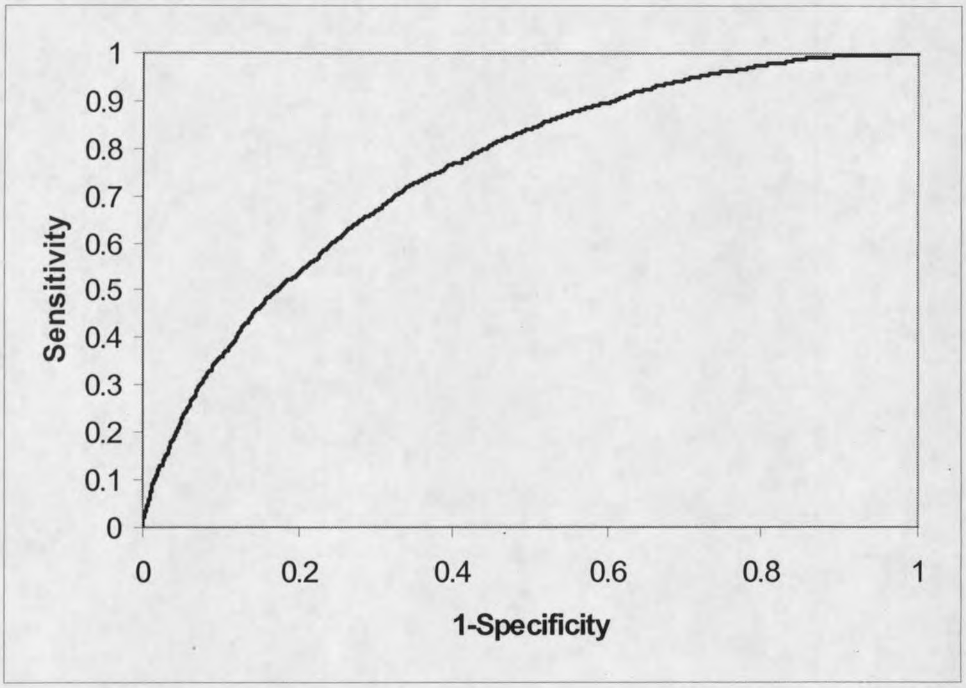
Figure 3.8. Odds ratio of a point being a nest site vs. a random point in relation to the proportion of a 0.65 km^2- circle centered on the point that is comprised of crop fields



Three models, all with many structural similarities, appear to be plausible alternatives (all have AIC values within 1 unit of each other (Table 3.8). Our second best model (ΔAIC = 0.54) was identical to our best model with the exclusion of the 2-way interaction between patch size and distance from a wetland. The third best model (ΔAIC = 0.81) was identical to our best model with the addition of a quadratic term for edge density.. Because these models are structurally similar and have similar AIC scores, they should be considered plausible alternatives.

Despite choosing a rather complex model as our most parsimonious, other unmeasured factors apparently influence mallard nest-site selection. Our most complex model, fit as part of our exploratory analysis, had a significant lack of fit (H-L G-o-F, $?^2 = 24.25$, 8 d.f, $p = 0.0021$). Nevertheless, our best model did a reasonable job of discriminating between nest sites and random points. For our best approximating model AUC = 0.76 (Figure 3.9). In other words, a randomly selected pair of points, one representing a nest site the other a random point, will be classified correctly by our model in 76% of instances. In contrast, an AUC=0.5 would indicate no discriminatory ability (SAS Institute 1995, Pearce and Ferrier 2000).

Figure 3.9. Receiver operator characteristic (ROC) curve for best approximating model of mallard nest-site selection.



Discussion

By using new approaches to modeling selection and examining a number of complex models, we were able to substantially improve our understanding of mallard nest-site selection in a highly altered environment. If nest-site selection is adaptive, we would expect birds to choose nest sites in a manner that maximizes their likelihood of successfully hatching a nest (Clark and Shutler 1999). Mallards in this study, while demonstrating selection, provide limited evidence that current patterns of nest-site selection in Canadian parklands confer adaptive benefits. With the exception of nests in grass, mallards tended to nest away from habitat edges, while hatching rates are positively related to distance from edge. Similarly, mallards nests tended to be in areas with greater edge density than random points, and nests in areas with a greater edge density tended to have a greater likelihood of hatching than nests in areas with less edge (Chapter 2). In contrast, mallards tended to select small patches of habitat despite the fact that, in general, hatching rates were higher in large patches of cover (Chapter 2) and mallards tended to nest near wetlands, despite the fact that nests in close proximity to wetlands suffered high predation.

