

THE INFLUENCE OF LANDSCAPE CHARACTERISTICS ON DUCK NESTING
SUCCESS IN THE MISSOURI COTEAU REGION OF NORTH DAKOTA

by

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ABSTRACT

Because of the importance of nesting success to avian population dynamics, and the extensive and ubiquitous nature of habitat fragmentation, many studies have attempted to address the relationship between fragmentation and nesting success. However, an overall theory of fragmentation effects on nesting success has remained elusive. First, we reviewed published literature to examine fragmentation effects on nesting success at three spatial scales (i.e., edge, patch, and landscape scales). We identified 86 relevant manuscripts that provided 117 individual tests of hypotheses regarding the effects of fragmentation on nesting success. Fragmentation effects were more likely to be detected if fragmentation was examined at a landscape scale and if research was conducted over several years. Next, we examined the influence of habitat and landscape variables on duck nest survival ($n \sim 4200$ nests) on 18 10.4-km² sites in the Missouri Coteau Region of North Dakota. We evaluated competing models of nest survival that considered combinations of habitat features measured at nests, within nesting patches, and at multiple landscape scales. We used generalized non-linear mixed-modeling techniques to model nest survival. Information-theoretic techniques were used to select among competing models. Models that included random effects of individual sites and covariates measured at multiple landscape scales were dramatically better than models that included nest-level, patch-level, or landscape-scale covariates measured at a single spatial scale. Nest survival was positively related to the amount of grassland habitat, negatively related to the wetland density and related to the amount of grassland edge in a complex quadratic manner. Finally, we combined our nest survival model with existing models of mallard pairs using spatially-explicit GIS models and applied them to the entire Coteau region of North and South Dakota to guide conservation programs. Important trade-offs existed between pair density and nest survival; source populations were dominated by low pair-density areas while sink populations were dominated by high and medium pair-density areas. Based on the complex suite of factors influencing nest survival, a unifying paradigm of fragmentation across taxa and habitat types may not exist. Thus, research on the species and habitats of interest may be necessary to guide successful conservation efforts.

CHAPTER 1.

INTRODUCTION TO DISSERTATION

For many avian species and groups, nesting success is an important vital rate that exerts strong influence on population dynamics (Lack 1954, Ricklefs 1969, Martin 1992, Newton 1998, Sæther and Bakke 2000, Hoekman et al. 2002). As a result, many empirical studies have examined the influence of numerous factors on avian nesting success (e.g., Clark and Nudds 1991, Santos and Telleria 1992, Robinson et al. 1995, Hartley and Hunter 1998, McKee et al. 1998). However, over the past 15 years, fragmentation of habitats has been the dominant theme throughout the literature (Saunders et al. 1991, Andrén 1994, Debinski and Holt 2000, Haila 2002).

Fragmentation of breeding habitats for birds has been extensive and continues to occur across many areas (Richards 1990, Skole and Tucker 1993, Hansen et al. 2002). Habitat fragmentation typically reduces total habitat area, size of individual habitat patches, proximity of habitat patches, and can increase the amount of habitat edge with important potential impacts on nest survival rates and bird population dynamics (Rolstad 1991, Lawton 1995, Franklin et al. 2000).

Thus, developing an understanding of the effects of habitat fragmentation on avian nesting success is critical to conserving bird populations. Although many empirical studies have attempted to address the topic (e.g., Martin 1988, Fahrig and Merriam 1994, Robinson et al. 1995, Donovan et al. 1997, Marzluff et al. 2000), an overall theory of the effects of habitat fragmentation on nesting success has remained elusive.

Dissertation organization

Chapter 2 reviews the evidence for fragmentation effects on nesting success. The primary objective in this review was to examine patterns among studies of habitat fragmentation and avian nesting success in relation to the spatial scale that fragmentation was measured. Studies of fragmentation effects on nesting success can be categorized into three spatial scales (i.e., edge-, patch-, and landscape-scale), each of which represents unique, scale-dependent hypotheses about how fragmentation affects nesting success. We hypothesized that studies that measured fragmentation at landscape scales would be more likely to detect fragmentation effects than studies that measured fragmentation at either edge or patch scales. Chapter 3 represents a field study designed to examine questions about how scale-specific (i.e., nest, patch and landscape) habitat factors influence nesting success. This work was focused on duck nesting success in the Missouri Coteau region of North Dakota; the core of the breeding range for ducks in the Prairie Pothole Region (Batt et al. 1989). The duck species we studied were ideal for investigating our hypotheses of interest because they nested in relatively high densities across a diversity of habitat and landscape conditions. Landscapes within the Coteau region vary from large areas of native grassland to extensive areas of mostly cultivated lands. As a result, the Coteau is comprised of a diverse gradient of landscape types that provided a unique opportunity to understand how various habitat characteristics affect duck nesting success. In Chapter 4, we apply (1) our statistical model of how landscape characteristics affect duck nesting success, developed in Chapter 3, and (2) an existing model of landscape factors that affect duck density to the entire Missouri Coteau region

of North and South Dakota to develop a spatially explicit conservation planning tool using GIS. Because of the large grassland base that remains in the Coteau region, it is a priority region where large amounts of conservation programs are focused. Thus, correctly identifying the areas that result in the best nesting success rates is critical to the effectiveness and efficiency of conservation programs. Chapter 5 summarizes the key findings of the previous chapters and identifies areas where continued research should focus. A common theme throughout all chapters is the importance of the spatial scale at which habitat characteristics are measured in order to best explain and predict variation in nesting success rates. Because the research described in my dissertation was done in cooperation with a diverse team of colleagues, the text is written in third person to accommodate submission of individual chapters as journal articles with a number of co-authors.

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CHAPTER 2.

EFFECTS OF HABITAT FRAGMENTATION ON AVIAN NESTING SUCCESS:
A REVIEW OF THE EVIDENCE AT MULTIPLE SPATIAL SCALESIntroduction

Fragmentation of wintering and breeding habitats for birds has been extensive and continues to occur at a rapid rate across many areas (Richards 1990, Skole and Tucker 1993, Hansen et al. 2002) with negative demographic implications (e.g., Terborgh 1989, Saunders et al. 1991, Robinson et al. 1995, Donovan et al. 1997, Askins 2000, Boulmier et al. 2001). Habitat fragmentation typically reduces total habitat area, size of individual habitat patches, and proximity of habitat patches, and it can increase the amount of habitat edge. Reduction in the area of suitable habitat can result in population declines by simply reducing adequate space for territories, nest sites, and other critical resources (Rolstad 1991). Changes in habitat patch size, proximity of habitat patches, and the amount of edge-habitat also can affect bird populations by negatively affecting reproductive success, survival, emigration and/or immigration rates in the remaining habitat (Rolstad 1991, Lawton 1995, Franklin et al. 2000).

Because of the importance of nesting success to avian population dynamics (Lack 1954, Ricklefs 1969, Sæther and Bakke 2000), many empirical studies have attempted to address the effects of habitat fragmentation on nest survival (e.g., Martin 1988, Robinson et al. 1995, Donovan et al. 1997, Marzluff et al. 2000). However, different studies have considered fragmentation at different scales, and results have been inconsistent. Thus, an

overall theory about the effects of habitat fragmentation on nesting success has remained elusive; although such theory is further developed for some regions and orders (Robinson et al. 1995, Donovan et al. 1997).

In this review, we examine patterns among studies of habitat fragmentation and avian nesting success with a focus on the spatial scale at which habitat fragmentation was measured. We found we could effectively categorize past research as having examined three spatial scales (edge, patch, and landscape scale. A study was classified as having been done at the edge scale if it quantified fragmentation by measuring factors such as distance from a nest to a habitat edge. Patch-scale studies quantified metrics of fragmentation such as the size and shape of the habitat patch where nests were located. Landscape-scale studies quantified metrics of fragmentation such as the amount of habitat, edge, and variation in patch size across a defined spatial extent (e.g., 1 km, 10 km). Although the measures of fragmentation at the edge-scale are typically distance measures and the patch- and landscape scales measure fragmentation at different extents, we believed that the different measures are inherently ordinal in nature. Each of these distinct scales suggests different scale-specific hypotheses about the effects of fragmentation on nesting success. The first hypothesis predicts that nest-predation rate is a function of proximity to a habitat edge (edge-scale effects) (e.g., Gates and Gysel 1978, Wilcove et al. 1986, Yahner 1988, Paton 1994, Cooper and Francis 1998, Lahti 2001). The second hypothesis states that patch-level attributes are key determinants of nest-predation rate within a patch (patch-scale effects) (Duebbert and Lokemoen 1976, Wilcove 1985, Faaborg et al. 1995). Debate about edge- versus patch-scale hypotheses

continues because some authors have found a relationship between nesting success and patch area without detecting an edge effect (Small and Hunter 1988, Arango-Velez and Kattan 1997), while others have found the opposite (Rudnicki and Hunter 1993). The third hypothesis suggests that it is critical to consider fragmentation in a broader context (landscape-scale effects; e.g., total amount of edge in a landscape, density of habitat patches, configuration of habitat patches, and variance of habitat patch size) when trying to predict nest-predation rate (Andrén et al. 1985, Robinson et al. 1995, Dooley and Bowers 1998, Hartley and Hunter 1998, Tewksbury et al. 1998). Several previous studies found effects of landscape-level factors. However some did not detect patch or edge effects while others found that patch and/or edge effects were landscape dependent (Kurki and Linden 1995, Donovan et al. 1997). Also, Chalfoun et al. (2002) suggest that factors operating at larger scales may be more influential than smaller-scale factors on the abundance and behavior of nest predators.

Although Lahti (2001) conducted a thorough review of studies that examined the edge-scale hypothesis, no review has evaluated patterns in findings across multiple scales. Thus, we used the numerous studies that have been conducted on the effects of habitat fragmentation on nesting success to search for scale-dependent patterns in results, and provide suggestions for conservation and future research.

Methods

Our overall approach was to (1) choose taxonomic groups of interest, (2) review the relevant literature and locate studies that examined habitat fragmentation and nesting

success, (3) summarize the results of all studies, and (4) evaluate the evidence for a consistent relationship between habitat fragmentation and nesting success with respect to spatial scales. We focused our review on avian taxa (e.g., anseriformes, ciconiiformes, galliformes, passeriformes, and tinamiformes) where nesting success is highly variable, strongly influenced by predation, and has the potential to strongly affect population growth rate and mean fitness (Sæther and Bakke 2000). Therefore, we excluded studies of raptors and cavity- or colonial-nesting species (e.g., cavity nesting songbirds, colonial nesting waterbirds) from our search.

Because we were primarily interested in the effect of habitat fragmentation on avian nesting success, we limited our search to 22 peer-reviewed journals (Table 2.1) that we believed were most likely to contain articles on the subject. We searched each issue of the 22 journals published from January 1990 through January 2000 to locate articles and then examined the citations of each article to ensure adequate sampling coverage of previously published relevant articles. As a result, our review encompassed studies published as early as 1984.

For each study that examined habitat fragmentation and avian nesting success, we recorded the following: 1) taxonomic order of birds studied, 2) nest type(s) used in the study (i.e., real and artificial), 3) study duration (i.e., the number of years in the study), 4) sample size of nests monitored, 5) geographic region of study, 6) physiographic habitat type of study, 7) scale(s) at which habitat fragmentation was examined (i.e., edge, patch, or landscape treated as an ordinal treatment of increasing scale) with respect to nesting success, and 8) whether an effect of habitat fragmentation on nesting success was

detected at each scale considered. Studies that detected effects counter to the hypothesized predictions were classified as finding an effect but were noted in Appendix A1. Some studies that used artificial nests did not make it clear which taxonomic order they were attempting to mimic. Additionally, several have shown that artificial nests cannot accurately represent the nests of any specific taxa (Martin 1987, Willebrand and Marcstrom 1988, Roper 1992, Haskell 1995, Major & Kendal 1996, Butler and Rotella 1998, Ortega et al. 1998). Thus, we categorized artificial nests by the type of eggs [e.g., domestic chicken (*Gallus gallus*) or Japanese quail (*Coturnix japonica*)] used in the study. We used the following geographic regions: Canada/Alaska, Fennoscandia, Eurasia, Eastern U.S., Middle U.S., Western U.S., and Other. For our purposes, we considered the Eastern U.S. to include the states of Ohio, Kentucky, Tennessee, Mississippi and all states east; the Western U.S. to include the states of Montana, Wyoming, Colorado, New Mexico and all states west; and the Middle U.S. to include those states between the Eastern and Western states. We classified physiographic habitat types as forest, grassland, marsh, and shrubland dominated systems (excluding agricultural activity). For studies that examined hypotheses across multiple spatial scales or nest types, we used the individual hypothesis test at each scale and for each nest type as a sample in our analysis.

Because field and statistical methodologies were inconsistent across reviewed publications, we could not conduct a formal statistical meta-analysis. Instead, we modeled the probability of a study detecting an effect of habitat fragmentation on

Table 2.1. Journals reviewed for relevant articles on fragmentation effects on avian nesting success from January 1990 – January 2000.

Auk
Biological Conservation
Canadian Field Naturalist
Canadian Journal of Zoology
Condor
Conservation Biology
Conservation Ecology
Ecology
Ecological Applications
Ecological Monographs
Ecography
Journal of Animal Ecology
Journal of Applied Ecology
Journal of Field Ornithology
Journal of Wildlife Management
Ibis
Landscape Ecology
Oikos
Oecologia
The Wildlife Society Bulletin
Wildlife Monographs
Wilson Bulletin

nesting success with logistic regression (McCullagh and Nelder 1989, Collett 1991). In the modeling process, we predicted that the aforesaid probability would increase with the spatial scale examined. We then evaluated the amount of support in our data for this hypothesis by comparing it to the support for alternative *a priori* hypotheses (Platt 1964). Our list of *a priori* hypotheses (models) included the univariate spatial-scale model, a null model, as well as additive and interaction models that considered (1) spatial scale and (2) one of the following covariates: nest type, study duration, geographic region, and physiographic habitat type. We considered these additive and interaction models to see if these covariates added information to our primary hypothesis regarding spatial scale. Further, with the subset of studies that examined real nests, we examined the support for the aforementioned models alongside additive and interaction models of spatial scale and taxonomic order. Although we believe that spatial scale is inherently ordinal in nature, we first treated spatial scale as a nominal predictor variable in the analysis and then treated the scale variable as continuous to examine whether our hypothesized trend was better fit by a continuous model than the simple nominal model of spatial scale. To evaluate the amount of support in our data for each model in our candidate list, we used Akaike's Information Criterion adjusted for sample size (AIC_c) (Akaike 1973, Burnham and Anderson 1998: 51, 124), which employs maximum-likelihood theory, information theory, and the principle of parsimony (Akaike 1973). Among the models in our candidate list, we considered the best approximating and most informative model to be that with the lowest AIC_c value. To assess the goodness-of-fit of each candidate model, we used the area under the receiver-operating-characteristic (ROC) curve, which ranges

from 0 to 1 and measures the ability of the model to discriminate between effect and no-effect (i.e., success and failure) detections given the covariate values (Hosmer and Lemeshow 2000).

Although our vote-counting strategy has problems if publication biases exist, we agree with Chalfoun et al. (2002) that potential biases should be similar across studies at the three spatial scales of interest. Additionally, the probability of detecting significant results could be confounded with sample size of nests (Gurevitch and Hedges 1993). Therefore, we considered models that examined whether sample size of nests was related to detection of significant results.

Results

Our literature survey identified 86 publications with 117 hypothesis tests of the effects of habitat fragmentation on avian nesting success. Of these, 33 examined real nests yielding a total of 42 hypothesis tests. Among the studies that examined artificial nests, 40% of the hypothesis tests were done using chicken eggs and 60% with Japanese quail eggs. Four orders of birds were represented in the literature that examined real nests: Anseriformes (7.1% of tests), Ciconiiformes (2.4%), Galliformes (14.3%), and Passeriformes (76.2%). The mean duration of study was 2 years (SE = 0.17). Many geographic regions and physiographic habitat types were represented poorly in the literature (Table 2.2). However, the journals we selected to review likely introduced a North American bias into our results.

Table 2.2. The number of hypothesis tests contained in the studies at each spatial scale and nest type across the geographic regions and physiographic habitat types.

	Edge		Patch		Landscape	
	Nest Type		Nest Type		Nest Type	
	Real	Artificial	Real	Artificial	Real	Artificial
Region						
Canada/Alaska	4	7	1	3	1	1
Eurasia	0	3	0	3	0	0
Fennoscandia	2	6	2	3	0	3
Eastern U.S.	5	10	3	8	1	6
Middle U.S.	10	6	6	1	4	2
Western U.S.	1	2	1	1	1	1
Other	0	6	0	3	0	0
Total	22	40	13	22	7	13
Physiographic Habitat Type						
Forest	13	33	8	17	5	12
Grassland	9	5	5	4	2	0
Marsh	0	1	0	0	0	0
Shrubland	0	1	0	1	0	1
Total	22	40	13	22	7	13

* Some studies examined multiple nest types and spatial scales of habitat fragmentation and the results for each nest type and scale examined are included in the table. See Appendix 1 for specific studies.

Most studies ($n = 62$ hypothesis tests) examined effects of habitat fragmentation on nesting success at the edge scale, whereas fewer studies examined effects at patch ($n = 35$) or landscape ($n = 20$) scales (see Appendix A for details of studies that examined multiple scales and nest types). The beta estimates from the nominal spatial-scale model ($\beta_{\text{edge}} = -0.392$, $\text{SE} = 0.6776$; $\beta_{\text{patch}} = 0.2877$, $\text{SE} = 0.7133$; $\beta_{\text{landscape}} = 1.7346$, $\text{SE} = 0.6262$) suggest nearly linear increases in the probability of detecting an effect of fragmentation as the spatial scale increases for the full data set. As a result, the model that treated spatial scale as continuous variable was a better model than the nominal spatial-scale

model ($\Delta\text{AIC}_c = 1.38$ for the full data set and $\Delta\text{AIC}_c = 1.83$ for real nest data set). Thus, hereafter we used only the spatial-scale model where scale was treated as a continuous variable in all remaining models. The spatial-scale model (continuous) was a better model than the null model ($\Delta\text{AIC}_c = 10.78$). However, when covariates were considered in addition to spatial scale, only the model with spatial scale and study duration (Fig. 2.1) performed better than the spatial-scale model ($\Delta\text{AIC}_c = 1.42$; $\beta_0 = -1.82$, $\text{SE} = 0.55$; $\beta_{\text{spatial scale}} = 0.93$, $\text{SE} = 0.28$; $\beta_{\text{study duration}} = 0.22$, $\text{SE} = 0.13$; $\text{ROC} = 0.62$) making it the best approximating model in our candidate list.

When we examined the subset of studies that used real nests, the results were similar to those using the complete data set. Again, the spatial-scale model was better than the null model ($\Delta\text{AIC}_c = 4.70$). When models with other covariates were considered, the model with spatial scale and study duration (Fig. 2.2) performed better than the spatial-scale model ($\Delta\text{AIC}_c = 4.00$; $\beta_0 = -3.48$, $\text{SE} = 1.20$; $\beta_{\text{spatial scale}} = 1.19$, $\text{SE} = 0.53$; $\beta_{\text{study duration}} = 0.46$, $\text{SE} = 0.24$) and had better predictive power than the same model using the complete data set ($\text{ROC} = 0.77$). The model with an interaction between spatial scale and study-duration was better than the spatial scale model ($\Delta\text{AIC}_c = 2.60$). However, the model that contained spatial scale and study duration without the interaction term was still the best model by 1.42 AIC_c units. We did not find support for models that included geographic region, physiographic habitat type, or nest type ($\Delta\text{AIC}_c \geq 2.58$). Additionally, the trends observed did not appear to be confounded by sample size ($\Delta\text{AIC}_c \geq 2.47$).