Hence, mallards provide only equivocal evidence that nest-site selection is adaptive. Clark and Shutler (1999) also reported equivocal evidence for mallard nest-site selection leading to fitness benefits. A number of explanations may explain a lack of correspondence between chosen nest sites and reproductive success; some related to the dynamic and, therefore, unpredictable nature of the prairie environment, while others consider the fact that the parklands have been altered at a rapid rate in recent decades.

Orians and Whittenberger (1991) suggested that birds often may not have sufficient time to sample from available nest sites to select one that ultimately will be safe. Anecdotal evidence suggests that this may be the case with mallards. Often during this study, we found mallards nesting within just a few days of wetlands becoming ice-free in the spring. Similarly, mallards, if they have a nest destroyed early in the laying period, often will immediately select a new nest site and continue laying within one day of the first nest being destroyed (Arnold et al 2002). It would be extremely difficult to assess the safety of a given site given this short time frame and the diversity of predators that prey on duck eggs (i.e., avian and mammalian; diurnal, crepuscular, nocturnal).

Fryxell (1997) suggested that unpredictable environments do not favor strong selection but rather flexible behavioral responses. Mallards are very flexible in their nest choices; in addition to choosing a variety of vegetation types within which to place nests, mallards during this study also located nests under abandoned cars and buildings, on top of hay bales and, occasionally, arborally in abandoned American crow (*Corvus brachyrhynchos*) nests. Given current landscape configurations in the parklands and the diverse suite of generalist predators (both avian and mammalian) that prey on duck eggs, perhaps it is just not possible to reliably select a nest site in an area that will remain predator-free for the 35 days necessary on average to lay, incubate and hatch a clutch of eggs (Orians and Whittenberger 1991). Flexible behavior could be especially pertinent if predators have the ability to develop search images of likely nest sites (Clark and Shutler 1999). While little research has been conducted on whether mammalian nest predators have the ability to recognize likely nesting areas, Lariviere and Messier (1998) working with striped skunks (*Mephitis mephitis*)—a common duck nest predator—concluded that skunks were likely unable to recognize high density nesting areas at densities common to our area (usually <2.5 nests/ha). Further, because we studied each site for only a single year, it is possible that short-term variability may mask long-term trends in nest success (Clark and Shutler 1999).

Another possible reason patterns of nest-site selection did not match patterns of nests success may relate to the underlying assumptions that went into our model-building efforts. Perhaps nest sites weren't selected to maximize hatching rates but instead to minimize female mortality or another vital rate or combination of rates (e.g., a trade-off between hatching rates and duckling survival). Several studies have documented increased mortality for nesting birds (Johnson et al. 1987, Ducks Unlimited Canada, unpubl.). Ducks may face a trade-off between locating nests in the most secure locations versus choosing a site that allows quick escape in the event a predator locates them. Despite the fact that mallard population growth is most sensitive to variation in hatching rates, obviously, losing one's life represents a much greater cost to an individual than losing a single nest. Others have suggested that ducks select certain locations for nests to maximize duckling survival (Poysa et al. 2000).

Finally, we may not have good correspondence between our models of nest-site selection and hatching rates because, due to anthropogenic changes to the landscape and the predator community, the conditions under which preferences for certain habitat attributes evolved, no longer exist (Misenhelter and Rotenberry 2000). Mallards tend to select thick cover (Joyce 2001), but in our analyses such sites were not necessarily safer. Such a preference may have been adaptive in the past when natural parkland habitats were more contiguous, and thick cover was the only reliable way of improving your chances on any single nesting attempt. Mallards are persistent renesters (Arnold et al. 2002), initiating up to 6 nests in a single season if previous nests are destroyed. We may be able to infer from this that nest predation has been high through evolutionary time. However, by reducing the top predator (wolves), other predators that are more efficient at finding nests (e.g., red foxes, skunks) may be more abundant than they were previously. Thus, when coupled with reduced attractive cover, it seems quite possible that the best strategy for hatching nests in landscapes of the past is no longer effective.

For instance, we documented a preference for small patches of habitat. We speculate that these patches were selected not for their size, but for their thicker cover, which occurs there because small patches are less likely to be grazed or hayed annually. Similarly, we believe that mallards likely select hay fields more commonly later in the season, because by then the hay crop provides dense vegetative characteristics. However, in today's environment these fields are very dangerous locations and thus, should be avoided. In other words, it seems entirely likely that mallards are selecting structural characteristics of the vegetation that no longer reflect the security of the habitat.

An area where patterns of nest-site selection matched predictions was regarding the scale at which habitat variables were selected. As with models of hatching rates (Chapter 2), models of nest-site selection generated from attributes at the patch scale performed better than models generated from landscape attributes aggregated at either 0.65 km^2 or 10.36 km^2 surrounding nest sites. Bergin (1992) noticed a similar phenomenon for western kingbirds (*Tyrannus verticalis*). Nevertheless, similar to our models of hatching rates, the inclusion of habitat covariates from multiple scales improved the predictive capability of our models of nests site selection. This supports the idea that habitat choice in birds is a hierarchical process (Johnson 1980, Orians and Whittenberger 1991). Interestingly, however, landscape attributes generated at the scale (10.36 km^2) thought to represent the home range of a mallard did not add appreciably to our models of nest-site selection.

Our best models of nest-site selection were generated using our most detailed habitat classification scheme. This is consistent with our analysis of hatching rates

(Chapter 2). Planners and managers should strive to acquire detailed habitat information, where possible.

Valid inference requires that investigators not introduce bias through the methods used to collect the data. In some cases, (especially prior to 31 May 1994 – see methods) our activity around nests caused the female to abandon her nest and subsequently select another site. In these instances we included both nests in our sample. While this had the potential to cause biases in our estimates, we believe these biases were small, because up to 95% of nests were unsuccessful due to other causes. Therefore, birds commonly select multiple sites for nesting within a single nesting season. We can think of no reason why investigator-induced abandonment should be qualitatively different than other forms of nest loss.

Despite this limitation, we feel that the models presented here provide advancements in our understanding of nest-site selection processes in several important ways. First, we used patterns of hatching rates to generate testable predictions about the adaptive consequences of nest-site selection. The models were generated using a large sample of radiomarked birds, which avoids the biases that can occur as a result of differential detection probabilities among habitats that are inherent in studies that document nest-site selection using nests located through traditional searching methods. In addition, we demonstrated that covariates collected at multiple scales improved our predictive models. Earlier works have described microhabitat characteristics of mallard nest sites (Gloutney and Clark 1997, Joyce 2001). Instead of duplicating that work here, we concentrated on potential covariates that can be remotely sensed, thereby facilitating incorporation into large-scale conservation planning models. Furthermore, we established that nest-site selection models are affected by various habitat classifications.

Our best approximating model, while complicated, reflects the most thorough analysis on nest-site selection of which we are aware. Regardless, uncertainties remain as our best model failed to explain much of the variation in nest-site selection. It seems likely that future attempts at modeling selection will need to consider even more complex models.

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CHAPTER 4.

CONCLUSIONS, MANAGEMENT AND RESEARCH IMPLICATIONS, AND AN APPLICATION OF THE MODELS

Management and Research Implications

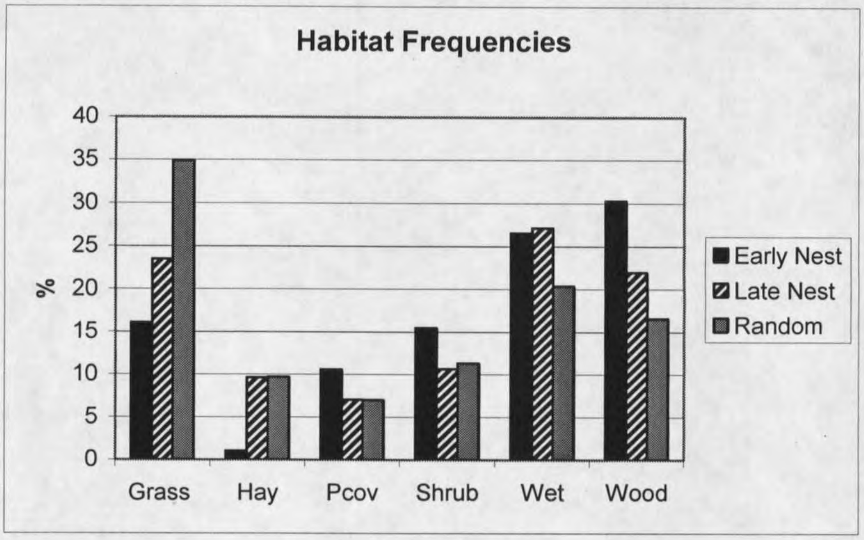
Hatching rates of nests are the thought to be the most important determinant of mid-continent duck population dynamics (Johnson et al 1987, Hoekman et al. 2002). In response to apparent declines in hatching rates caused by landscape changes as a result of agricultural and urban expansion, managers use a variety of interventions designed to provide relatively safe habitats for nesting ducks. Examples of such interventions include providing financial incentives for landowners to delay harvesting hay crops until after most ducks have completed nesting, or converting annual crop fields to a mixture of grasses and legumes and removing them from agricultural production. For these interventions to be cost-effective, however, the resulting habitat must be safer than surrounding habitats *and* be attractive to nesting ducks. Thus, a more complete knowledge about how upland-nesting ducks choose nest sites and the hatching rates they achieve in those habitats will allow managers to make better decisions about which type of interventions are likely to succeed. This information is essential for estimating the cost-effectiveness of various management options.