Figure 2.1. The effect of the spatial scale of study, and the duration of study (measured in years) on the probability of detecting a significant effect of habitat fragmentation on nesting success for studies that used real and artificial nests ($n = 117$).

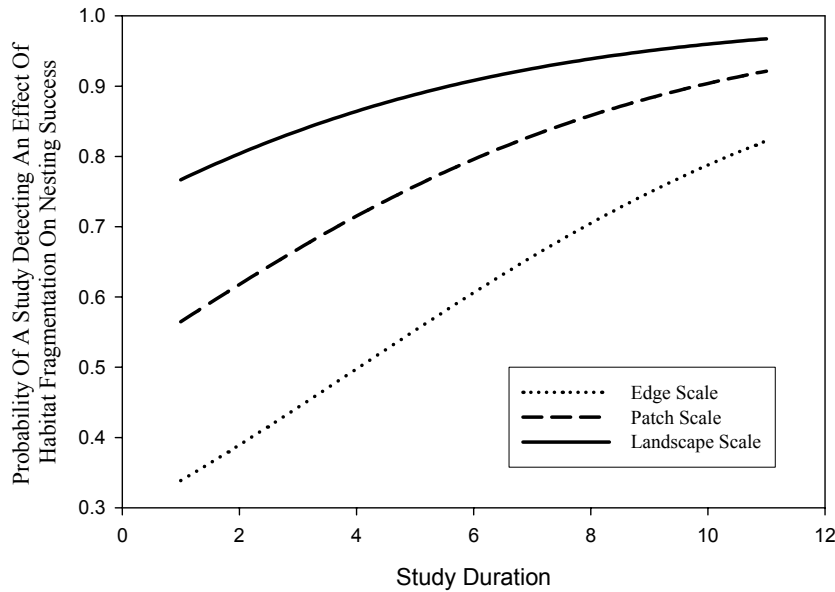
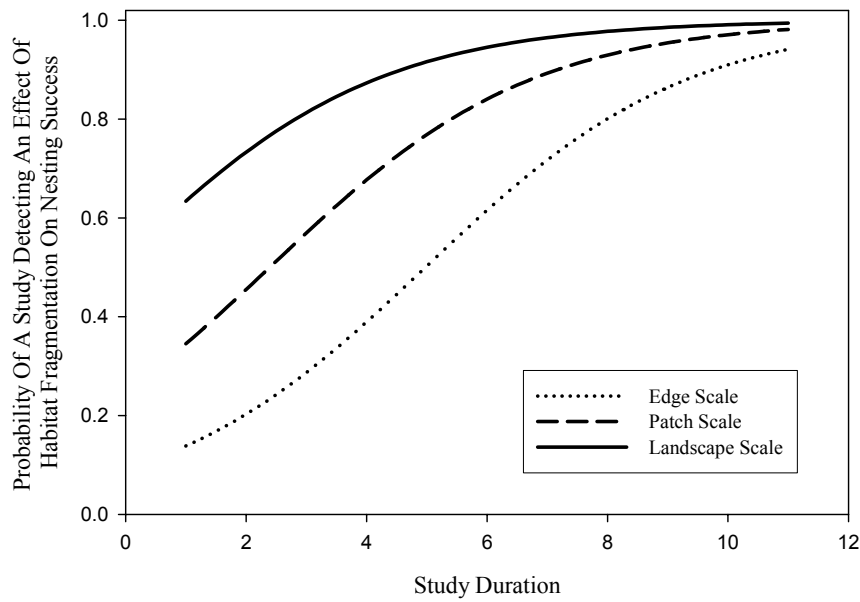


Figure 2.2. The effect of the spatial scale of study, and the duration of study (measured in years) on the probability of detecting a significant effect of habitat fragmentation on nesting success for studies that used real nests ($n = 42$).



Discussion

From our review of the literature, it is evident that habitat fragmentation studies have not been evenly distributed across species, geographic regions, or physiographic habitat types. In addition to Lahti's (2001) review on the edge-effect hypothesis, our multi-scale review of habitat fragmentation and its effect on avian nesting success provides a broad-based perspective that illuminates gaps in our knowledge. Based on this information, we identify directions for continued research on the topic and implications for conservation programs.

Overall, the proportion of studies detecting relationships between habitat fragmentation and nesting success increased as the scale at which habitat fragmentation was measured increased from edge to patch to landscape scale. Further, the data were best modeled treating the spatial-scale variable as continuous which suggests that the probability of detecting relationships between fragmentation and nesting success changed by similar magnitudes from edge, to patch, to landscape scales. We believe this trend represents compelling evidence that fragmentation effects are manifest at the larger landscape scales that have only recently begun to receive attention (Robinson et al. 1995, Donovan et al. 1997, Tewksbury et al. 1998). Interestingly, Chalfoun et al. (2002) recently conducted a literature review of nest predator responses to habitat fragmentation and noted the following general pattern across studies: nest predators were more likely to show a positive response to fragmentation (increased abundance, activity, or species richness) when fragmentation was measured at the landscape scale than at finer scales. Responses at local scales were more variable and dependent upon the landscape context

within which the study was conducted, as was previously suggested by Andrén (1995) and Donovan et al. (1997). We believe our results, coupled with Chalfoun et al.'s (2002) findings, provide new insight into the scale-dependent mechanism responsible for fragmentation effects on nesting success. Specifically, it appears that the response of nest predators is most sensitive to fragmentation at a landscape scale, and consequently, variation in nesting success is best explained by landscape-level metrics of fragmentation. When fragmentation only occurs at a local scale, however, the results are less predictable. Despite the consistent findings between our study and that of Chalfoun et al. (2002), it is important to realize that (1) the appropriate landscape scale (e.g., 1-km, 10-km, 100-km) will likely vary for different groups of nest predators and has not been explicitly examined (Mitchell et al. 2001), (2) some studies of nesting success conducted at the landscape scale failed to detect effects of fragmentation, and (3) many landscape settings, biogeographic regions, species groups, and physiographic habitat types remain poorly studied (see below).

Chalfoun et al. (2002) found no studies that examined species richness of nest predators in relation to landscape type. But, it seems plausible that patterns of predation on nests may be driven by the diversity of nest predators present in a landscape. We hypothesize that in settings with diverse predator communities, it will be important to consider multiple landscape scales when trying to predict nesting success rates because different species or groups of nest predators (e.g., squirrels vs. coyotes) likely respond to fragmentation at different scales. Thus, empirical investigations that concurrently examine predator-community composition and nesting-success rates across a range of

landscape types at multiple spatial scales may be necessary to elucidate the true effect of habitat fragmentation on nest predators and nesting success.

Our results also suggest that the short duration of most studies may be partly responsible for the inconsistent results among studies. Given the nature of temporal variation in predator populations, alternate prey populations, and thus, predation rates (see Holmes and Sherry 2001), research conducted for at least five years will offer greater ability to separate real effects of fragmentation from those due to inherent environmental stochasticity. Additionally, spatially and temporally replicated studies will be necessary to accomplish the important task of partitioning variance into process and sampling components (White 2000, Franklin et al. 2000). Thus, conservation decisions will be best informed by longer-term efforts to monitor the effects of fragmentation on nesting success, and correspondingly, decisions made based upon short-term evaluations may be misleading.

There is little information on the effects of habitat fragmentation on nesting success for most orders of birds, making it difficult to draw conclusions across taxa even in the same geographic regions or physiographic habitat types (see Results). For example, this is particularly relevant in the western U.S. where the rate of habitat loss is accelerating (Hansen et al. 2002) but where few studies on habitat fragmentation effects have been conducted (Franklin et al. 2000).

Chalfoun et al. (2002) found that nest-predator response was inconsistent and variable across geographic areas. Thus, for reliable inference and conservation decisions to be made across poorly studied regions and physiographic habitats, more work will be

required. To improve our understanding of the relationship between habitat fragmentation and nesting success, future studies should consider studying avian species and orders where little or no information currently exists. Also, future study designs should focus on using real nests (Butler and Rotella 1998), consider necessary sample sizes of nests (Rotella et al. 2000), and ensure spatial and temporal replication of sites to rigorously examine alternative hypotheses.

Because on the results of our review (e.g., $\geq 85\%$ of studies that examined landscape-scale habitat fragmentation detected an effect of habitat fragmentation on avian nesting success), we believe that examination of fragmentation at landscape scales offers the greatest utility. Furthermore, the effects of habitat fragmentation on avian demographics at smaller spatial scales may be dependent on the larger landscape context (Andr n 1994, Donovan et al. 1997, Chalfoun et al. 2002). However, the lack of an experimental design across the available studies prevents strong inference on the causal nature of the association between fragmentation, scale, and avian nesting success. We strongly believe that future studies designed to address fragmentation effects on nesting success should: 1) focus on sampling across landscape gradients, 2) measure predictor variables at multiple landscape-scales, and 3) as suggested by Lahti (2001), conduct corresponding research on the dominant nest predators.

Our results indicate that habitat fragmentation at larger scales may affect nesting success more than fragmentation at smaller scales. If this is true, then management of avian populations will have to consider management of human development as well. Thus, we suggest that avian conservation plans should focus on developing reserves

comprised of large blocks of unfragmented habitats. Negative impacts on bird populations will be minimized if human-induced fragmentation (e.g., home development, logging, agriculture) is concentrated in one locale rather than dispersed across a large spatial extent. Furthermore, the cumulative effects of multiple small anthropogenic developments, which may occur across socio-political boundaries of ownership and management, will have to be considered in the landscape context when trying to manage fragmentation of avian habitat to minimize demographic impacts.

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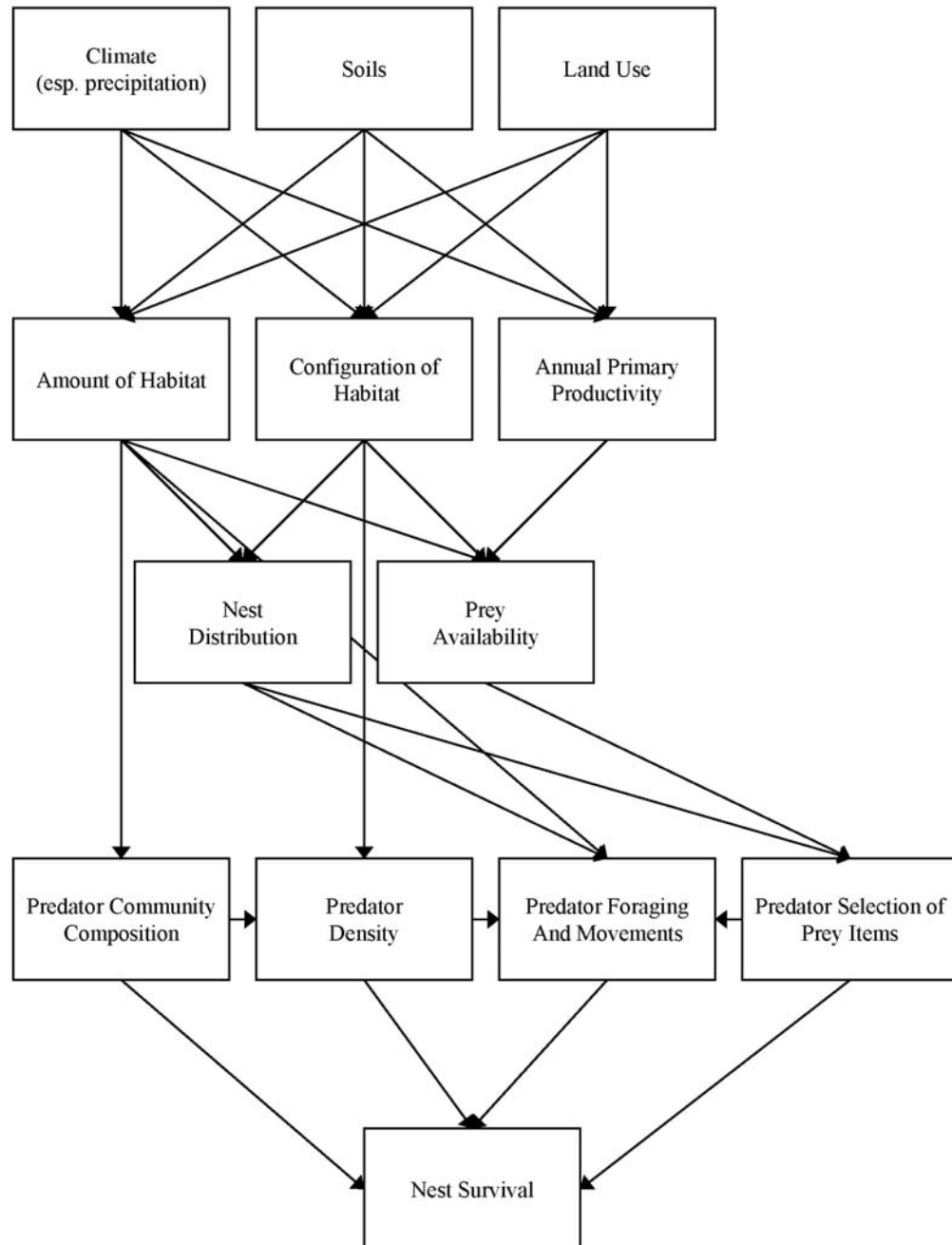
CHAPTER 3.

LANDSCAPE CHARACTERISTICS AFFECTING DUCK NESTING SUCCESS IN
THE MISSOURI COTEAU REGION OF NORTH DAKOTAIntroduction

Ducks breeding in the Prairie Pothole Region (PPR) of the Northern Great Plains evolved life-history characteristics in landscape settings typified by numerous small wetlands and expansive native grasslands (Kuckler 1964, van der Valk 1989, Rohwer 1992, Ostlie et al. 1997). However, over the past 100 years, the PPR has been dramatically altered by large-scale agriculture (Higgins 1977, Archibold and Wilson 1980). Wetland loss and degradation across the PPR have been substantial (Tiner 1984, Boyd 1985), and most native grasslands that existed historically in the PPR have become increasingly fragmented or lost through conversions to agriculture (Higgins 1977, Sugden and Beyersbergen 1984, Greenwood et al. 1995, Miller and Nudds 1996).

These large-scale changes are hypothesized to have affected predators, which are the primary cause of nest loss (Klett et al. 1988, Sargeant and Raveling 1992, Sovada et al. 2000). Predators may influence nest survival based upon 1) the species composition of the predator community, 2) the density of predators present, 3) how predators forage and move throughout the landscape, and 4) selection of different prey items as a result of differing availability of prey items (Figure 3.1). As a result of the landscape-level change to habitats of the PPR, predators encounter more nests in altered landscapes, which results in reduced nesting success (Higgins 1977, Cowardin et al. 1985, Greenwood 1995,

Figure 3.1. Conceptual diagram of hypothesized interrelationships between landscape/habitat characteristics, nest predators, alternate prey and duck nest survival in the Prairie Pothole Region.



Beauchamp et al. 1996, Reynolds et al. 2001). If this hypothesis is correct, we would expect important negative consequences for duck populations because population growth rates appear most sensitive to changes in nesting success (Johnson et al. 1992, Hoekman et al. 2002). Accordingly, most conservation programs for breeding ducks in the PPR seek ways to increase nesting success (PPJV Implementation Plan 1995, Williams et al. 1999) by restoring habitats so they more closely approximate historic conditions.

To design successful habitat management strategies, we need to understand how predator responses are affected by habitat features and thereby, understand how altering habitat will influence nesting success. However, predators are difficult and expensive to reliably monitor directly (Diefenbach et al. 1994, Sargeant et al. 1998, Warrick and Harris 2001). As a result, researchers are forced to use a more indirect approach that identifies habitat features strongly correlated with nesting success. Previous research into habitat features affecting nesting success focused on small-scale variables such as vegetation at the nest site or characteristics of the habitat patch where the nest was located (e.g., Kirsch et al. 1978, Higgins et al. 1992, Klett et al. 1988). But these studies did not find strong and consistent patterns (Livezey 1981, Clark et al. 1991, Clark and Nudds 1991).

Landscape-scale factors may be better predictors of nesting success. For example, nesting success has been shown to be negatively related to the amount of cropland on a site (Greenwood et al. 1995) and positively related to the amount of grassland present (Reynolds et al. 2001). However, these studies left a large amount of variation in nesting success unexplained. Recent studies suggest that variation in nesting

success may be better explained by considering multiple landscape features (Howerter 2003). Landscape features have also been shown to influence foraging patterns of predators of duck nests (Phillips et al. 2003). Thus, structure and configuration of landscapes may have important influences on predation rates of duck nests. Additional landscape characteristics such as wetland density and the number of human settled sites may also influence predators (Larivière et al. 1999) and thus, nest-predation rates.

Nesting success might also be affected by landscape features measured at a variety of spatial scales. To date, most studies that have examined the influence of landscape characteristics on nesting success have only quantified landscape-level metrics at a single scale (Greenwood et al. 1995, Reynolds et al. 2001). But, diverse communities of nest predators are common throughout the PPR (Greenwood et al. 1995). Different species of nest predators, which can have very different home range sizes, are likely to respond to landscape characteristics at different spatial scales (Chalfoun et al 2002; Stephens 2003, Chapter 2). Thus, determining the appropriate scale(s) at which to measure landscape-level variables may be as important as identifying which variables to measure (Levin 1992, May 1994, Mitchell et al. 2001).

In an effort to improve our ability to explain variation in nest survival, we designed this study with the following objectives: 1) evaluate competing models of nest survival that consider different combinations of habitat features measured at nest sites, within nesting patches, and at broader landscape scales; 2) determine the spatial scale(s) at which landscape-level covariates best explain variation in nest survival. To achieve these objectives, we used a factorial design to establish study sites that varied in

grassland extent as measured at different spatial scales. We then monitored nest survival on each site and measured other landscape-, patch- and nest-level covariates that we thought were potentially related to nest survival. Because ducks nest across broad areas of the PPR, we were able to sample large numbers of nests across a variety of habitat and landscape settings. Finally, using new analysis methods (Rotella et al. 2000, Dinsmore et al. 2002, this study), we conducted multiple-regression analyses of continuous and categorical factors potentially related to nest survival. These methods allow simultaneous consideration of multiple continuous and categorical covariates. As a result, these new methods facilitate a more thorough exploration of factors related to nest survival and are a substantial improvement over simple Mayfield estimators that have previously received the majority of the use.

Study Area

This study was conducted on 18 sites in the northern half of the Missouri Coteau region (hereafter, Coteau) of North Dakota. The Coteau is a 19- to 80-km wide glaciated area with moderate relief (30-90 m) that extends from southern Saskatchewan to southern South Dakota. This region is comprised of “knob and kettle” topography (Stewart and Kantrud 1973) deposited by the Wisconsin glacier (Clayton and Cherry 1967, Bluemle 1991). The soils are mostly thin, gravelly, and loamy soil types (Bluemle 1991). Study sites were distributed across McLean, Ward, Mountrail, Burke and Divide Counties.

Prior to settlement, the Coteau region was comprised of native mixed-grass prairie (Kuckler 1964, Ostlie et al. 1997) and supported large herds of grazing ungulates (Roe

1951, Coues 1965). Today, landscapes within this region vary from large areas comprised almost exclusively of native grassland used for cattle production to extensive areas of mostly cultivated lands devoted to production of small grains and oilseeds. This gradient of conditions makes the Coteau an ideal area for investigating relationships between habitat features and nest survival because of the diverse gradient of landscape characteristics that exist across the region.