In the previous chapters, we have demonstrated that patterns of both hatching rates and nest-site selection are complex. Nevertheless, a number of patterns were consistent across both analyses. For both analyses of hatching rates and nest-site selection, models using a detailed habitat classification scheme were more parsimonious than models using simpler classifications, despite the fact that models with more complex habitat classifications required the estimation of more parameters. This provides insights into how ducks, and perhaps predators perceive parkland habitats. Models based on a classification that included vegetation physiognomy and floristics performed better than models built solely on land use. Joyce (2001) provided evidence that even more detailed (within-patch) vegetation attributes influenced the selection of nest sites by mallards. Therefore, we recommend that habitat managers and planners use the most detailed habitat information available when designing or implementing management plans. We recognize, however, that the acquisition of detailed habitat information is costly. The models we present allow objective assessments of the trade-offs between the loss of information planners can expect when using simpler habitat information and the cost of obtaining more detailed information.

Another pattern that was consistent for analyses of both hatching rates and nest-site selection was that models built using patch-scale information were superior to models built using landscape metrics measured within either 0.65- or 10.36-km^2 circles centered on nest sites. Subsequently, however, including variables measured at both that patch-scale and the 0.65 km^2-scale improved model fit, indicating that the patch-scale patterns were context-specific to some extent. Again, planners and habitat managers should be mindful of this complexity and should consider both patch-scale and landscape factors when designing habitat programs.

The analyses conducted in the previous chapters provide considerable insight into the design of successful habitat programs. For example, planted cover—where crop fields are secured by purchasing them or through long-term leases and converted to a mixture of grasses and legumes—is one of the cornerstone programs of the Prairie Habitat Joint Venture (PHJV). We demonstrated (Chapter 2) that large fields of planted cover have very high hatching rates early in the nesting season. In our analysis of nest-site selection, we did not include a covariate for seasonal effects; however, figure 4.1 indicates that planted cover fields are relatively more attractive to nesting mallards early in the nesting season than later. Therefore, early in the nesting season planted cover fields provide both attractive and relatively safe nesting cover. This is particularly important given increasing evidence that early-hatched ducklings are more likely than later-hatched ducklings to be recruited to the breeding population (Dawson and Clark 2000, Anderson et al. 2001, Blums et al. 2002). In contrast, hay fields also have high hatching rates early in the season but are only attractive to nesting birds later (Figure 4.1) when hatching rates have declined substantially (Figure 2.7a). Therefore, programs that convert crop fields to hay may be counter-productive by attracting nesting birds into a dangerous habitat type unless hay cuts are delayed until after the majority of nesting is complete.

Figure 4.1. Comparison of proportion of early nests, late nests and random points within each habitat type. Early nests were those initiated prior to the median initiation date of all nests; late nests were those initiated after the median initiation date.



The choice of a given habitat type for nesting depended on the composition of the surrounding landscape. The likelihood of selecting a given habitat for nesting was dependent on the amount of annual crop fields in the surrounding 0.65 km^2. This, too, has important implications for habitat management efforts. Birds were much more likely to select planted cover in areas with abundant crop fields (Figure 3.8) while there was little evidence that the amount of crop fields surrounding nests influenced hatching rates. Thus, planted cover may be most cost effective in highly cropped areas. Also, we documented that hatching rates were reduced near wetlands (Chapter 2). Therefore, while high densities of wetlands are required to attract nesting ducks to a given area

(Cowardin et al 1983), it may be more productive to convert individual crop fields to planted cover that have few wetlands embedded within them.

In addition to management implications, this research suggests several topics that require additional research. Despite making important advancements in our understanding, our models of hatching rates and nest-site selection left considerable variation unexplained. The inclusion of study site as a random effect in our analysis of hatching rates improved the fit of our best approximating model substantially ($\Delta QAIC_c >$ 140, Chapter 2). This indicates that other uncontrolled and/or unmeasured factors were affecting hatching rates. Because predation is the primary cause of nest loss, additional research is needed to identify what factors influence predator compositions, abundances, and foraging patterns. Similarly, additional work is required to discern how abundances of alternative prey items (e.g., small mammals, invertebrates, waste grain) influence predation of duck nests.

In several instances our models of nest-site selection demonstrated that mallards were not selecting the safest habitats within which to place their nests. This will challenge both research scientists and habitat managers to design habitat programs that more closely mimic the ecological functions of pre-settlement parklands and, therefore, restore the conditions under which nest-site selection patterns presumably evolved.