Methods

Study-Site Selection

We sought a set of study sites that varied in the extent of grassland cover. To increase our ability to detect relationships between nest survival and habitat conditions measured at different spatial scales (McGarigal and Cushman 2002), we employed a factorial design that considered 2 spatial scales and three levels of grassland extent at each scale. We chose to examine spatial scales of 10.4 km² (4 mile²) and 93.2 km² (36 mile²). We selected the 10.4-km² scale because previous work suggested that nest survival was positively related to percent grassland measured at that scale (Reynolds et al. 2001). We chose the larger 93.2-km² scale to gain information that would provide a substantial contrast to the finer 10.4-km² scale. We only considered sites with 20-100% grassland cover at each of the spatial scales. We expected that sites with less than 20% grassland would not provide adequate nest-searching opportunities and, based on our *a priori* thinking about factors related to nest survival, would be difficult locations to manage for duck production.

To choose sites, we first used Landsat satellite imagery to identify the locations of the respective grassland/scale combinations, and then randomly selected 2 replicate sites from each grassland/scale treatment level from the population of potential sites (Table 3.1). This approach allowed us to control multiple sources of variation *a priori* and ensured our sample was representative of the larger region of interest (McGarigal and Cushman 2002). Because the treatment of low grassland at the 10.4-km² scale and high grassland at the 93.2-km² scale did not exist in our area of interest, we randomly selected two additional study sites from the remaining treatments (Table 3.1). Selected study sites also had to meet 2 other criteria for inclusion in our sample. First, to maintain spatial independence of study sites, we required that the centers of study sites were ≥ 10.36 km apart (because of the Coteau's linear nature some study sites did overlap one another at the 93.2-km² scale). Second, we only considered sites that were predicted, based on their wetland composition and density (Cowardin et al. 1995; Ron Reynolds, unpublished data), to have at least 50 females/2.59 km² (1 mi²).

For the 18 sites selected, grassland cover ranged from 19 to 96% of the total upland area at the 10.4- km² scale and from 19 to 85% at the 93.2-km² scale (Table 3.2). Other landscape characteristics of our sites also varied widely at each of the two spatial scales (Table 3.2), which allowed us to examine the influence of the suite of landscape variables on duck nest survival. The values for the various habitat metrics that we considered in our models were not strongly correlated (see Results). During the two years of this study, we observed similar and excellent wetland conditions across our study

sites: all semi-permanent and permanent wetlands contained water year-round, and many seasonal wetlands held water throughout each nesting season.

Table 3.1. Factorial design used to select study sites in the Missouri Coteau region of North Dakota, USA with different levels^a of grassland at 10.4- and 93.2- km² spatial scales.

10.4- km ² scale	93.2- km ² scale	Number of study sites selected
Low	Low	2
Low	Medium	2
Low	High	Did not exist
Medium	Low	2
Medium	Medium	2
Medium	High	2
High	Low	3
High	Medium	3
High	High	2

^aLow levels of grassland were defined as landscapes containing from 20-47% grassland, medium levels of grassland were defined as landscapes containing from 48-74% grassland, and high levels of grassland were defined as landscapes containing from 75-100% grassland.

Table 3.2. Range of landscape characteristics for 18 study sites in the Missouri Coteau region of North Dakota, USA measured at the 10.4- and 93.2- km² spatial scale.

Study Site	10.4-km ² scale	93.2- km ² scale
Percent Grassland	19 - 96	19 – 85
Grassland Edge	50,237 - 134,303 m	417,222 – 975,434 m
Density of Grassland Patches	0.0004 - 0.0042 /m ²	0.0010 – 0.0045 /m ²
Grassland Patch Size Variance	244,588 – 3,958,983 m ⁴	422,526 – 5,008,703 m ⁴
Grassland Patch Count	4 - 43	77 – 411
Wetland Area	576,845 – 3,327,629 m ²	9,148,897 – 17,461,287 m ²
Wetland Count	101 - 500	1,271 – 3,090
Human settled sites	1 - 11	10 – 57

Nest Searching and Monitoring

We located nests using standard nest-searching techniques for waterfowl (Higgins et al. 1969, Klett et al. 1986) from late April through mid-July in 2000 and 2001. A nest was defined as ≥ 1 egg in a scrape or bowl. When a nest was found, we marked its location by placing an individually numbered stick (1-1.5 m tall, 1-3 cm diam.) 5 m to the north of the nest and recorded the following information: duck species, number of eggs, incubation stage (i.e., nest age, Weller 1956), date, nest location, habitat type, and type of vegetation within 1 m of the nest. We plotted nest locations on aerial photographs and recorded nest coordinates with Trimble Geo-Explorer 3 GPS units. We revisited each nest at intervals of 3-9 days until ≥ 1 egg hatched or the nest was abandoned or destroyed. Both destroyed and abandoned nests were classified as unsuccessful. If we could not relocate a nest, determine a nest's fate with certainty, or a nest was abandoned before the first re-visit, the nest was not included in analyses.

Habitat and Landscape Characteristics

We measured habitat characteristics at multiple spatial scales. At each nest site we recorded a modified Robel-pole reading (Robel 1970) of the height and density of vegetation within 0.5 m of the nest (nest robel). For each field that contained a nest, we quantified the following patch-level features: 1) average Robel reading (averaged across a minimum of 10 random sites within the patch) and 2) habitat type (i.e., grassland [native pasture], Conservation Reserve Program [CRP] fields, Hayland, Planted Cover [introduced grass and forbs typically occurring on federal Waterfowl Production Areas [WPA's] or National Wildlife Refuges [NWR's], Cropland, Wetland, Right-of-ways

[roadside ditches], and Other). For landscape characterization, we measured seven variables at each of 5 spatial scales (10.4-, 23.3-, 41.4-, 64.7, and 93.2-km²). The seven landscape variables examined were: 1) Percent Grassland (grassland area/total upland area), 2) Grassland Edge (length of edge between grassland cover types and other upland cover types or wetlands), 3) Grassland Patch Density (1000 x number of grassland patches/total upland area; Saura and Martinez-Millan, 2001), 4) Variance of Grassland Patch Size, 5) Wetland Count (number of wetlands derived from National Wetlands Inventory [NWI]; U.S. Fish and Wildlife Service 1994a, 1994b, 1995), 6) Wetland Area (sum total of wetland area derived from NWI) and 7) Number of Human Settled Sites. We also included several other non-habitat variables that we thought might be related to nest survival; these were Year, Species of duck, Observer Effect of visiting nests, Nest Age and Julian Date.

Model Justification and Predictions

We considered which habitat features might be related to predator abundance and foraging behavior and thereby, influence nest survival. The predator responses to variation in habitat features occur as: 1) variation in the composition of predator communities, 2) variation in the densities of predator species, 3) variation in predator foraging behavior and nest-finding efficiency, 4) variation in prey selection and availability of different prey items, and 5) interactions among all four. Based on these ideas, we developed a variety of competing models (Burnham and Anderson 1998, 2002) that related habitat features to nest survival.

Most previous research investigated how fine-scale habitat factors related to nest survival. Klett et al. (1988) found evidence that nests in different habitat types had different survival rates. Height and density of vegetation within nesting patches and at nest sites have also been found to affect nest fates (Livezey 1981); the hypothesized mechanism is that predator foraging efficiency is reduced in taller, thicker vegetation.

Investigations of the influence of landscape-level metrics on nest survival have only recently begun. Thus, we do not yet know whether or not knowledge of such factors will substantially improve our ability to explain variation in nest survival. Here, we sought to explore a variety of ways by which landscape level factors might influence nest survival. We hypothesized 1) that landscapes with different amounts of grassland habitat would consequently have different communities of predator species (Sovada et al. 1995, Sargeant 1993, Chalfoun et al. 2002) and 2) that landscapes with greater grassland extent would have higher nest survival than less-intact landscapes. Landscapes with more intact grassland tend to be dominated by predator communities comprised of species such as coyotes and badgers which have larger home ranges, and have been shown to have higher nest survival for waterfowl (Sovada 1993, Sargeant et al. 1993). In contrast, landscapes with substantial amounts of cropland are believed to be comprised of smaller predator species such as red fox, skunks and raccoons that have been shown to depress duck nesting success rates to low levels (Sargeant et al. 1993, Sovada et al. 1995).

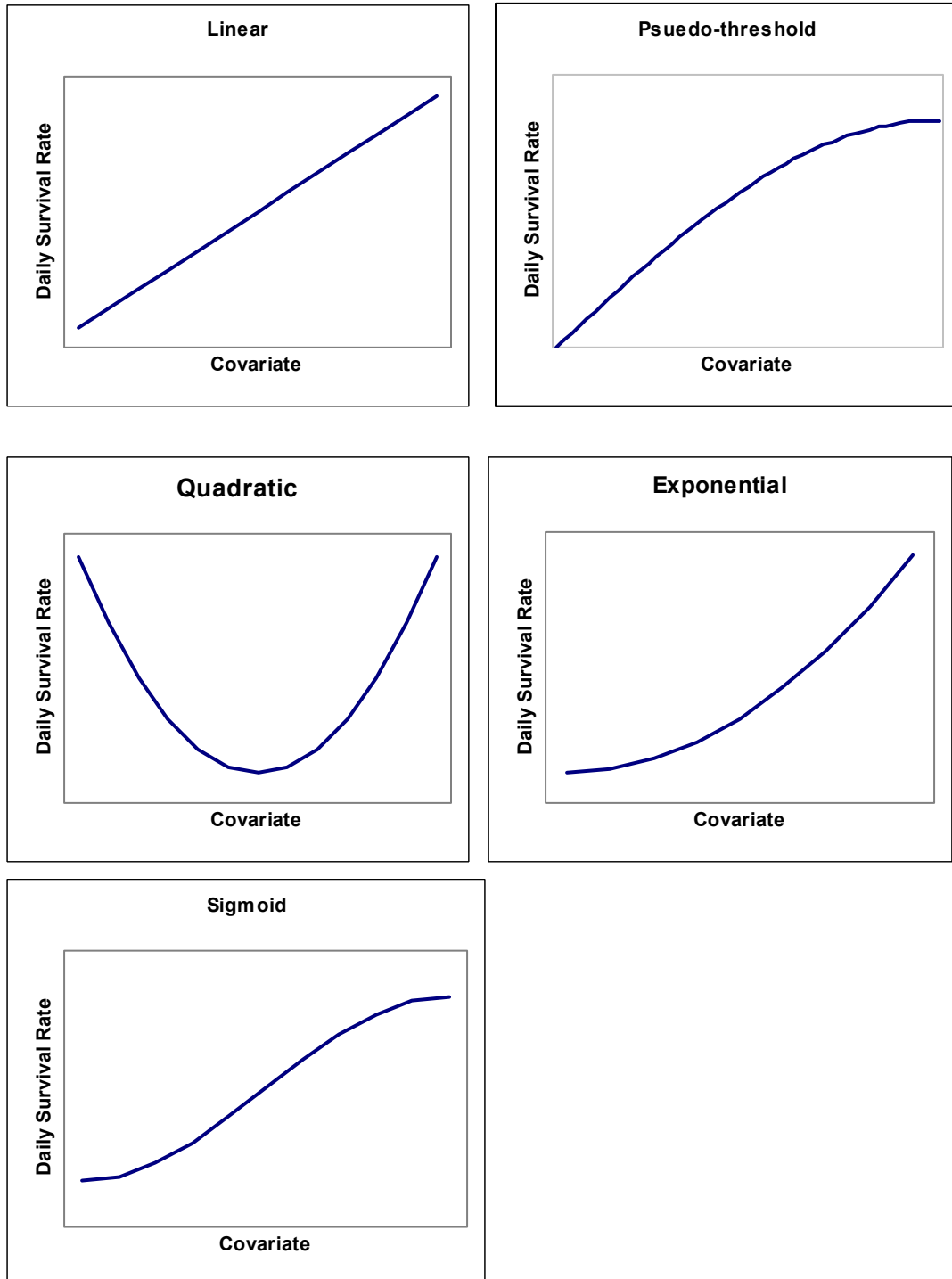
Configuration of habitats within a landscape may also influence predator community composition and foraging strategies of the predator species present and as a result, affect nesting success (Andren 1995, Ims 1995). Size and shape of patches can

impact the survival of nests if predators spend more time foraging along patch edges (e.g., Clark et al. 1999, Phillips 2001) or use edges as travel corridors (Andren 1995, Lahti 2001). Similarly, the amount of habitat edge has also been reported to be an important factor influencing nest survival for avian taxa in general (Andren et al. 1985, Robinson et al. 1995, Donovan et al. 1997) and waterfowl specifically (Howerter 2003) with landscapes comprised of more edge typically resulting in lower nesting success. As a result, we predicted that nest survival would generally decrease as landscape-level habitat fragmentation increased.

Other landscape features may also influence nest survival. Outbuildings associated with farmsteads may provide additional den sites for some predator species (Lariviere and Messier 1998, Lariviere et al. 1999) and thus, allow increased abundance of species such as striped skunk, raccoon, and perhaps red fox. Accordingly, we predicted a negative relationship between the number of buildings and nest survival. Because many nest predators focus their foraging efforts around wetlands (Phillips 2001, Lariviere 1999), and because wetlands may, through their high primary productivity, support a greater abundance of predators, we also hypothesized that sites with more wetlands (number or areal extent) would have lower nest survival.

For each continuous habitat or landscape variable, we considered those functional forms of the relationship between the variable and nest survival (Figure 3.2) that we believed were reasonable. For all variables, we considered linear forms (Table 3.3). However, we also considered pseudo-threshold, exponential, and sigmoid forms of relationships for many predictor variables (Table 3.3) because we believed non-linear

Figure 3.2. Model forms used in hypothesized models relating covariates to daily survival rate.



forms of relationships, such as positive or negative relationships that asymptote, were more biologically realistic than simple linear forms. We believed that the quadratic form was compelling only for variables that quantified the fragmentation level of the landscape because optima might exist at both high and low levels of fragmentation (Table 3.3). We hypothesized that intermediate levels of fragmentation (i.e., a patchwork of grassland and cropland) would support the most diverse predator communities, and thereby result in the lowest nesting success.

Table 3.3. Hypothesized models relating habitat covariates to nesting success in the Missouri Coteau region of North Dakota, USA.

Variable	Form of Relationship Examined				
	Linear	Pseudo-threshold	Exponential	Sigmoid	Quadratic
Percent Grassland	X	X	X	X	
Grassland Edge	X	X	X		X
Grassland Patch Density	X	X	X		X
Grassland Patch Variance	X	X	X		X
Wetland Area	X	X	X	X	
Wetland Count	X	X	X	X	
Human settled sites	X	X	X		

Modeling Daily Nest-Survival Rate

We evaluated competing models of daily survival rate (DSR) of nests using generalized non-linear mixed models (Proc NLMIXED, SAS Institute Inc. 2002). We chose Proc NLMIXED in SAS because it allowed us to model our binomially distributed data while considering the effects of nest-level covariates, in addition to patch- and landscape-level covariates, on nest survival along with a single random effect. Non-linear mixed models also allowed us to consider complex, non-linear relationships between the covariates of interest and nest survival using multiple fixed effects and

random effects attributed to a single random factor (e.g., study site). Non-linear mixed models can include quantitative and categorical covariates. Whether the effect of a covariate on the response is considered fixed or random depends upon both the understanding and the intent of the researcher. If an effect is conceived of as being drawn from some random probability distribution and the researcher is interested in inference on the greater population from which the effects are drawn, i.e., not only on the specific cases themselves, then the effect should be considered random (LaMotte 1983, Robinson 1991). Fixed effects are those not drawn from a random distribution or effects for which the value of the covariate can be quantified when making predictions to new sites. In this modeling effort, we considered all landscape, habitat and other variables such as Percent Grassland, Grassland Edge, Wetland Count and Nest Age to be fixed-effect variables because they could be quantified on new sites. Because of the broad distribution of sites that we had across the Coteau region, we chose to include the unmeasured effects of individual study sites as our random effect. However, ultimately year effects will need to be estimated as random effects when data from additional years are available and when the software is capable of supporting multiple random effects. The random effect of study sites encompasses all of the factors associated with that site that are not quantified by any of the fixed effect covariates. Thus, when making predictions to new sites we cannot quantify these un-measured vagaries of the individual sites. However, the estimate of the process variance associated with individual study sites does provide a measure of 1) the process variation in nest survival not explained by other covariates that we measured and 2) the level of uncertainty that we can expect when

using the model to make predictions for new sites. Because study sites were stratified to maximize the power to discriminate among fixed-effect covariates, our overall estimate of the random effects variance associated with individual study sites had the potential to be inflated. As a result we conducted diagnostic tests to examine possible differences in the means and variances of the estimated random effect among strata at the 10.4-km², 41.4- km², 93.2- km², and 10.4- and 93.2-km² scales combined. We used Tukey's test among strata to examine differences in means and Levene's test to examine differences in the variances among strata. We also tested for spatial autocorrelation among the beta estimates of the random effects for each study site. We used a Geary's C-statistic to measure the amount of spatial autocorrelation. Geary's C-statistic ranges from 0 – 2 with a value of 0 indicating perfect positive spatial autocorrelation, a value of 1 indicating no spatial autocorrelation and a value of 2 indicating perfect negative spatial autocorrelation.

We modeled the relationship between DSR and both time-varying (e.g, covariate values change across days in the interval) and time-invariant (e.g., covariate values remain constant across days in the interval) covariates with a logit link function:

$$DSR_{ij} = \frac{e^{(B_0 + u + B_1 * (NA + i) + B_k * X_k)}}{(1 + e^{(B_0 + u + B_1 * (NA + i) + B_k * X_k)})},$$

where DSR_{ij} is the daily survival rate for the i th day ($i = 0, 1, \dots, t - 1$) of the j th interval (Dinsmore et al. 2002) between visits to the nest with length t days; B_0 is the intercept term, u is the random effect of study area on the intercept of the model (normally distributed with mean = 0.00), B_1 is the slope coefficient for the nest age, NA is the age of the nest at the beginning of the interval and is then incremented by a day for each day in the interval ($i=0, 1, \dots, t-1$), B_k is the slope coefficient for the k th time-invariant covariate

and X_k is the value of the k th time-invariant covariate. We used 2 approaches to model the complex non-linear relationships between covariates and nest survival that were of interest to us (Figure 3.2). First, we used the logit link function that is very flexible and can accommodate a variety of forms while constraining DSR between 0 and 1. Second, we transformed some covariates (e.g., $\ln$ covariate, $e^{\text{covariate}}$) to allow the non-linear relationships between covariates and duck nest survival even greater flexibility and asymmetry in form. Example code is provided in Appendix B1.

Survival probability for any interval (S_j) is estimated as the product of DSR 's for that interval:

$$S_j = \prod_{i=0}^{t-1} DSR_i$$

and nesting success is the product of the daily survival rates for the length of the nesting period (e.g., 35 days for mallards):

$$NestSuccess = \prod_i^{35} DSR_i .$$

We used Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 1998) to evaluate models (Burnham and Anderson 1998, Franklin et al. 2000). We compared models using ΔAIC values, where for each model i :

$$\Delta AIC_i = AIC_i - AIC_{\min}$$

We used AIC instead of AICc because with our sample size, the values for both AIC and AICc were the same. The ΔAIC values compare the relative distances between the best approximating model ($AIC_{\min}$) and each competing model (AIC_i). Generally, models

with ΔAIC values ≤ 2 have strong support while those with ΔAIC values > 10 have little support (Burnham and Anderson 1998, 2002).

We first analyzed 466 models using a reduced dataset. We did this because Robel readings at nest sites and random sites were not available for all nests. Thus, to assess the importance of Robel readings, we worked with data for those nests for which we had obtained both nest- and field-Robel readings. No model containing field or nest Robel had an ΔAIC value ≤ 21.6 . Thus, models containing nest Robel and field Robel were not considered further, and the full data set was used to examine which of the remaining variables were most strongly related to duck nest survival.

Although we initially developed a limited number of *a priori* models that combined nest-, patch- and landscape-level covariates, our model list grew exponentially when multiple landscape scales were considered (a total of over 1,000 *a priori* models). Additionally, because run times for estimating parameters in models that included a random-effect of study site exceeded 20 hours, we used a modeling strategy whereby we included covariates in models in a hierarchical manner (Langtimm et al. 1998). We first evaluated the simple, *a priori* models, which included fixed-effects and only a limited number of interactions between habitat covariates measured at 10.4- and 93.2-km² scales, which was in keeping with our *a priori* interest in what could be learned about variation in nest survival using habitat information from small versus large landscape scales. Next, we examined nuisance variables (see below) to determine which needed to be included to appropriately assess the habitat variables of interest. Then, for each fixed-effects model that had ΔAIC values ≤ 25 , we added study area as a random effect. To further evaluate

the spatial scale at which landscape characteristics best-explained variation in nest survival, we subsequently examined all *a priori* models that contained scale-specific landscape variables at 23.3-, 41.4-, 64.7, and 93.2- km² landscape scales. We included the 93.2-km² scale because our original *a priori* models included only a limited number of models at the 93.2-km² scale.

Several non-habitat covariates may introduce important sources of heterogeneity in survival rates of nests. For the purposes of this study, we considered these variables to be “nuisance variables” that needed to be dealt with appropriately in order to accurately assess the importance of the habitat covariates of interest. These variables included Observer Effects, Nest Age, and Julian Date. Researchers may influence the DSR of nests visited, which if ignored would result in biased estimates of nest survival (Rotella et al. 2000). Thus, we added an observer effect variable that allowed DSR’s to be different on the days that each nest was visited. Techniques recently became available to examine the influence of time-varying covariates such as Nest Age and Julian Date on nest survival (see Dinsmore et al 2002). Therefore, we included Nest Age and Julian Date in our *a priori* models, although we did not have preconceived ideas on how they might influence nest survival.

In addition to the suite of factors we measured, we recognized that many other latent variables might influence nest survival. We took advantage of the ability to examine the random effect of study site to quantify the amount of variation in nest survival that was not explained by the covariates we measured. We modeled the random

effect of study site as a change in the intercept of relationships between nest survival and the covariates of interest.

To generate new hypotheses from the dataset, we built exploratory models that 1) combined those covariates that were in top-ranked *a priori* models but that had not been combined in any single model, 2) explored two-way interactions between landscape covariates and year, and 3) combined information from those spatial scales shown to be most useful based on results for single-scale models (AIC comparisons among single-scale models).

Model Diagnostics

To evaluate which variables had the greatest influence on nest survival, we measured the change in nesting success (sensitivity) to changes in each predictor variable in the most parsimonious model. Because relationships between nesting success and predictors were non-linear, sensitivity values depended on the baseline value of the covariate that was chosen. We chose to calculate the sensitivity of nesting success to each covariate for values where the change in the covariate value resulted in the maximal change in nesting success. We changed each covariate value by 10% while all other covariates were set to their mean values.

Nest survival is known to vary spatially (Greenwood et al 1995, Reynolds et al. 2001), but previous work has not explicitly accounted for site-specific variation unaccounted for by measured fixed effects. Recent availability of models that allow estimation of random effects provides a means to quantify how much variation in nest survival is due to fixed versus random effects, i.e., factors that are difficult to measure

(e.g., diverse community of nest predators) or have yet to be identified. Separating these two components is important for 1) understanding the relative contributions of fixed effects included in the model and random effects, 2) generating ideas for new covariates that can be identified or measured to capture additional unexplained variation, thus reducing unexplained residual variation, and 3) appropriately estimating the degree of deviations from predictions that can be expected when the model is applied to new sites.

In order to interpret the estimates of spatial process variation in nest survival, we first had to back-transform the logit-transformed estimates that resulted from our model to the spatial process variance in nesting success. This allowed us to consider variation in the vital rate itself, which provided for more straightforward biological interpretation. Additionally, we were also interested in quantifying how well our model performed by estimating the proportion of spatial process variation in nesting success in our data explained by 1) the fixed-effect covariates included in the model, and 2) residual variation not explained by any measured covariates. To accomplish this, we compared the results of two models run on our data set. The first model was our best approximating model. Thus, the estimated random-effect variance from this model represented residual spatial variation in nest survival (σ_s^2 residual) not explained by any other covariates. The other model contained all non-spatial covariates (e.g., species of duck, nest age) from our best approximating model but no covariates that could explain spatial variation in nesting success (e.g., Percent Grassland, Wetland Count). Because it contained no covariates that could explain spatial variation in nest survival, the estimated random-effect variance from this model represented the total spatial variation in nest survival (σ_s^2 total) present

in our data set. Thus, the proportion of spatial variance in nesting success captured by our model ($R^2_{S,model}$) was calculated as follows:

$$R^2_{S,model} = (\sigma_S^2 \text{ total} - \sigma_S^2 \text{ residual}) / \sigma_S^2 \text{ total}.$$

To estimate the amount of spatial process variation (σ_S^2) in nesting success associated with each of the two models, we used a simulation-based approach. We estimated the variance in nesting success from 10,000 simulation runs where the mean of the random effect of study site was zero and the variance was equal to our estimate from the respective models. Estimates for the variance in nesting success were calculated separately for each year with all covariate values set to their mean, nest age at its mid-point of 18 days, and with mallards as the species. For these simulations, daily survival rate (DSR) was converted to nesting success as follows:

$$\text{Nesting Success} = \text{DSR}^{35}.$$

Results

We monitored 4,188 duck nests across 18 study sites during the course of our study. The number of nests on individual sites ranged from 48-279 in 2000 and 48-269 in 2001 (mean = 116 nests/site in both years). The composition of nesting species varied across sites and years but was dominated by blue-winged teal, mallards, and gadwall across all sites during both years.

A Priori Models

Here, we review general results regarding predictions made *a priori*. We do not provide further details of the results from *a priori* models because our best exploratory

models, which included both *a priori* hypotheses and patterns suggested by the data, were dramatically better than our best *a priori* models. Accordingly, for efficiency's sake, we prefer to only provide detailed results for the best exploratory models.

Models containing landscape-level covariates provided the best explanation of variation in nest survival data. Evaluation of 1,036 *a priori* models indicated the percent grassland in the landscape and landscape configuration were important factors related to survival rates at each of the 5 landscape scales. The variables Percent Grassland and Grassland Edge occurred in the best models at each landscape scale: nest survival was positively related to Percent Grassland and negatively related to Grassland Edge (Table 3.4, Appendix B). The best models at each scale also included the non-habitat variables Nest Age, Species and Year. Nest Age was positively related to daily survival rate of the nest. The categorical variables Species and Year, which allowed intercept values to vary, indicated that blue-winged teal experienced the highest nest survival followed by northern pintails, other dabblers (i.e., American wigeon and green-winged teal), northern shovelers, gadwall, mallards and divers (primarily lesser scaup), and nest survival was higher in 2000 compared to 2001 (Appendix B). Models that incorporated study site as a random effect were dramatically better than models with only fixed effects. Adding study site as a random effect resulted in dramatic improvement of the models; AIC values decreased by > 100 AIC units.

Our *a priori* predictions regarding influences of patch- and nest-scale habitat covariates received little support. The variable Habitat Type occurred in only one model within 2 AIC units of the best model at any spatial scale (Appendix B). There was no

evidence that models that contained Nest Robel or Field Robel were related to nest survival ($\Delta AIC \geq 21.6$ for models containing these variables at the 10.4- and 93.2-km² scales). Finally, our results did not indicate that our visits to nests affected their survival: all models that included an observer effect were approximately 2 AIC units worse than a model not including the effect, and point estimates of the observer effect suggested none was present.

Exploratory Models

Based on the results of the *a priori* modeling, we explored 88 additional random-effect models across the 5 landscape scales. Exploratory models resulted in substantially improved explanation of variation in nest survival over our *a priori* models (Appendix B). Our hypotheses regarding positive relations between Percent Grassland and nest survival, and a quadratic relationship between Grassland Edge and nest survival received strong support (Table 3.4). At each spatial scale, the most parsimonious exploratory models contained the variables Percent Grass and Grassland Edge (Table 3.4). The best approximating model at each spatial scale also contained the non-habitat variables of Nest Age, Species and Year. Nest Age was positively related to daily survival rate of nests while nest survival varied among Species and between Years similar to the *a priori* results (see above).

Our data provided some support for the hypothesis that wetland numbers negatively affect nest survival. At the 10.4-km² scale, 2 models that contained the variable Wetland Count were within 2 AIC units of the best model, and at the 23.3-km² scale, the best approximating model contained the variable Wetland Count (Table 3.4,

Appendix B). Nest survival was negatively related to density of wetland basins in each model. Results regarding our hypothesis that human dwellings provide subsidized den sites for predators, and thus negatively affect nest survival were equivocal. The variable Human Settled Sites was included (in an additive form and in an interaction term with year) in the best approximating model at the 10.4- km² scale, however, the number of Human Settled Sites was related to nest survival negatively in 2000 and positively in 2001 (Appendix B). Given these results and the fact that the coefficients for Human Settled Sites were poorly estimated (95% confidence limits on the estimates contained zero in both years), we are unable to come to any strong conclusions about the influence of Human Settled Sites on nest survival.

Table 3.4. Variables included in best approximating *a priori* and exploratory models of duck nesting success in the Missouri Coteau region of North Dakota, USA for 10.4-, 23.3-, 41.4-, 64.7, and 93.2-km² spatial scales.

Type of Models	Spatial Scale	Habitat Variables in Best Approximating Model				
		Percent Grassland	Grassland Edge	Grassland Edge ²	Wetland Count	Human Settled Sites
<i>A priori</i>	10.4-km ²	X	X			
<i>A priori</i>	23.3-km ²	X	X			
<i>A priori</i>	41.4-km ²	X	X			
<i>A priori</i>	64.7-km ²	X	X			
<i>A priori</i>	93.2-km ²	X	X			
Exploratory	10.4-km ²	X	X	X	X	X
Exploratory	23.3-km ²	X	X	X	X	
Exploratory	41.4-km ²	X	X			
Exploratory	64.7-km ²	X	X	X		
Exploratory	93.2-km ²	X	X	X	X	X
Exploratory	Multi-scale	X	X	X	X	X

Comparisons Among Scales. The model containing landscape variables measured at the 10.4-km² scale was the best overall model, and a model containing information

collected at the 41.4-km² scale was a close competitor ($\Delta AIC = 0.9$, Appendix B).

Models that measured landscape characteristics at 23.3-, 64.7, and 93.2-km² spatial scales were much less parsimonious ($\Delta AIC \geq 11.2$). Thus, we suggest that variables measured at both the 10.4- and 41.4-km² provided similar explanation of variation in nest survival and warranted further consideration.

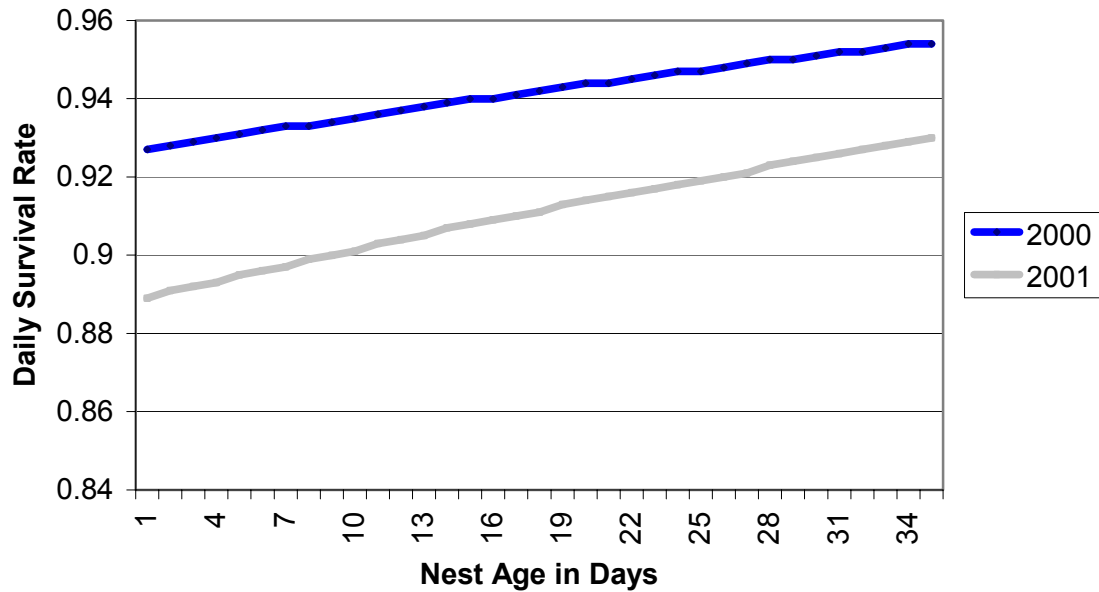
Multi-scale Models. Based on the results of models that only considered habitat information measured at a single spatial scale, we developed and evaluated 12 additional models that included covariates measured at 10.4- and 41.4-km² scales. These models contained various combinations of the following variables: Percent Grassland, Wetland Count, Human Settled Sites and Grassland Edge measured at either the 10.4- or 41.4-km² scale. All models included Nest Age, Species and Year. These results provide evidence that it may be important to consider habitat features at multiple spatial scales when trying to understand variation in nest survival. The best multi-scale model had an AIC value that was 32.3 units better than that for the best single-scale model (Appendix B). This overall best model largely consisted of covariates measured at the 10.4-km² scale: Wetland Count, Human Settled Sites, Grassland Edge, Grassland Edge², and the number of Human Settled Sites (Table 3.5, Appendix B). The only variable included that was measured at the broader 41.4- km² scale was Percent Grassland. Thus, this model suggests that a broader-scale measurement of the amount of grass coupled with finer-scale measurement of other important landscape variables provided the best explanation of variation in nest survival.

Table 3.5. Beta estimates, standard errors and 95% Confidence Limits for the best exploratory model of duck nesting success in the Missouri Coteau region of North Dakota, USA, 2000-2001.

Covariate	Year	Estimate	Standard Error	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Intercept		2.411	0.083	2.248	2.573
e percent grassland at 41.4-km ² scale	2000	0.429	0.111	0.211	0.646
	2001	1.099	0.106	0.892	1.306
e human settled sites at 10.4-km ² scale	2000	-1.527	1.244	-3.965	0.911
	2001	6.587	1.185	4.266	8.910
Species 1		-0.007	0.241	-0.481	0.467
Species 2		0.235	0.074	0.090	0.379
Species 3		-0.338	0.399	-1.119	0.443
Species 4		-0.059	0.075	-0.206	0.088
Species 5		-0.083	0.072	-0.224	0.058
Species 6		0.081	0.093	-0.102	0.264
Ln (wetland count at 10.4-km ² scale)		-0.585	0.098	-0.779	-0.392
Nest age		0.015	0.003	0.009	0.020
Year (2000)		0.335	0.044	0.249	0.421
Grassland edge at 10.4-km ² scale		-0.405	0.071	-0.544	-0.266
Grassland edge ² at 10.4-km ² scale		0.021	0.004	0.013	0.029

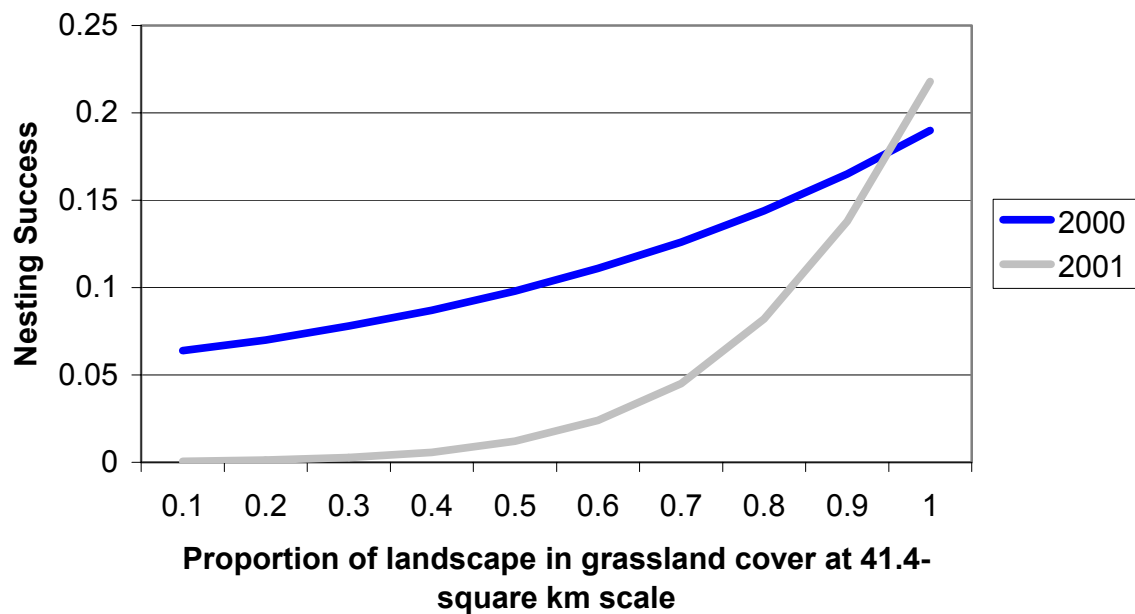
According to this model (Table 3.5), survival rate of duck nests was positively related to Nest Age ($\hat{\beta} = 0.015$, SE=0.003; Figure 3.3). In accordance with our *a priori* hypothesis, nest survival was positively related to Percent Grassland in each year, although the relationship was weaker in the first year ($\hat{\beta}_{2000} = 0.428$, SE₂₀₀₀ = 0.111) than in the second year ($\hat{\beta}_{2001} = 1.099$, SE₂₀₀₁ = 0.106). Although nest survival was lower overall in 2001 (9.4%) than in 2000 (20.5%), sites with high Percent Grassland maintained high nesting success in 2001 (Figure 3.4). We interpret this result as evidence that the amount of grassland had a stronger influence on nesting success rates in years when the average nesting success was low. Thus, landscapes with more intact grassland

Figure 3.3. Nest age in relation to daily survival rate of duck nests in the Missouri Coteau region of North Dakota, USA, 2000-2001^a.



^arelationship shown is for mallards with all other covariate values set at their means.

Figure 3.4. Duck nesting success in the Missouri Coteau region of North Dakota, USA 2000-2001 in relation to the amount of grassland cover measured at a 41.4-km² scale^a.



^arelationship shown is for mallards with all other covariate values set at their means.

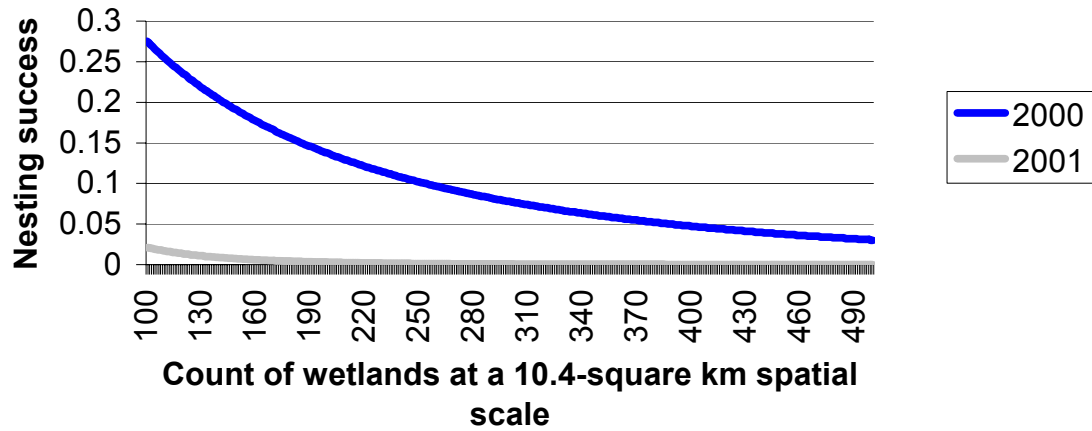
may buffer the effects of predation in years with low, overall nest survival. As we predicted *a priori*, nest survival was negatively related to the Wetland Count (10.4-km² scale; Figure 3.5). In accordance with our *a priori* hypothesis, we observed a curvilinear relationship between nest survival and Grassland Edge (10.4-km² scale; Figure 3.6) with the lowest nest survival occurring at intermediate levels of grassland edge. We obtained equivocal results regarding our hypotheses about Human Settled Sites as the coefficient for this variable was imprecisely estimated (Table 3.5). Additionally, none of the variables contained in this model were strongly correlated (Table 3.6).