Application of the Models

Because our models of both hatching rates and nest-site selection are complex and include landscape attributes measured at multiple scales, application of the models likely will require them to be incorporated into a spatially explicit decision support system (DSS). This is facilitated with our models because, with the exception of nest initiation date (IDATE), all other covariates we considered can be remotely sensed. In the following section, we provide an example of how our models could be used to provide guidance to managers. We chose the Baldur, Manitoba study site to demonstrate this process; however, we do not consider the following example to be an exhaustive treatment of how to build these models into a DSS. The most appropriate method for incorporating these models will depend on the specific management questions(s) being asked, the spatial extent of area being modeled, and the computing resources available. Figure 4.2 provides a map of our basic cover types for the Baldur site as a reference. For each of the subsequent maps, we first generated a uniform grid of 2,500 points. These points were overlaid onto our base habitat map and landscape attributes—measured at both the patch- and 0.65 km^2-scales—were appended to each point. From these attributes we applied either our best approximating nest-site selection (Figure 4.3) or hatching rate models (Figures 4.4-4.6) to each point to generate a predicted value. We then fit an isotropic semivariogram to the predicted values and used punctual kriging (Issaks and Srivatava 1989) to generate predictive surface representations.

Figure 4.3 represents the application of our best approximating nest-site selection model to the Baldur study site. Warm colors indicate selection, while cooler colors indicate areas that we expect to be selected as nest sites less frequently. Because we did not consider cropland in our models of nest-site selection points that fell within this habitat type were deleted for this example. Accordingly, we have masked this habitat type in Figure 4.3. The open-water portion of wetland habitats was treated similarly. In accordance with our model structure, planted cover fields are expected to be most strongly selected, grass fields most weakly selected, and other habitat types to have intermediate levels of selection.

Figure 4.2. Map of Baldur, Manitoba study site

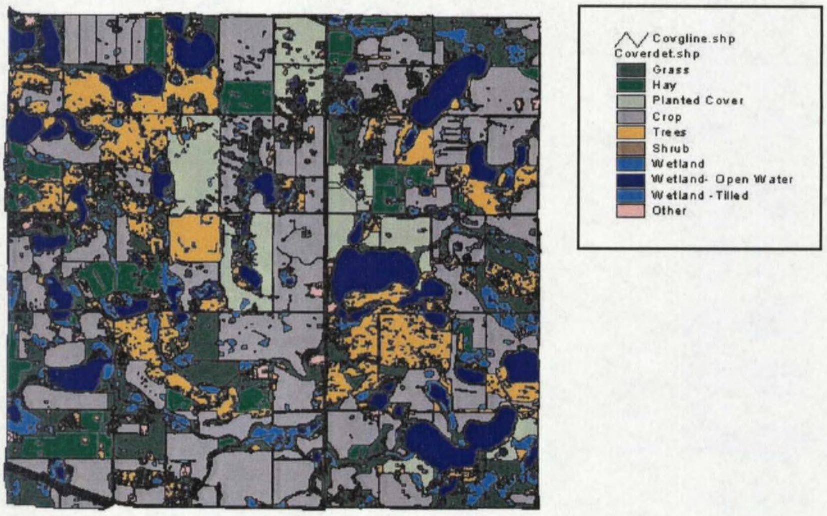
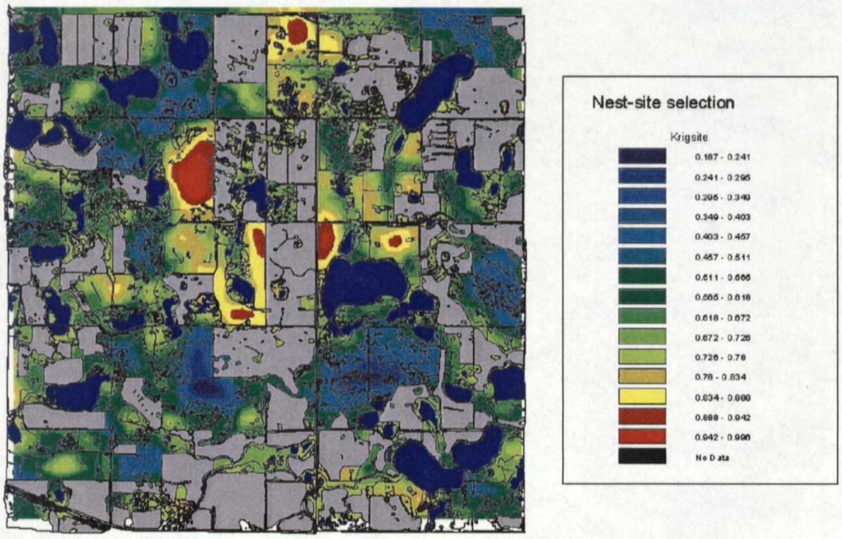


Figure 4.3. Application of the best approximating nest-site selection model to the Baldur, Manitoba study site.



Because there was a strong seasonal effect for a number of habitat types in our models of hatching rates, we applied our best approximating model of hatching rates to represent early- (initiation date = 10th percentile of all initiations dates; Figure 4.4), mid- (initiation date = median of all initiation dates; Figure 4.5), and late-season hatching rates (initiation date = 90th percentile of all initiation dates; Figure 4.6).