Table 3.6. Correlations among landscape variables in the best exploratory multi-scale model.

	Percent Grass 41.4- km ²	Wet Count 10.4- km ²	Human Settled Sites 10.4- km ²	Grassland Edge 10.4- km ²
Wet Count 10.4- km ²	-0.04			
Human Settled Sites 10.4- km ²	-0.42	0.14		
Grassland Edge 10.4- km ²	0.60	0.52	-0.46	
Grassland Edge ² 10.4- km ²	0.59	0.57	-0.39	0.99

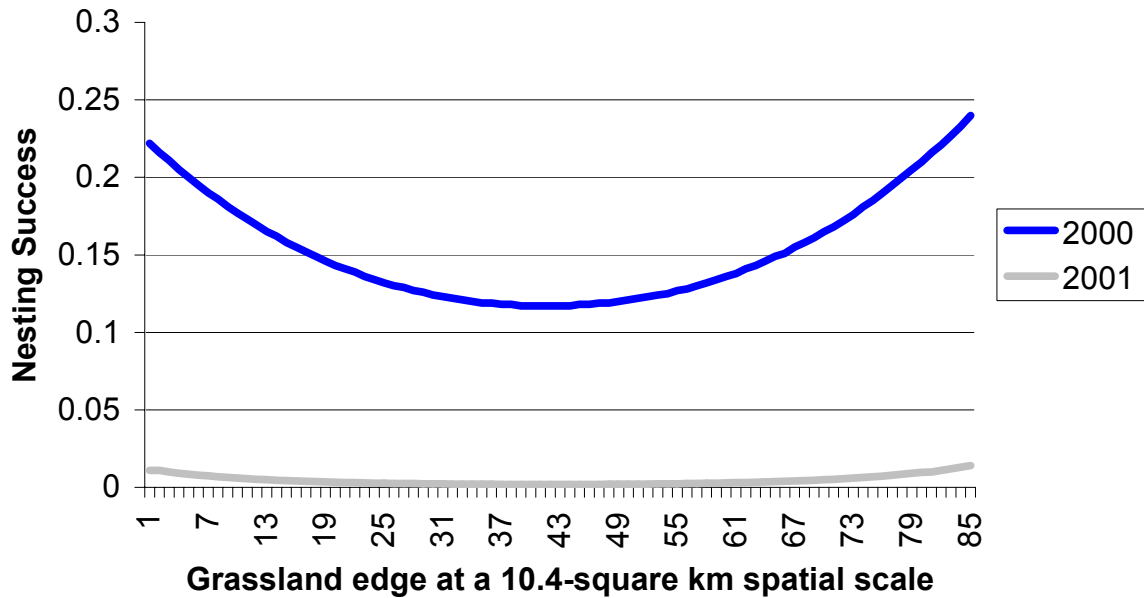
Neither of the two multi-scale models within 2 AIC units of the best model represents major departures in the important covariates from the best model described above but rather subtle changes. The second-ranked model ($\Delta\text{AIC} = 0.3$) was simply the most parsimonious multi-scale model with the addition of Grassland Edge measured at the 41.4-km² scale to the model that already included Grassland Edge metric at the 10.4-km² scale (Appendix B). The third-ranked model ($\Delta\text{AIC} = 2.0$) was similar to the best

Figure 3.5. Duck nesting success in the Missouri Coteau region of North Dakota, USA, 2000-2001 in relation to the number of wetland basins measured at a 10.4-km² scale^a.



^arelationship shown is for mallards with all other covariate values set at their means.

Figure 3.6. Duck nesting success in the Missouri Coteau region of North Dakota, USA, 2000-2001 in relation to the amount of grassland edge measured at a 10.4-km² scale^a.



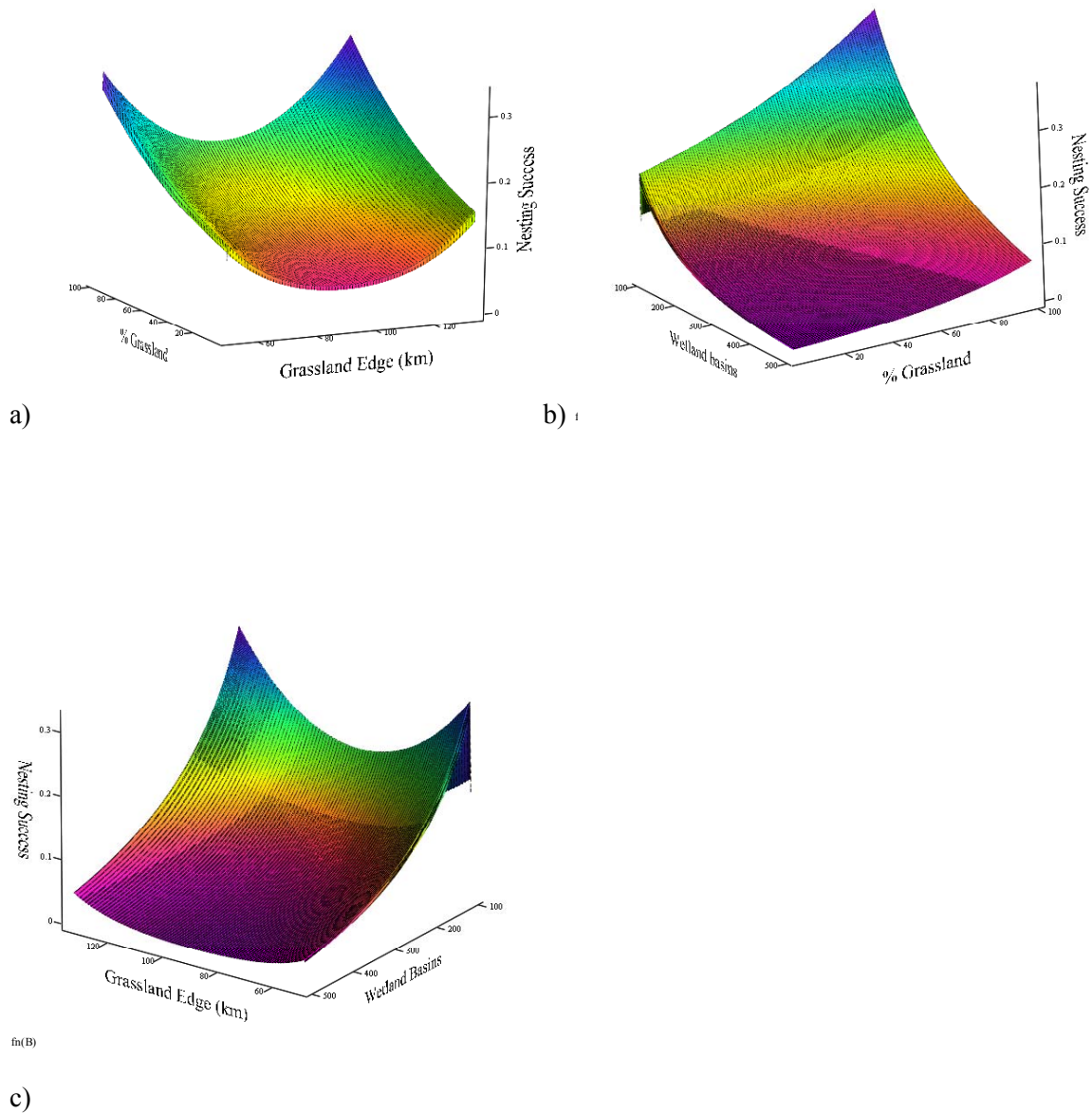
^arelationship shown is for mallards with all other covariate values set at their means.

approximating multi-scale model but treated the Species of duck as two groups (i.e., blue-winged teal vs. all other species, Appendix B). All other multi-scale models examined were much poorer approximations to our data than the above-described models ($\Delta AIC \geq 27.8$)

Model Diagnostics

Examination of the relative importance of each covariate to nesting success suggested the following. Nesting success is most sensitive to changes in Percent Grassland measured at the 41.4-km² scale (50% increase in nesting success for 10% increase in Percent Grassland and 37% decrease in nesting success for a 10% decrease in Percent Grassland; Figure 3.7a and 3.7b). Nesting success was moderately sensitive to the amount of Grassland Edge at a 10.4-km² scale (15% increase in nesting success for a 10% increase in Grassland Edge and 12% decrease in nesting success for a 10% decrease in Grassland Edge; Figure 3.7a and 3.7c), followed by the Wetland Count at a 10.4-km² scale (9% increase in nesting success for a 10% change in Wetland Count and 8% decrease in nesting success for a 10% decrease in Wetland Count; Figure 3.7b and 3.7c). Nesting success was least sensitive to the number of Human Settled Sites at a 10.4-km² scale (5% increase in nesting success for a 10% increase in Human Settled Sites and 4% decrease in nesting success for a 10% decrease in Human Settled Sites). Thus, loss or addition of grassland will have the largest impact on nesting success as both the Percent Grassland and Grassland Edge variables will be affected.

Figure 3.7. Nesting success in the Missouri Coteau region of North Dakota, USA in relation to a) percent grassland at 41.4-km² scale and grassland edge at 10.4-km² scale, b) wetland basins at 10.4-km² scale and percent grassland at 41.4-km² scale and c) grassland edge at 10.4-km² scale and wetland basins at 10.4-km² scale, during 2000^a.



^a relationship shown is for mallards with all other covariate values set at their means.

Although accounting for unmeasured site-specific factors dramatically improved our models, our habitat covariates accounted for most of the spatial process variation in nest survival in our data set. Our estimate of the residual variation in nesting success in our data set that was associated with the random effect of study site was σ_s^2 residual = 0.126 (SD = 0.034, 95% CL = 0.065, 0.200) in 2000; σ_s^2 residual = 0.041 (SD = 0.017, 95% CL = 0.015, 0.081) in 2001. We found no evidence of differences in the means ($p > 0.092$) or variances ($p > 0.114$) of the estimated random effects among strata at any spatial scales. We also found no evidence of spatial autocorrelation (Geary's $C = 1.007$, $SE = 0.273$; $p = 0.9791$). Our best model explained an estimated 87.8% in 2000 and 94.3% in 2001 of the total spatial process variation in nesting success in our data set. This suggests that variation in nesting success, among sites in our data set, was more a result of changes in the important habitat covariates than it was due to the effects of unmeasured, site-specific factors.

Discussion

The duck species we studied were ideal for investigating our hypotheses of interest because they nested in relatively high densities across a diversity of habitat and landscape conditions. Based on a contemporary analysis of nest-survival data, our results supported a number of *a priori* hypotheses, suggested several new hypotheses, and provide insight into factors affecting duck nest survival in the Coteau region. We believe that this work may also help generate hypotheses for how grassland fragmentation influences avian nest survival for other grassland nesting birds. Because of the large samples of nests obtained for each site, we had the potential to pick up even small effects

that may not be possible with smaller data sets typically available for other species. Thus, we believe researchers investigating factors influencing nest survival for other grassland nesting birds should test for some of the effects we discovered with the caveat that smaller sample sizes will make discerning more subtle effects challenging.

Effect of landscape characteristics

There was strong evidence that it was important to consider landscape features when attempting to explain variation in nest survival data. Also, it was evident that it was important to examine landscape features at multiple scales. These results supported our *a priori* thinking that nest survival would be related to the amount of grassland habitat, how that habitat was configured and wetland density. Although the importance of fragmentation effects on nest survival has received considerable attention in the avian literature, research conducted in prairie areas is quite limited (Stephens 2003, Chapter 2), and thorough examinations of how landscape level metrics of fragmentation influence nest survival for ducks are just beginning (Howerter 2003, this study).

Percent Grassland. There seems to be mounting evidence that the amount of grassland habitat present in a landscape strongly influences nest survival for ducks in the PPR. In accordance with our *a priori* hypotheses, we found strong evidence that nest survival was positively related to the amount of grassland habitat. Reynolds et al. (2001), who worked in CRP fields across the U.S. portion of the PPR, also found a positive relationship between survival of duck nests and the amount of grassland habitat measured at a 10.4-km² scale. Greenwood et al. (1995), who worked in both the prairies and Aspen

Parklands within the PPR of Canada, took a slightly different approach to examining the influence of the amount of grassland habitat. He related nesting success to the percent cropland present on 1.6 x 16 km study sites. He found that nest survival on sites from the prairie region was negatively related to percent cropland, which has a strong negative correlation with the amount of grassland present. However, both Reynolds' (2001) and Greenwood et al.'s (1995) results from prairie sites left substantial variation in nest survival unexplained. This may be the result of not examining the amount of grassland at multiple spatial scales and considering additional landscape covariates.

Predator communities of the PPR are comprised of a diversity of nest predators (Sargeant et al. 1993). Each species of predator has different impacts on nest survival rates (Sovada et al. 1993, Sargeant et al. 1993). We speculate that the species composition of nest predators present in a given landscape may be influenced by the amount of grassland present and in turn, influence nest-survival rates. We suspect that landscapes with more intact grasslands tend to favor endemic species like coyotes and badgers over red fox, raccoons, and skunks. As a result, nest survival is higher because species like coyotes and badgers typically have larger home ranges and occur at lower densities than species like red fox, raccoons, and skunks (Sargeant et al. 1987). If true, this would provide a mechanism for higher nest survival in intact grassland landscapes.

Further, nesting success on intact sites was quite high even in a year when overall nesting success was poor – thus indicating a very important role for landscapes with intact grassland. We speculate intact grassland sites maintained high nesting success rates in a year with poor overall nesting success because of the predator community

present. Sites with more intact grassland and few roads have predator communities comprised of endemic prairie species like coyotes and badgers that exert lower predation pressure on nests (Sargeant et al. 1987, Sovada et al. 1995). Additionally, species like coyotes and badgers tend to occur at low density in the PPR (Sargeant et al. 1987). As a result, we speculate that populations of coyotes and badgers are less subject to large variation in abundance over time compared to species such as red fox, and skunks that commonly occur at higher densities (Sargeant et al. 1993), and thus nest survival rates in intact grassland landscapes may be higher and less variable. However, alternative hypotheses are possible. Fluctuations in abundance of alternate prey (e.g., mice and voles) across landscape gradients in the PPR are currently poorly understood, as is how the different predator communities response to fluctuations in prey. Thus, more detailed research on alternate prey and the response of predator communities to fluctuations in food availability will be necessary to better understand causal mechanisms for temporal variation in nest survival.

An important question is how well the models developed in prairie areas apply to the broader PPR that includes the Aspen Parklands of Canada. Results from studies of factors influencing nest survival conducted in the Parklands suggest important differences exist between Parkland and prairie regions. In contrast to prairie sites, on Aspen Parkland study sites, Greenwood et al. (1995) found only weak evidence for a relationship between the amount of grassland and nest survival. Howerter (2003), who worked in the Parklands as well, also failed to find a relationship between the amount of grassland habitat and nest survival. Thus, although it seems clear that the amount of

grassland influences nest survival in the prairie region, in the more complex landscapes of the Parklands the amount of grassland may be inadequate. Howerter (2003) suggests that a more complex suite of factors influences nest survival in the Parklands.

Grassland Edge. We hypothesized that predator communities would be most diverse at intermediate levels of habitat fragmentation and that, accordingly, the relationship between measures of fragmentation and nest survival would be curvilinear. Our results were consistent with this as nest survival was lowest for locations with intermediate levels of grassland edge. Of course, our explanation for the mechanism behind the relationship is purely speculative because we had no information on nest predators, and several other viable explanations exist. We speculate that predator foraging strategies may be influenced by the amount of edge in the landscape. Additionally, intermediate levels of edge may concentrate nests in a few moderate size patches that are very profitable for predators to forage in contrast to a few large patches or many small patches. Thus, interactions between foraging strategies and nest distribution could be responsible for the landscapes with moderate amounts of edge experiencing the poorest nest survival. Further, configuration of the landscape may affect both which predator species are present and how those respective species forage. More detailed information on how predators forage in different landscapes setting will be difficult to obtain but very useful in understanding the mechanisms behind how edge influences nest survival.

Studies of how the amount of edge in the landscape influence duck nest survival in the PPR has been rare: we are only aware of our study and Howerter's (2003). Both

studies found the amount of edge to influence nest survival but in different ways. Howerter (2003), who worked in the aspen parklands of Canada, found a positive relationship between edge density and nest survival, whereas we found a quadratic relationship in the prairies.

However, landscapes of the prairies and Parklands differ in how the amount of edge changes with habitat alteration. Thus, it is important to consider fragmentation in the context of the region under study (Haila 2002). In prairies, where natural landscapes consisted of large expanses of a single habitat type, agricultural conversion of land tends to increase the amount of edge up to the point that the amount of habitat comprised of agriculture and grassland are equal. Then, as agriculture becomes the dominant land-use the amount of edge declines again. In contrast, unaltered Parkland landscapes inherently have high amounts of edge, and edge is initially reduced as multiple patches of natural habitat are converted to large agricultural fields (Dave Howerter, personal communication). As a result, in the Parklands the unaltered areas have high amounts of edge and the best nesting success. Howerter (2003) also found distance to habitat edges was positively related to nest survival. Parkland areas are thought to have more diverse predator communities that contain both avian and mammalian species, whereas, prairie areas are primarily dominated by mammalian nest predators (Sargeant et al. 1993). However, Howerter (2003) measured edge density at a 0.65-km^2 scale whereas we measured edge at a 10.4-km^2 scale. Thus, different relationships between edge and nest survival could be indicative of varying predator response at different scales.

Wetland Density. As we hypothesized *a priori*, we found nest survival to be negatively related to wetland density. Although this represents a novel finding for factors influencing waterfowl nest survival, we believe that our proposed underlying mechanism is consistent with what is known of PPR ecology. First, several species of nest predators have been shown to preferentially select wetland areas for foraging (Greenwood 1999, Lariviere and Messier 2000, Phillips 2001). Second, distance to wetland edge has been shown to positively influence nest survival (Howerter 2003). Thus, we speculate that in landscapes with more wetlands, ducks are more likely to nest nearer to wetlands and to consequently suffer greater nest mortality than they are in areas with fewer wetlands. Additionally, we speculate that landscapes with more wetlands also support a greater number of predators and are thus, inherently more difficult settings in which to successfully nest. Wetlands are the most productive components of the prairie landscapes where our work was conducted (van der Valk 1989, Mitsch and Gosselink 1986). Information on predator abundance across a gradient of wetland densities will be required to test our hypothesized explanation and will be difficult to obtain given the diversity of predators involved and the difficulty of obtaining reliable estimates of density for such species.