Figures 4.4-4.6 demonstrate a number of important practical implications of our hatching rate models. First, one can see from looking at the figures that, not only is there spatial variability in hatching rates, but the spatial patterns change throughout the season. Thus, it clearly is important to consider both spatial and temporal variability in hatching rates when considering the results of management options. Second, there is a much wider range of variability in hatching rates early in the season than there is later. Therefore, early in the season there is the potential for a greater payoff for implementing management programs that would attract birds to specific habitat settings. Later, it may be possible to design habitat programs that are attractive to birds, but the likelihood of these birds experiencing higher hatching rates in these habitat programs is reduced. Third, habitat programs that only become attractive to birds late in the nesting season (e.g., delayed hay cut) are less likely to substantially improve waterfowl production because by that point in the season hatching rates are similar throughout the study area.

As a final consideration, it is important to recognize that we studied each site for only a single nesting season. Future studies need to be replicated spatially and temporally to ensure that the patterns we observed can be strengthened by including variation among seasons as well as within.

Figure 4.4. Application of the best approximating hatching rate model to the Baldur, Manitoba study site, initiation date fixed at 10th percentile.

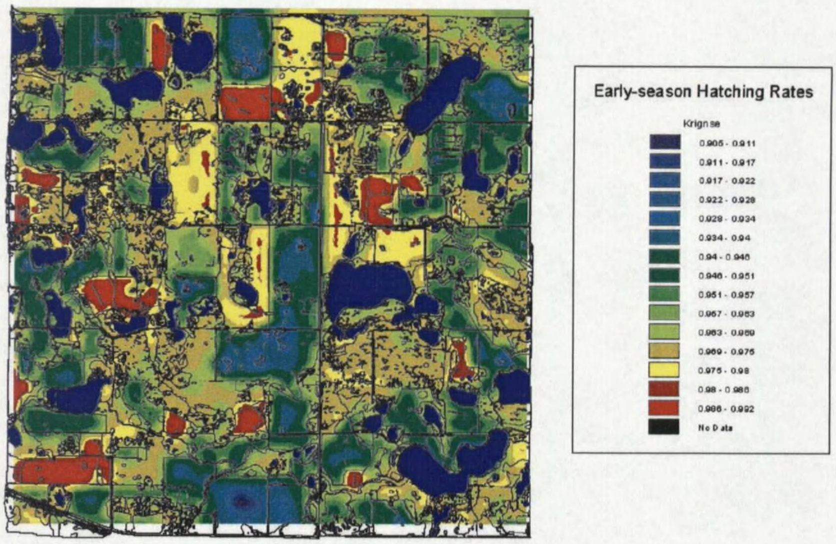


Figure 4.5. Application of the best approximating hatching rate model to the Baldur, Manitoba study site, initiation date fixed at 50th percentile.

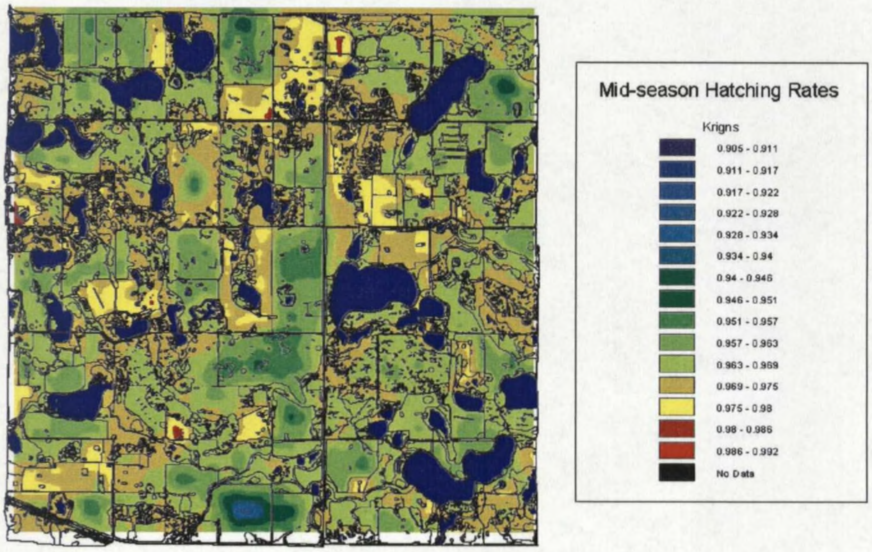
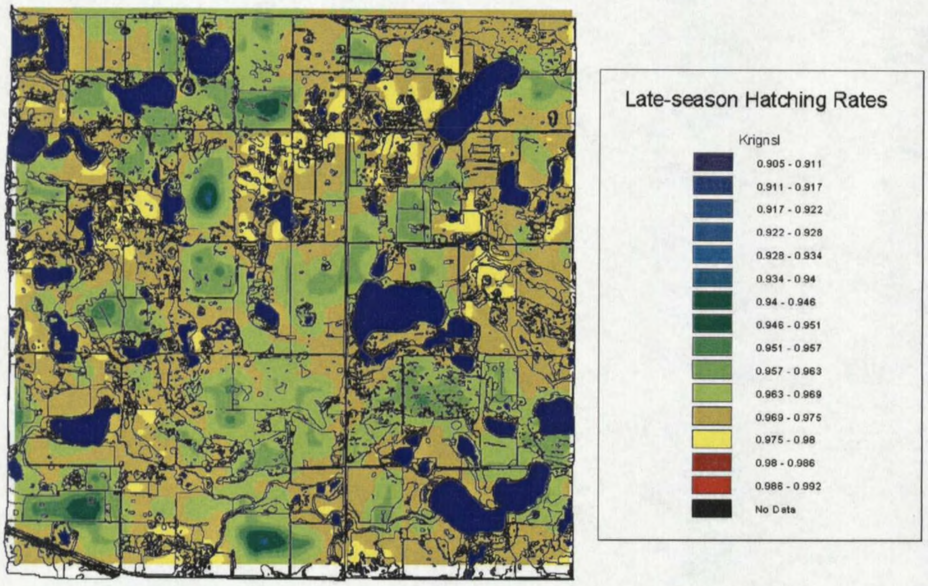