Research on duck nesting success in the PPR has commonly focused in areas with the highest wetland densities yet yielded lower than expected estimates of nesting success (Greenwood et al. 1995, Joynt 1998). The negative influence of wetlands on nesting success identified in our work may help explain why past results contradicted predictions in high wetland density areas. Additionally, Adaptive Harvest Management

models suggest recruitment rates of mallards breeding in the PPR are strongly density dependent (U.S. Fish and Wildlife Service 2003). The negative influence of wetlands on nesting success we identified would provide a mechanism for density dependence to occur spatially throughout portions of the PPR. However, it is important to point out our empirical data were collected over only 2 years during a period of extended wet conditions across the Coteau. Thus, we suggest that our model be validated across additional years under different wetland conditions.

Effect of Year

Large temporal variation in duck nest survival has been documented in the PPR (Higgins et al. 1992), and our results also support large variation in nest survival among years. Based on anecdotal information, we speculate that the high nest survival rates we experienced in 2000 were the result of high small mammal populations, which buffered predation on nests.

Despite large annual changes in nesting success, the estimated effects of Grassland Edge and Wetland Count were similar in both years, whereas the magnitude (but not the direction) of the relationship between Percent Grassland and nesting success differed by year. Thus, although the magnitude of the effects of some landscape covariates changed between years, all covariates that were well estimated had consistent positive or negative impacts on nest survival under the environmental conditions our data encompassed.

Because we only had data for 2 consecutive years and we were limited to including only a single random effect in our models, we treated year as a fixed effect.

However, estimation of the random effect of year would be appropriate and desirable if data were available from a larger sample of years. The random effect of year, which represents variation that is not accounted for by other covariates and not due to random site effects, would be useful to know because it allows researchers to predict how much nesting success may change across years on individual sites due to non-habitat factors such as weather. Regardless of the potential importance of year effects, available data do not allow variation in nesting success to be partitioned into spatial and temporal components. Most previous studies have conducted research on most study sites for only a year or two (Greenwood et al. 1995, Reynolds et al. 2001), and long-term research (≥ 5 years) on the same individual sites is rare (Higgins et al. 1992). As a result, amounts of temporal and spatial variation have been confounded in most studies conducted to date. However, understanding whether high nesting success can be attributed to the characteristics of the site or is due to year-specific effects is important. Thus, partitioning the amount of variation in nest survival that can be attributed to temporal (year-to-year) variation versus how much is spatial (site-to-site) variation is important for accurately identifying the landscape characteristics of sites that result in the highest nest success over the long-term. Further, this partitioning of variance should facilitate a better understanding of factors that may be responsible for annual deviations in nest-survival rates given covariate values for individual sites.

Random Effect of Study Sites

In this paper, we introduce methods for adding random effects to models of nest survival. We believe that this extension of existing modeling tools (Rotella et al. 2000,

Dinsmore et al. 2002) will be valuable to future studies of nest survival. Inclusion of random effect of site improved our models substantially. Random effects allow the amount of unexplained variation due to unmeasured factors to be quantified. The decomposition of variance in nest survival into components explained by the model and residual unexplained variation not accounted for by covariates also provides a rigorous way to quantify model performance. Additionally, estimates of random site variation allow more rigorous inference to be made to the population of sites rather than only to the sites in the sample, which has important implications to applied conservation. As a result, we believe the inclusion of random effects represents a significant advance in the analysis of nest survival data and will facilitate a much more thorough understanding of factors influencing nest survival.

In this study, models that included study area as a random effect were substantially better than models that contained only fixed effects because they account for unmeasured, site-specific factors that influence nest survival. It is easy to envision site-specific factors that are difficult to quantify that might exert important influences on nest survival. For example, factors such as the composition of predator communities and density of predators likely exert important influences on nest survival but are very difficult to quantify reliably. The flexibility provided by random-effect models was important for fitting our nest survival data and allows more appropriate inference to be made to population of sites that are of interest for applied conservation. Additionally, we found no evidence that our stratified random selection of study sites biased our estimate of the random effect variance associated with individual study sites. However, further

work to examine the influence of such stratified random site selection procedures on estimated random effects is warranted.

Effect of measuring habitat metrics at multiple spatial scales

Selecting an appropriate scale for investigation of ecological processes is important (e.g. Levin 1992, May 1994, Mitchell et al. 2001). For landscape-level analyses, selection of the spatial extent at which to measure landscape variables is critical because different patterns emerge at different spatial scales (Wiens 1989, Kareiva 1994, Bissonette 1997, Villard 2002, Haila 2002). As a result, multiple scales need to be examined to determine the scale that provides the best explanation of the response variable of interest (Mitchell et al. 2001, McGarigal and Cushman 2002). Despite this fact, we are only aware of 3 other studies (Hartley and Hunter 1998, Tewksbury et al. 1998, Howerter 2003) that formally investigated relationships between nest survival rate and habitat characteristics measured at multiple spatial scales. Hartley and Hunter (1998) found that percent forest cover measured at a 5-km spatial scale provided better explanation of nest predation rates for artificial nests than did 10-km or 25-km scales. Tewksbury et al. (1988) found similar results at both 1-km and 2-km spatial extents when examining relationships between nest predation and parasitism rates for forest breeding songbirds. Howerter (2003) found that edge density measured at the 0.65-km² scale entered top-ranked models while edge-density measured at the 10.36-km² scale was included in none of the top-ranked models. In our study, landscape metrics from the 10.4- and 41.4-km² scales provided much better explanation of variation in nest survival than other scales. Further, models that combined landscape metrics measured at these

two spatial scales were dramatically better than models that only considered habitat information from any single scale. We believe this is because the response of nest predators to landscape structure is complex and occurs at multiple spatial scales.

Chalfoun et al. (2002) found nest predators were most sensitive to landscape level measures of fragmentation. However, we are aware of no studies that have examined responses of nest predators to landscape characteristics at multiple spatial scales.

Nonetheless, we speculate that multiple scales will be needed to account for factors influencing diverse predator communities that are comprised of species with very different home range sizes such as those in the PPR.

In our study, landscape-scale metrics explained variation in nest survival better than did features measured at the nest site or for the patch of habitat containing the nest. We argue that this is because nest predators are most strongly influenced by landscape level habitat factors (Chalfoun et al. 2002). However, we do not have data on the response of predators to landscape characteristics and obtaining that information across a gradient of landscapes will be challenging.

Modeling Methods

We believe that the non-linear random-effect models used here represent a significant advance in analysis of nest survival data. First, we explored a variety of relationship types between covariates at multiple scales and all of the landscape variables that were included in our best models were non-linearly related to nest survival. Further, as was also found by Dinsmore et al. (2002) for Mountain Plovers (*Charadrius montanus*), these new analysis techniques allowed us to identify and estimate the effects

of important non-habitat variables such as nest age. Accounting for heterogeneity in nest survival due to variables such as nest age reduces bias in nest-survival estimates and allows the influence of the habitat covariates of interest to be more accurately estimated (Dinsmore et al. 2002). Despite these advances, further improvements in analysis are needed. Specifically, current methodologies for assessing model fit with binomially distributed data and for estimating extra-binomial variation are unsatisfactory. Thus, it is currently not possible to obtain a measure of the fit of the global model or to adjust for overdispersion (Dinsmore et al. 2002).

Our best model was largely based on *a priori* thinking but was also the result of a limited amount of exploratory modeling. Specifically, the variables in the final model were all considered *a priori*, but some of the covariates contained in the final model were measured at different spatial scales than those that we considered when designing the study's sampling scheme. This occurred because few studies and little information existed to guide our *a priori* thinking with respect to scale. Thus, we have less certainty in the results than if the model had been completely developed *a priori*, and we recommend that future research evaluate those hypotheses that we developed through exploratory modeling. Specifically, the influence of wetland density was added in exploratory modeling to the models that contained variables Percent Grassland and Grassland Edge that were identified as important variables in *a priori* models in various forms.

Implications for Conservation and Future Research

Landscape variables identified by our best model hold important implications for conservation programs. Our results indicate that natural resource managers should maintain large, intact grassland areas and restore grassland to re-create intact areas to achieve high nesting success for breeding ducks. During our study, sites with more intact grassland maintained high nesting success rates even in a year with poor overall nesting success. We find this result intriguing and believe it has important conservation implications for protection of intact grassland landscapes.

Intermediate levels of edge resulted in the lowest nesting success rates so conservation implications are more complex for this variable; in order to understand the implications of more or less grassland edge, the baseline level for a given landscape must be taken into account. However, the amount of grassland edge can be quantified and accounted for across broad scales using remotely sensed satellite imagery.

The number of wetland basins negatively impacted nest survival. But positive relationships between wetland density and both pair density (U.S. Fish and Wildlife Service 2003) and duckling survival (Rotella and Ratti 1991) suggest that inherent trade-offs exist for the effects of wetlands on net duck production. However, we suggest that the population-level effect of wetlands should not simply be assumed to be neutral because population growth rates of mallards are most sensitive to nesting success rates (Hoekman et al. 2002). Research designed to examine relationships between brood survival and wetland density will be necessary to fully examine the net effect of different wetland densities on duck recruitment. To date, conservation planning in the PPR has

been based upon simplistic, single-factor models of relationships between landscape characteristics and nest survival. Our results suggest that more complex spatially explicit models that consider habitat features at multiple scales will provide improvements over previous tools and capture more biological reality. The parameter estimates from our best model can easily be incorporated into a Geographic Information System and used with remotely sensed habitat data to (1) prioritize areas for protection efforts and (2) develop landscape-specific restoration and management prescriptions.

Future research should focus on addressing important uncertainties that remain in our understanding of factors influencing nest survival. First, because the best model developed here resulted from exploratory analysis, validation and refinement of our model will be important. Second, we believe that future studies should be designed so that variation in nesting success can be partitioned into temporal and spatial components at spatial scales that are most meaningful for conservation programs. Estimation of spatial and temporal components of variation will be critical to determining the characteristics of landscapes that yield the highest nesting success rates over the long term and should stimulate insight into why observed nesting success may deviate from predictions. Additionally, our data were collected during an extended wet period on the prairies. Because of the large impacts variation in precipitation has on prairie ecosystems, we suggest that initial years of wet cycles following drought periods may represent unique conditions that contrast those we encountered. Thus, validation of our model under different environmental conditions will be important. We suggest that long-term research (10-15 years) on a suite of study sites spread across gradients of the

important landscape variables (i.e., percent grassland, wetland density) will be necessary to better understand the robustness of our estimated relationships across different environmental conditions, and to estimate and partition variation in nest survival into spatial and temporal components.

Finally, collection of accompanying data on alternate prey and predators should prove valuable. We believe information on fluctuations in abundance of alternate prey will help explain temporal fluctuations in nest survival rates and may be influenced by the landscape characteristics. Understanding how species composition of predator communities and the foraging behaviors of different species change across landscape gradients would be especially valuable for understanding the mechanisms behind the patterns we observed in our nest survival data. However, this work will likely be extremely challenging; most predator species are at low density and are difficult to rigorously quantify, and information on foraging behavior via radio-marked animals is costly to obtain across multiple sites.

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CHAPTER 4.

SPATIALLY EXPLICIT PLANNING TOOLS FOR WATERFOWL CONSERVATION
IN THE MISSOURI COTEAU REGION OF NORTH AND SOUTH DAKOTAIntroduction

Historically, high densities of shallow, depressional wetlands scattered amidst expansive native prairie grasslands (Kuckler 1964, van der Valk 1989, Ostlie et al. 1997) characterized the Prairie Pothole Region (PPR). As a result of this unique mix of grasslands and wetlands, this ecoregion represents the primary breeding range for many species of waterfowl (Batt et al. 1989). However, dramatic alteration of the historic habitat base occurred with settlement of the region. Most of the region's native grasslands were fragmented or lost through conversion to agriculture (Higgins 1977, Sugden and Beyersbergen 1984). Prairie wetlands have also been significantly impacted across the region. A large percentage of the regions' wetland basins have been drained (Tiner 1984, Dahl 1990), and many others have been dramatically altered by cultivation (Cowardin et al. 1981) or agricultural run-off (Grue et al. 1996).

These dramatic changes to the landscape of the PPR have resulted in significant impacts on the endemic mammalian community (Sargeant et al. 1993). Wolves (*Canis lupus*) have been extirpated from the region, while several species of small- and medium-sized carnivores such as red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*) and striped-skunk (*Mephitis mephitis*) have either expanded their range or increased in abundance (Sargeant et al. 1993). These simultaneous changes to habitat and predator communities

are believed to have resulted in higher predation rates and lower nesting success rates for breeding waterfowl (Clark and Nudds 1991, Beauchamp et al. 1996, Reynolds et al 2001). Ultimately, nesting success rates are likely not sufficient to maintain populations of breeding waterfowl across much of the PPR (Cowardin et al. 1985). As a result, there is significant interest across the PPR in conservation programs that protect existing grasslands and restore grasslands to benefit breeding waterfowl (U.S. Department of the Interior and Environment Canada 1986, PPJV 1995). However, appropriate prioritization of areas for conservation is needed if natural resource managers are to achieve maximal benefits with limited resources.

Conservation planning for ducks in the PPR has been based on both broad- and local-scale data. Annual breeding population surveys, which have been conducted across the PPR since 1955 (Martin et al. 1979, U.S. Fish and Wildlife Service 2003b), have provided information on areas where breeding duck densities are high. Local-scale data from studies of nests and radio-marked birds have indicated that sites with high densities don't, however, necessarily have high production (Joynt 1998, Howerter 2003). Thus, defining the optimal planning tools to accurately identify conservation targets has been challenging.

To improve our understanding of the interplay among habitat, duck density, and duck productivity, Cowardin et al. (1988) developed a population model for the prairie region of the U.S. (i.e., Mallard Model). The Mallard Model predicts the effects of various management prescriptions on mallard reproductive output by modeling bird density as a function of wetland area and survival of nests and nesting hens as functions

of the habitat type in which nesting occurs. Recent analyses suggest that models comprised of habitat type alone, i.e., not spatially explicit, poorly explain variation in nesting success rates (Howerter 2003; Stephens 2003, chapter 3). Thus, it seems worthwhile to develop models that combine estimates of density and nesting success based on landscape characteristics. Models developed in this way should be an improvement over previous models because statistical analyses suggest that spatially explicit models of nesting success that include landscape covariates are dramatic improvements over simple models that only include habitat type (Howerter 2003; Stephens 2003, chapter 3). Also, if reliable estimates of nesting success and pair density can be derived by using covariates that can be measured across broad scales via remote sensing, then it will be possible to use a Geographic Information System (GIS) to extrapolate results across broad areas.

Previous population models have assumed that duck pair density and nesting success are independent. However, our recent analyses of nesting success suggest that the density of wetland basins, which is positively related to pair density, is negatively related to nest survival (Stephens 2003, Chapter 3). Thus, inherent trade-offs may exist between the density of breeding pairs and nesting success, which is commonly used as a proxy to population growth rate. However, dependencies of pair density and nesting success are not a foregone conclusion because (1) pairs are modeled as a function of wetland area, (2) nesting success is a function of wetland density, and (3) the strength of correlation between wetland area and density can vary greatly depending on the size and density of wetlands present on sites. Additionally, other landscape variables such as the

amount of grassland habitat present are not strongly correlated with wetland density but exert important influences on nesting success. Thus, understanding how pair density and nesting success interact in real landscapes will facilitate a thorough understanding of the trade-offs between the two.

To improve our understanding of relationships among landscape characteristics, duck pair density, and nesting success, we developed a spatially explicit population model of mallard population dynamics and examined model predictions for a range of landscape conditions that varied greatly in terms of wetland densities and upland cover characteristics. Our population model combined our newly created model of nesting success (Stephens 2003, Chapter 3) with existing models of pair density (Cowardin et al. 1995) using a GIS to achieve the following objectives: (1) examine trade-offs between nesting success and mallard pair density by quantifying the proportion of areas predicted to be below, at, or above population maintenance levels for nesting success rates across various densities of breeding pairs, (2) identify conservation priorities for protection efforts based on our model output using a conservation decision matrix, (3) examine how much our prioritization changes between years, and (4) identify additional research needs to refine and validate our model.

Methods

Our overall modeling strategy was to first develop a spatially-explicit predictive model of nesting success across the entire Coteau region based on important landscape characteristics (see Estimating Nesting Success). A continuous surface of estimated

nesting success was derived for the entire Coteau region (see Landscape Metrics). Next, we categorized nesting success based on predicted population performance (i.e., areas predicted to result in sink, stable and source populations; see Source-Sink Models) and built a frequency table of performance. Estimates of mallard pairs were calculated for each wetland in the Coteau (see Mallard Pair-Density Models). In order to assign pairs to population performance categories, pairs were aggregated to defined spatial areas. Mallard pairs were aggregated to each section (2.58-km² area) in the public land survey grid resulting in density estimates for each section (see Mallard Pair-Density Models). Double counting of pairs using extrapolation techniques was avoided by using this discrete approach. The 2.58-km² section was selected as the unit of analysis because it is an appropriate size unit for management purposes. To facilitate combining predicted population performance with pair density, each section was assigned sink, stable, or source population status based on the population performance category that comprised the majority of the area in the section. Next, we cross-tabulated the population performance and pair density frequency tables for each of the 15,704 sections in the Coteau and tested for association between predicted population performance and pair density across the landscapes of the Coteau. Finally, we developed conservation priorities (see Conservation Priorities) at the section scale based on both pair density and population performance, and we examined how these priorities changed across the Coteau between years.

Landscape Metrics

Landscape metrics used in our nesting success model (see Modeling Nesting Success) were measured using a land-cover classification based on Landsat TM imagery (28.5-m resolution). We identified wetland basins for each study site using National Wetlands Inventory (NWI) coverage (U.S. Fish and Wildlife Service 1994a, 1994b, 1995). The amount of grassland was calculated as the area of grassland cover types (i.e., native prairie, hayland, and fields enrolled in the Conservation Reserve Program [CRP]) divided by the total upland area. Upland area was the area of the study site not covered by wetlands. We computed grassland edge as the sum of the line lengths between grassland polygons and other upland cover types, and between grassland polygons and wetlands. Focal functions available in ArcGIS 8.3 Spatial Analyst module (ESRI 2002) were used to calculate each landscape metric for each pixel in the Coteau. Focal functions derived statistics in a defined analysis window (e.g., 10.4-km² and 41.4-km²) that was moved across the Coteau. Thus, nesting success was estimated across a continuous surface for the Coteau region using a cell size of 28.5 meters.

Habitat metrics used in the development of the nesting success model were based on fine-resolution (1-m resolution) aerial photography (Stephens 2003, Chapter 3), but this broad-scale effort necessitated use of Landsat imagery. We evaluated how well measures from the 2 approaches correlated. Estimates of all metrics were similar for both aerial-photo and Landsat-based methods with the exception of grassland edge (Stephens 2003, Chapter 3). Estimates of the amount of grassland edge that was calculated from Landsat satellite imagery were consistently lower than the estimates from fine-scale

aerial photography. Therefore, we adjusted the Landsat estimates via a regression model using data on both edge types from our 18 empirical study sites. The adjusted Landsat edge estimates yielded similar results to the aerial-photo based edge estimates ($r^2 = 0.468$, $p = 0.001$).

Mallard Pair-Density Models

We predicted densities of breeding mallards across the Coteau region by first identifying all wetlands within the Coteau based on the National Wetlands Inventory coverage of wetlands (U.S. Fish and Wildlife Service 1995). Pairs were then assigned to each wetland basin based on Cowardin et al.'s (1995) regression models using γ estimates (Cowardin et al. 1995:8) from 2001 data from the 4-square mile survey (Ron Reynolds, U.S. Fish and Wildlife Service, unpublished data). Because wetland conditions were similar in 2000 and 2001 (excellent conditions in both years) and thus, breeding population sizes were also similar, we simplified the density component by using the 2001 data to represent pair populations during both years. Mallard pair values were then aggregated up to the section in the public land survey grid to obtain density estimates of pairs/2.58-km² for each of the 15,704 sections in the Coteau. If a wetland overlapped multiple sections, duck pairs were considered to be on the section that contained the center of the wetland polygon. Estimated pairs were categorized into low (<40 pairs/2.58-km²), medium (40-80 pairs/2.58-km²), and high (>80 pairs/2.58-km²) pair densities for comparative purposes. All pairs were assumed to nest within the section their wetland was located.