Figure 4.6. Application of the best approximating hatching rate model to the Baldur, Manitoba study site, initiation date fixed at 90th percentile.



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APPENDICES

APPENDIX A

TABLES

Appendix A1. Effect of habitat classifications on certain study area characteristics

	Edge Density (km/km^2)			Mean Patch Size (ha)		
Study Area	8-Habitat	4-Habitat	2-Habitat	8-Habitat	4-Habitat	2-Habitat
Hamiota	29.7	25.0	24.8	1.3	3.6	3.7
Punnichy	41.1	27.7	25.6	0.9	3.1	3.3
Belmont	57.5	26.1	22.8	0.8	3.8	4.3
Davis	54.9	33.3	28.8	0.6	2.8	3.2
Erskine	44.4	21.6	19.5	0.7	4.3	4.8
Camplake	53.3	23.7	21.0	0.7	3.4	3.8
Kutawa	54.7	29.6	29.5	0.8	2.4	2.6
Shoal lake	53.3	27.1	26.9	0.6	3.2	3.2
Baldur	46.0	22.3	18.9	0.9	4.5	5.8
Parkside	33.9	22.5	20.2	1.3	5.4	6.2
Pinelake	61.3	23.6	19.9	0.5	3.2	3.7
Allan Hills W	53.4	31.3	26.2	0.9	3.3	4
Elnora	86.8	14.2	13.1	0.3	5.2	5.9
Mixburn	63.8	41.6	35.5	0.4	0.9	1
Willowbrook	57.6	32.6	28.9	0.6	2.7	3.1
Mean (SE)	52.8 (3.4)	26.8 (1.6)	24.1 (1.4)	0.8 (0.1)	3.5 (0.3)	3.9 (0.3)

Appendix A2. Hypothesized models relating habitat features to hatching rates.

Nest -Scale	
No.	Model[a]
N1	$H_{(HAB)}$
N2	$H_{(AREA)}$
N3	$H_{(HDIST)}$
N4	$H_{(SHAPE)}$
N5	$H_{(FDIST)}$
N6	$H_{(WDIST)}$
N7	$H_{(HAB+AREA)}$
N8	$H_{(HAB+HDIST)}$
N9	$H_{(HAB+SHAPE)}$
N10	$H_{(HAB+FDIST)}$
N11	$H_{(HAB+WDIST)}$
N12	$H_{(AREA+HDIST)}$
N13	$H_{(AREA+FDIST)}$
N14	$H_{(AREA+WDIST)}$
N15	$H_{(HDIST+FDIST)}$
N16	$H_{(HDIST+WDIST)}$
N17	$H_{(SHAPE+FDIST)}$
N18	$H_{(SHAPE+WDIST)}$
N19	$H_{(FDIST+WDIST)}$
N20	$H_{(HAB+AREA+HDIST)}$
N21	$H_{(HAB+AREA+SHAPE)}$
N22	$H_{(HAB+AREA+FDIST)}$
N23	$H_{(HAB+AREA+WDIST)}$
N24	$H_{(HAB+HDIST+FDIST)}$
N25	$H_{(HAB+HDIST+WDIST)}$
N26	$H_{(HAB+SHAPE+FDIST)}$
N27	$H_{(HAB+SHAPE+WDIST)}$
N28	$H_{(HAB+FDIST+WDIST)}$
N29	$H_{(AREA+HDIST+FDIST)}$
N30	$H_{(AREA+HDIST+WDIST)}$
N31	$H_{(AREA+FDIST+WDIST)}$
N32	$H_{(HDIST+FDIST+WDIST)}$
N33	$H_{(SHAPE+FDIST+WDIST)}$
N34	$H_{(HAB+AREA+HDIST+FDIST)}$
N35	$H_{(HAB+AREA+HDIST+WDIST)}$
N36	$H_{(HAB+AREA+FDIST+WDIST)}$
N37	$H_{(HAB+HDIST+FDIST+WDIST)}$

Nest -Scale	
No.	Model[a]
N38	$H_{(HAB+SHAPE+FDIST+WDIST)}$
N39	$H_{(AREA+HDIST+FDIST+WDIST)}$
N40	$H_{(AREA+SHAPE+FDIST+WDIST)}$
N41	$H_{(HAB+AREA+HDIST+FDIST+WDIST)}$
Aggregated Scales	
$B_1 1$, $B_2 1$[b]	$H_{(CROP)}$
$B_1 2$, $B_2 2$	$H_{(MEANAREA)}$
$B_1 3$, $B_2 3$	$H_{(EDGEDENS)}$
$B_1 4$, $B_2 4$	$H_{(MEANSHAP)}$
$B_1 5$, $B_2 5$	$H_{(CROP + MEANAREA)}$
$B_1 6$, $B_2 6$	$H_{(CROP + EDGEDENS)}$
$B_1 7$, $B_2 7$	$H_{(CROP + MEANSHAP)}$
$B_1 8$, $B_2 8$	$H_{(MEANAREA + EDGEDENS)}$
$B_1 9$, $B_2 9$	$H_{(CROP + MEANAREA + EDGEDENS)}$

[a] All models include a random effect for study area, and an effect for IDATE.

[b] Models numbered B_1N, and B_1N refer to models with covariates generated within 0.65 km^2 and 10.36 km^2 circular buffers centered on nest sites, respectively.

Appendix A3. Hypothesized models relating habitat features to nest-sites selection.

Nest -Scale	
No.	Model
N1	$H_{(\mathrm{HAB})}$
N2	$H_{(\mathrm{AREA})}$
N3	$H_{(\mathrm{HDIST})}$
N4	$H_{(\mathrm{SHAPE})}$
N5	$H_{(\mathrm{WDIST})}$
N6	$H_{(\mathrm{HAB+AREA})}$
N7	$H_{(\mathrm{HAB+HDIST})}$
N8	$H_{(\mathrm{HAB+SHAPE})}$
N9	$H_{(\mathrm{HAB+WDIST})}$
N10	$H_{(\mathrm{AREA+HDIST})}$
N11	$H_{(\mathrm{AREA+WDIST})}$
N12	$H_{(\mathrm{HDIST+WDIST})}$
N13	$H_{(\mathrm{SHAPE+WDIST})}$
N14	$H_{(\mathrm{HAB+AREA+HDIST})}$
N15	$H_{(\mathrm{HAB+AREA+SHAPE})}$
N16	$H_{(\mathrm{HAB+AREA+WDIST})}$
N17	$H_{(\mathrm{HAB+HDIST+WDIST})}$
N18	$H_{(\mathrm{HAB+SHAPE+WDIST})}$
N19	$H_{(\mathrm{AREA+HDIST+WDIST})}$
N20	$H_{(\mathrm{HAB+AREA+HDIST+WDIST})}$
Aggregated Scales	
No.	Model
$B_1 1$, $B_2 1$[a]	$H_{(\mathrm{CROP})}$
$B_1 2$, $B_2 2$	$H_{(\mathrm{MEANAREA})}$
$B_1 3$, $B_2 3$	$H_{(\mathrm{EDGEDEN})}$
$B_1 4$, $B_2 4$	$H_{(\mathrm{MEANSHAP})}$
$B_1 5$, $B_2 5$	$H_{(\mathrm{CROP + MEANAREA})}$
$B_1 6$, $B_2 6$	$H_{(\mathrm{CROP + EDGEDEN})}$
$B_1 7$, $B_2 7$	$H_{(\mathrm{CROP + MEANSHAP})}$
$B_1 8$, $B_2 8$	$H_{(\mathrm{MEANAREA + EDGEDEN})}$
$B_1 9$, $B_2 9$	$H_{(\mathrm{CROP + MEANAREA + EDGEDEN})}$

[a] Models numbered B_1N, and B_1N refer to models with covariates generated within 0.65 km^2 and 10.36 km^2 circular buffers centered on nest sites, respectively.