Estimating Nesting Success

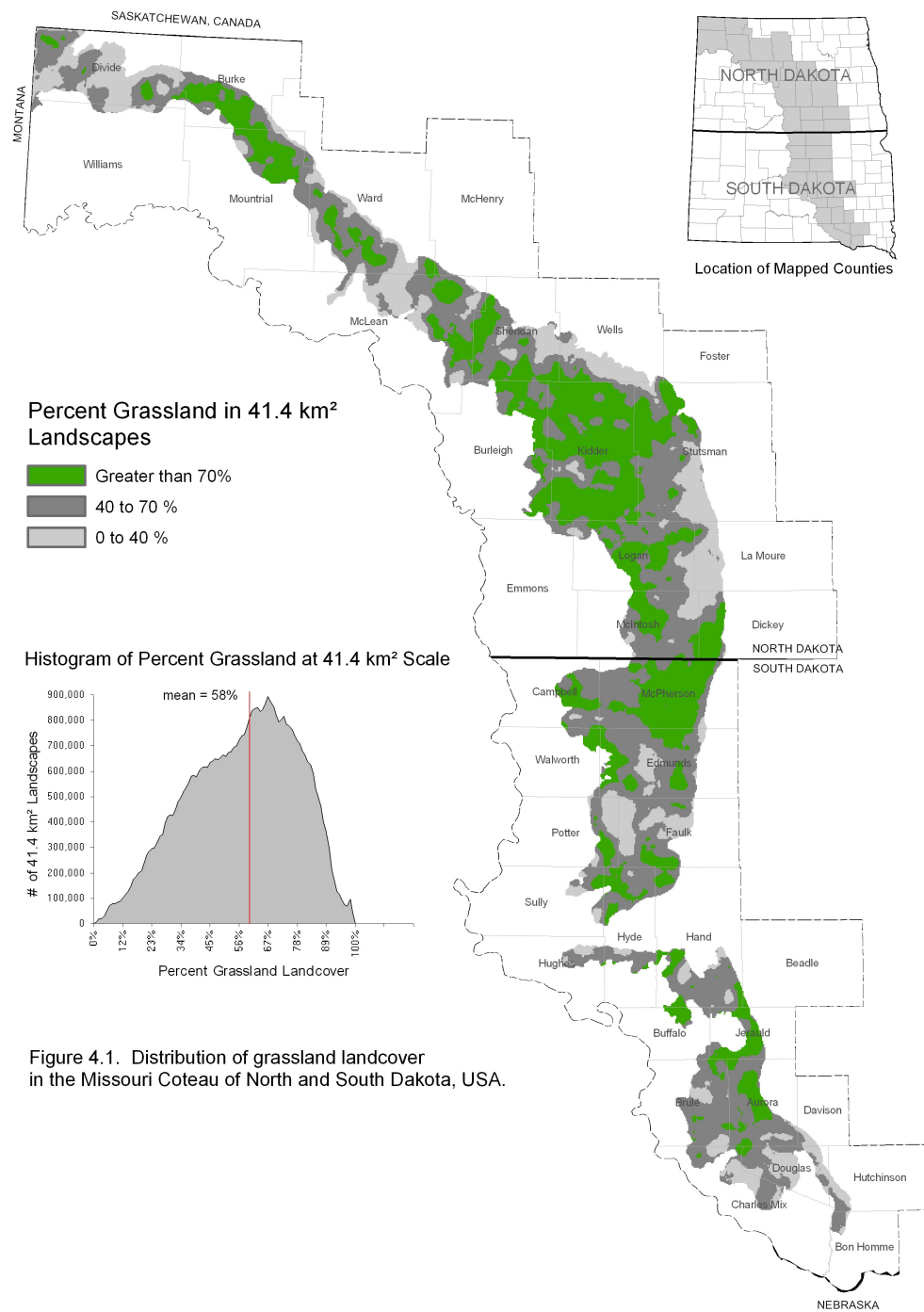
We predicted nest survival rates across the entire Coteau region of North and South Dakota by applying a modified version of the model of nest survival that we developed in the northern portion of the Coteau region of North Dakota (Stephens 2003, Chapter 3). This spatial extrapolation seemed reasonable because (1) the landscapes in the northern portion of the Coteau are similar to those in the remainder of the region, (2) we don't expect predator communities to differ in their species composition, and (3) we expect predators to respond similarly to the same set of landscape characteristics across the entire Coteau region.

The model that best explained variation in nest survival for the northern Coteau (Stephens 2003, Chapter 3) estimated nest survival as a function of (1) the amount of grassland within 41.4-km² of the center of each 10.4-km² site, and (2) the number of wetland basins within 10.4-km² of the center of the study site, (3) the amount of grassland edge measured within 10.4-km² of the center of the study site, and (4) the number of human-settled sites measured within 10.4-km² of the center of the study site. Although the number of human-settled sites was in the best model (Stephens 2003, Chapter 3), we did not consider that variable in this analysis because number of human-settled sites could not be remotely sensed with currently available imagery. Although the number of human settled sites did influence nesting success rates (10% decrease in number of human settled sites yields a 5% increase in predicted nesting success; 10% increase in number of human settled sites yields a 4% decrease in predicted nesting success [Stephens 2003, Chapter 3]), the estimated effects of grassland amount, wetland

basins, and amount of grassland edge, which we were able to incorporate here, were much larger (Stephens 2003, Chapter 3).

We modeled Daily Survival Rate (DSR) of mallard nests as a function of nest age, year (i.e., 2000 and 2001), and landscape metrics with a logit link function (Stephens 2003, Chapter 3). The best model included an intercept term ($\hat{\beta} = 2.4774$) and the following covariates and their respective coefficients: (1) $\exp(\text{Percent Grassland})$, ($\hat{\beta} = 0.6134$); (2) $\ln(\text{Wetland Count})$, ($\hat{\beta} = -0.6032$); (3) a dummy variable that was -1 if Year was 2000 and 1 if Year was 2001, ($\hat{\beta} = -0.1933$); (4) Grassland Edge, ($\hat{\beta} = -0.4654$); (5) Grassland Edge², ($\hat{\beta} = 0.02516$); (6) $\exp((\text{Percent Grassland}) * \text{year})$, ($\hat{\beta} = 0.1586$); (7) Nest Age, ($\hat{\beta} = 0.01487$) and (8) the random effect of study area on the intercept (normally distributed with mean = 0.00, variance = 0.021) (Stephens 2003, Chapter 3). Predicted nesting success was then calculated as the product of the respective daily survival rates for each of the 35 days (age 1 to 35) that a mallard nest must survive in order to hatch young.

The study sites on which empirical data were gathered and which were used to construct our statistical models encompassed most of the range of variation present in the Coteau for the variables percent grassland and grassland edge (Figures 4.1, and 4.2). However, a large proportion of the wetland densities across the Coteau fall below the range encompassed by the study sites used to develop the statistical model (Figures 4.3 and 4.4). As a result, the empirical range of values for wetland densities (101-500) used to develop the nesting success model encompasses only 54 % of the total range of values



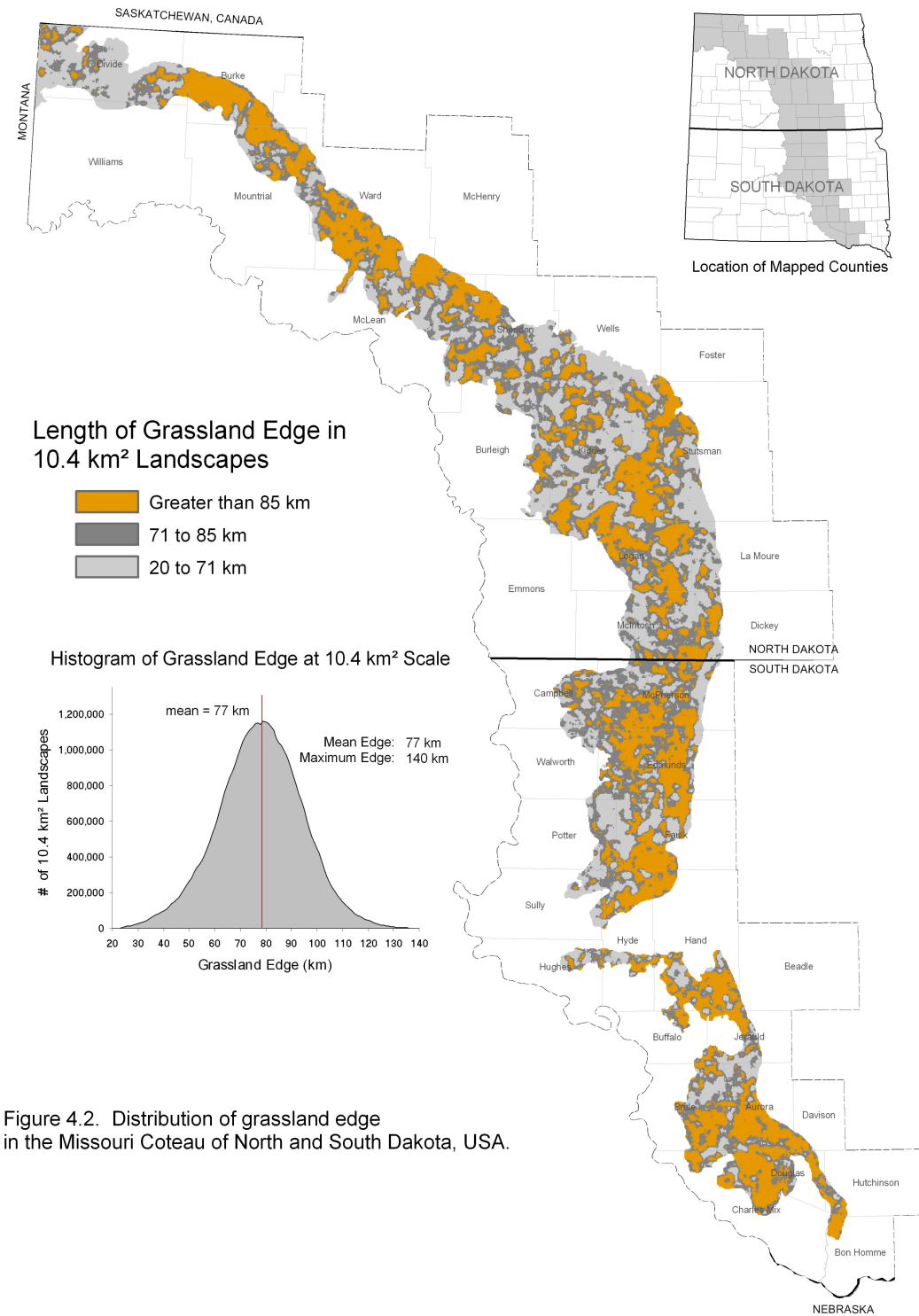
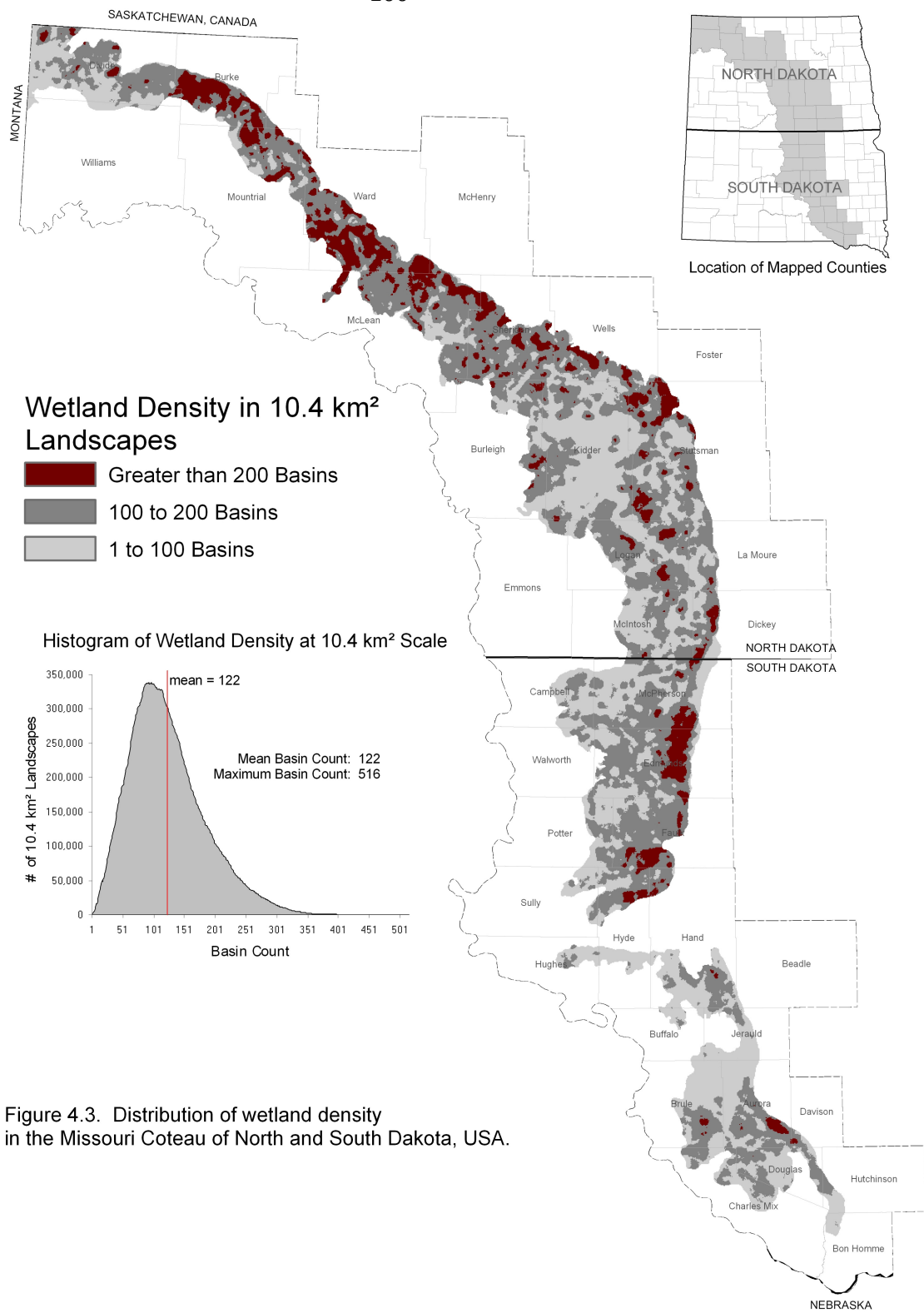


Figure 4.2. Distribution of grassland edge in the Missouri Coteau of North and South Dakota, USA.



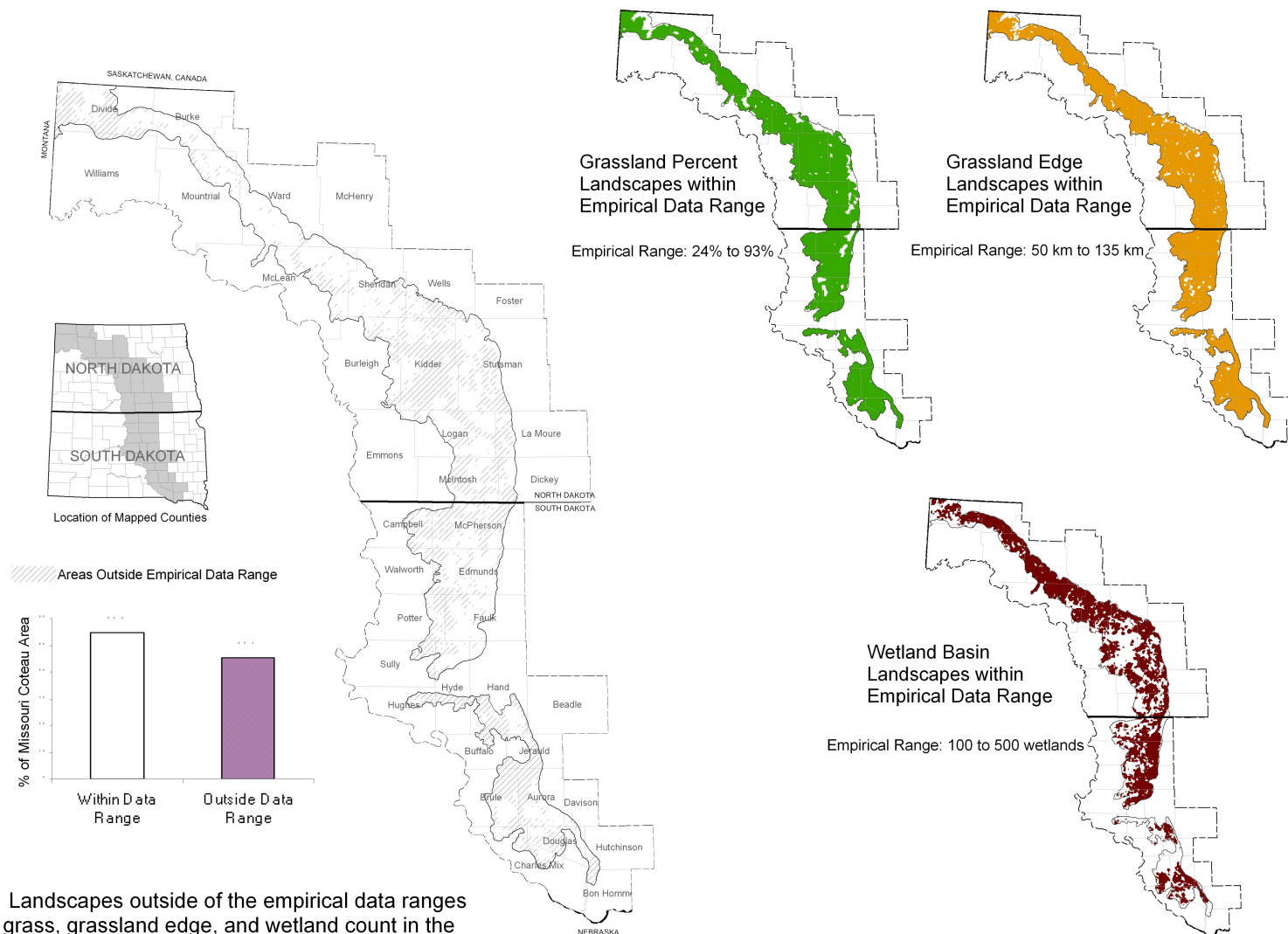


Figure 4.4. Landscapes outside of the empirical data ranges for percent grass, grassland edge, and wetland count in the Missouri Coteau of North and South Dakota, USA.

that exist in the Coteau region in North and South Dakota (Figure 4.4). Thus, further validation of our model, especially in landscapes with wetland densities below 100/10.4-km², would be valuable.

There is also uncertainty associated with estimates of nest survival because the various coefficients in the best model are estimates based on sample data. Thus, to accurately portray this uncertainty we calculated 95% confidence limits on the daily survival rate estimates using the delta method (Seber 1973) across a range of the important habitat covariates.

Source-Sink Models

To examine distribution of pairs among areas with different predicted nesting success rates, we also needed to categorize nesting success in a meaningful way. Using a population model based on empirical data (Cowardin and Johnson 1979), Cowardin et al. (1985) concluded that 15% nesting success was necessary to achieve population stability (i.e., population growth rate = 1), which has served as a management benchmark (Cowardin et al. 1985, Klett et al. 1988, Reynolds et al. 2001). We believe categorizing nesting success based on source-sink status is justified and reasonable because (1) population growth rates are most sensitive to variation in nesting success (Hoekman et al. 2002) and (2) nesting success rates are believed to be strongly, positively correlated with female breeding-season survival rates, which also strongly influences population growth rate. Population models that identified 15% nesting success as population maintenance level make assumption about other vital rates such as duckling survival, female breeding season survival and annual survival. However, empirical estimates for duckling survival

(Talent et al. 1983) and female summer survival (Cowardin et al. 1985) from prairie areas within the PPR are limited, and analyses have not been conducted of annual survival rates for mallards from the PPR during the recent period with more liberal harvest regulations. This population model was also developed prior to most research conducted on brood and duckling survival that used radio-marked hens (Talent et al. 1983, Orthmeyer and Ball 1990, Rotella and Ratti 1992). Thus, estimates of brood survival used in the model do not account for total loss of broods and are, therefore, likely biased high (Ringelman and Longcore 1982, Talent et al. 1983). Given the uncertainty and potential biases associated with the other vital rates used in the population model, we chose a more conservative rate of nesting success; we assumed 18% nesting success was necessary to maintain populations. Additionally, because we were interested in identifying sites for protection where breeding ducks are predicted to experience the highest nesting success, we felt this more conservative definition was justified. Accordingly, we considered three categories of nesting success defined as (1) moderate nesting success was between 13 and 23% which approximates predicted stable populations, (2) low nesting success was <13% and approximates predicted sink populations, and (3) high nesting success was > 23% which approximates predicted source populations.

Conservation Priorities

We first examined how categories of population performance (i.e., areas predicted to have high, medium and low nesting success) were distributed among pair categories (i.e., high, medium and low pair densities) during each of the two years. To test whether population performance was independent of pair density across real landscapes of the

Coteau, we conducted generalized linear regression using a log link function and Poisson error distribution (Proc GENMOD, SAS Institute Inc. 2002) to model the structure of cell counts within the tables. We used Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 1998) to evaluate models (Burnham and Anderson 1998). We compared models using ΔAIC values, where for each model i :

$$\Delta AIC_i = AIC_i - AIC_{\min}$$

We evaluated competing models that represented different hypotheses about distribution of sites across the Coteau region among the 9 individual categories of population performance and pair density. We compared a null model, which contained only an intercept, to models that included (1) population performance alone, (2) pair density alone, (3) additive effects of population performance and pair density, and (4) additive effects of population performance and pair density and an interaction between population performance and pair density. Because the year effect in our predictive model of nesting success created large differences in nesting success between the two years, we evaluated the distribution for each year separately.

We were ultimately interested in using the results from our models to guide conservation programs on the ground. Thus, we defined conservation priorities for grassland protection efforts based on a decision matrix (Figure 4.5) that considered both a site's population performance (categorized as high, medium, or low nesting success) and its pair density (categorized as high, medium, or low). Finally, we examined differences in conservation priorities between years.

Protection Prioritization Matrix

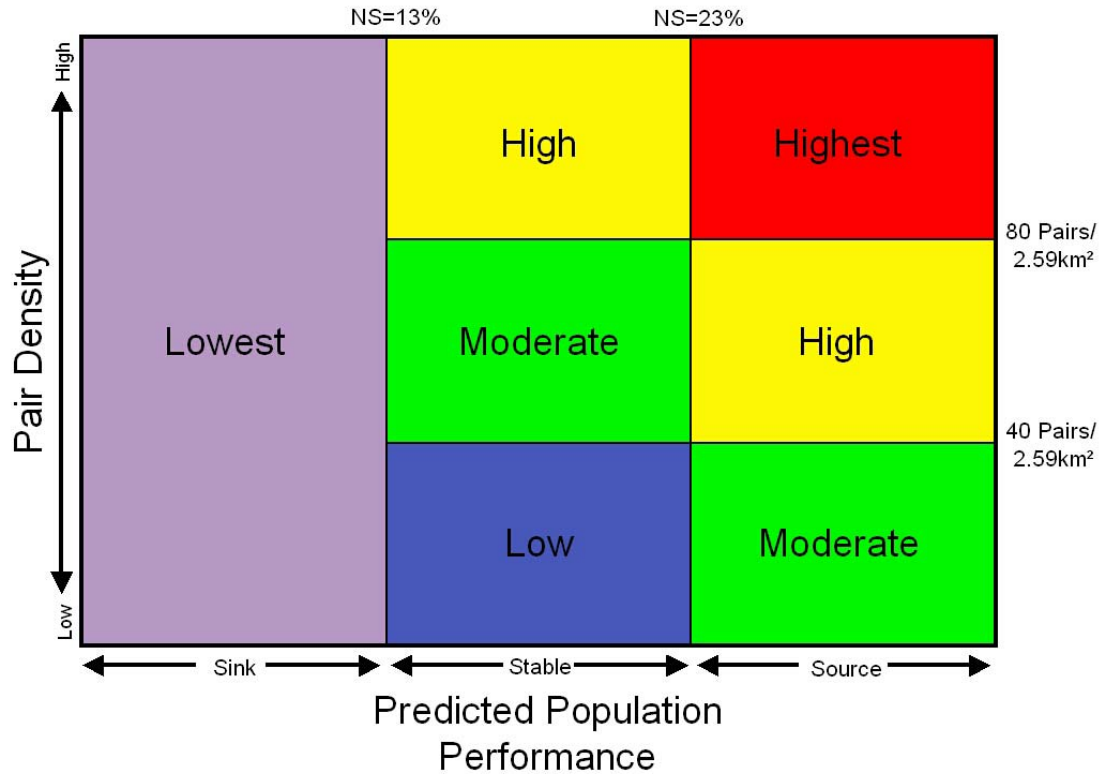


Figure 4.5. Conservation prioritization matrix for grassland protection efforts within the Missouri Coteau of North and South Dakota, USA.

Results

Landscapes across the Coteau varied dramatically in terms of upland features (Percent Grassland, mean = 58%, range 0-100%, Figure 4.1; Grassland Edge, mean = 77 km of edge/10.4-km², range 24-140 km of edge/10.4-km², Figure 4.2) and wetland density, (mean = 122 wetland basins/10.4-km², range 1-516 wetland basins/10.4-km², Figure 4.3). Given the strong spatial variation in landscape features, nesting success

(Figures 4.6 and 4.7) and pair density (Figure 4.8) varied across the Coteau region and thus, large variation existed in predicted population performance across density categories. During 2000, predicted nesting success was relatively high across the Coteau (mean = 26%). As a result, 54.5% of sites within the Coteau region were predicted to achieve high nesting success for mallards, while only 12.2% of the sites were predicted to have low nesting success (Table 4.1, Figure 4.9). In contrast, predicted nesting success during 2001 was relatively low across the Coteau region (mean = 15%). As a result, 20.2% of the sites within the Coteau were predicted to have high nesting success, while 55.9% were predicted to have low nesting success (Table 4.1, Figure 4.9). To quantify uncertainty in parameter estimates, we calculated confidence limits on daily survival rates across a range of landscape characteristics (Table 4.2 and 4.3). Predicted mallard pair density across the Coteau varied from 1 - 212 pairs/2.59 km² (mean = 49 pairs/2.59-km², Figure 4.8).

Evaluations of regression models suggest that population performance and pair density were associated on sites across the Coteau. The model that contained population performance, pair density, and an interaction between these two variables was clearly the best during both 2000 and 2001 ($\Delta AIC > 4,000$ for all other models, Table 4.4). The distribution of sites among categories of population performance and pair density suggests that strong negative relationships exist between pair density and population performance across sites (Figure 4.10 and 4.11).

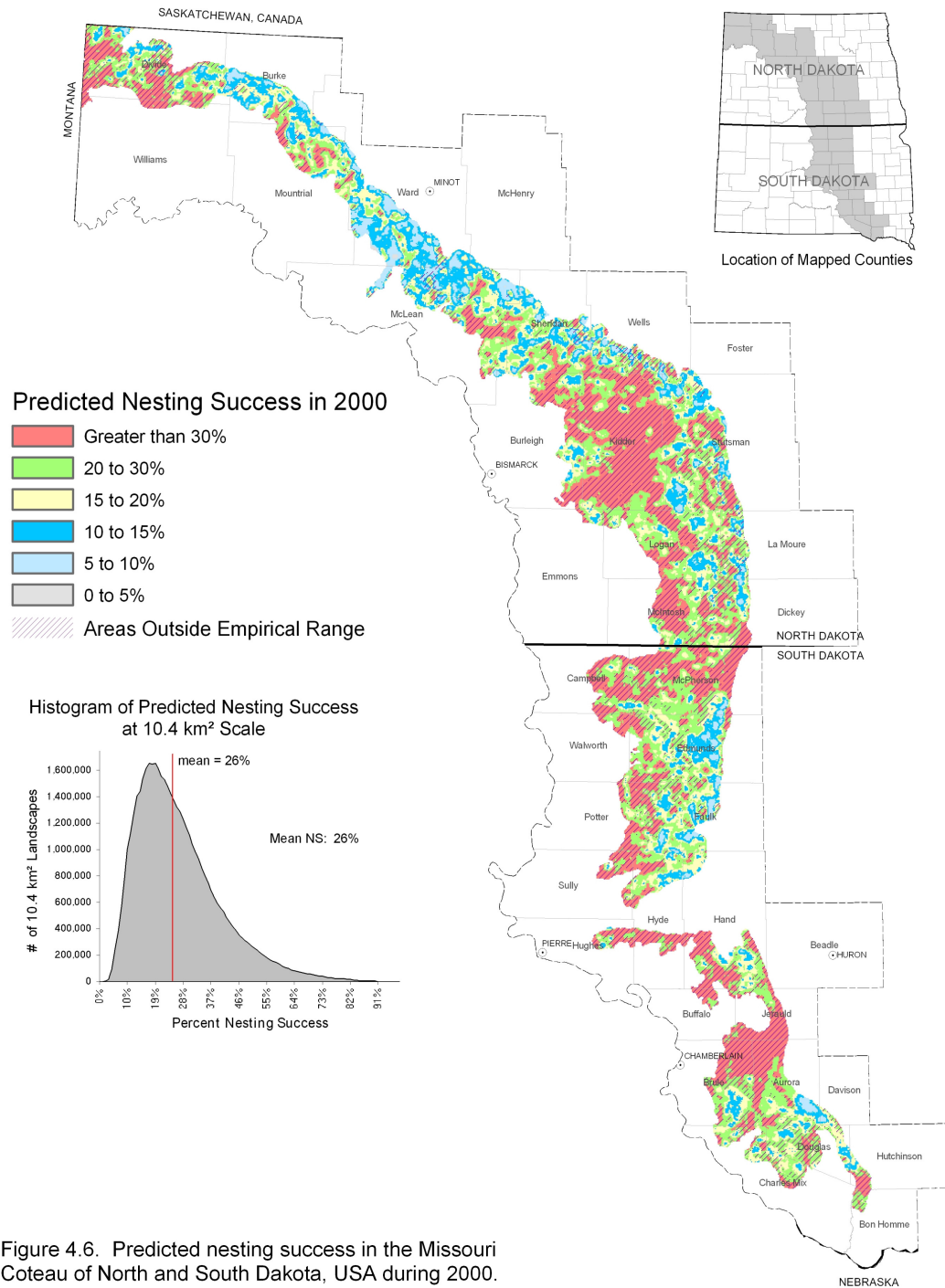


Figure 4.6. Predicted nesting success in the Missouri Coteau of North and South Dakota, USA during 2000.

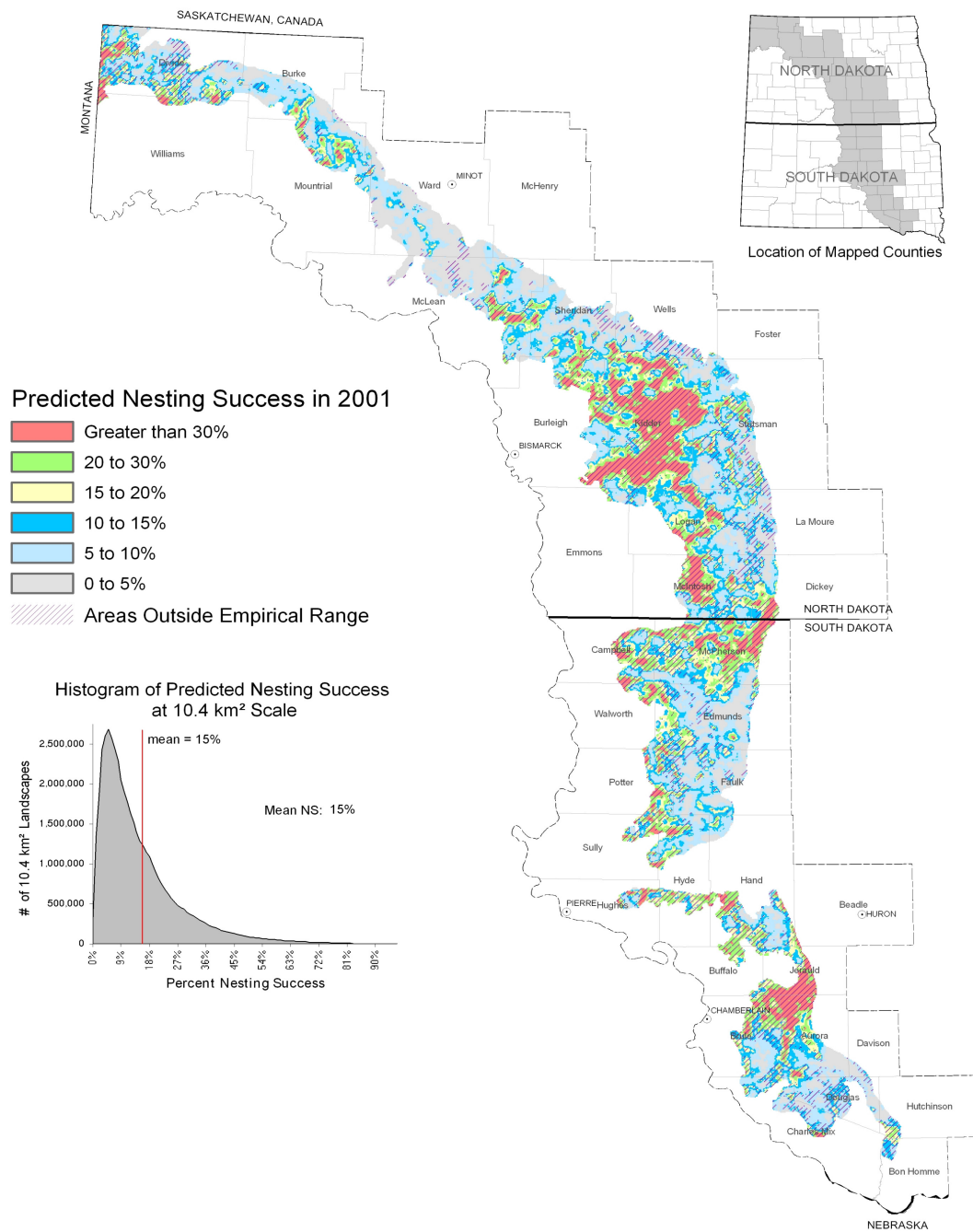


Figure 4.7. Predicted nesting success in the Missouri Coteau of North and South Dakota, USA during 2001.

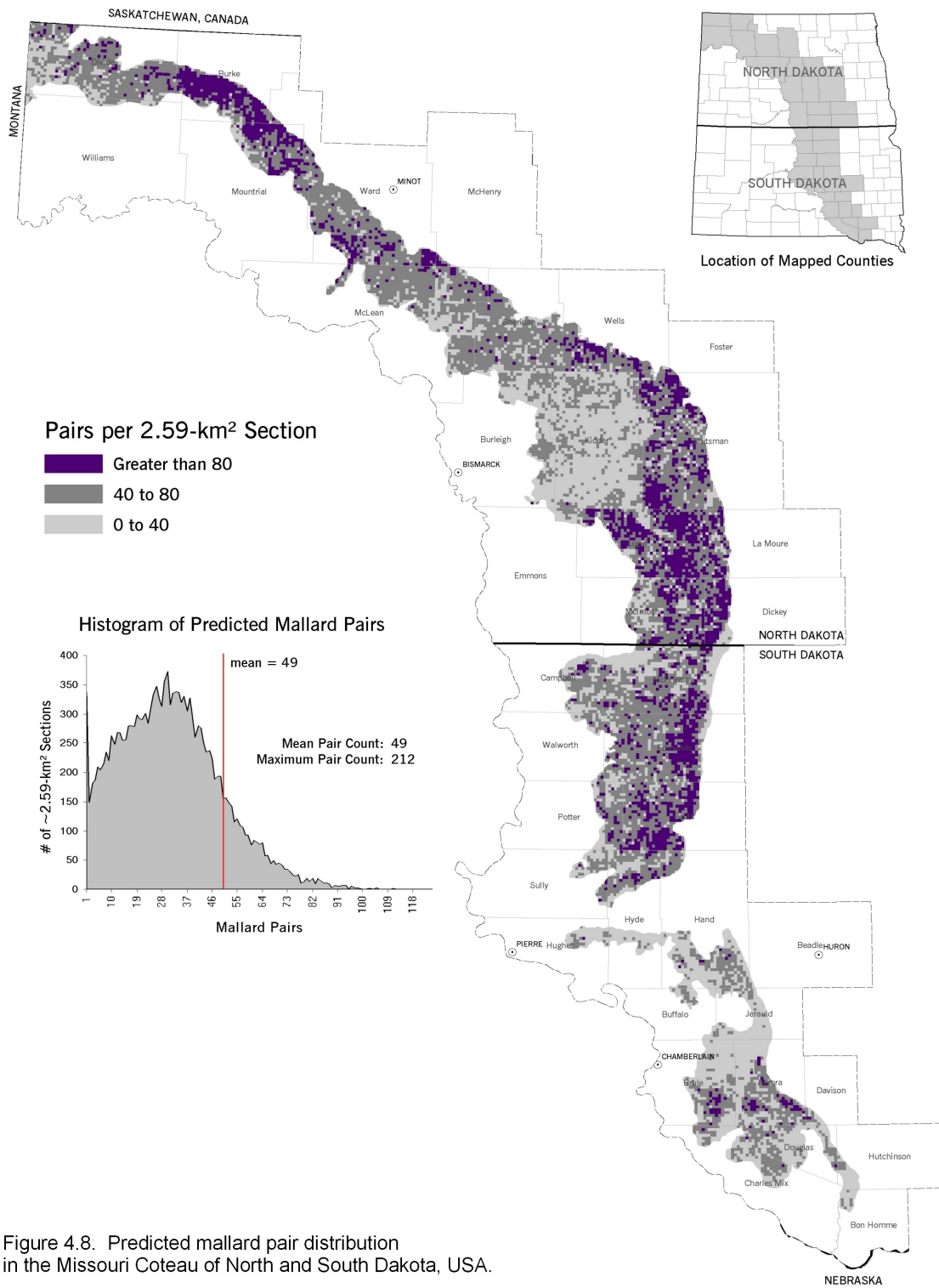


Figure 4.8. Predicted mallard pair distribution in the Missouri Coteau of North and South Dakota, USA.

Table 4.1. Distribution of 2.59- km² sites among predicted high, medium, and low nesting success areas and pair-density categories for mallards in the Missouri Coteau region, USA, 2000-2001.

Year	Pair Density	Population Performance Categories			Totals
		Low Nesting Success	Medium Nesting Success	High Nesting Success	
2000	Low (< 40 pairs/2.59 km ²)	167 (1.1%) ^a	975 (6.2%) ^a	5,137 (32.7%) ^a	6,279 (40.0%)
	Medium (40 - 80 pairs/2.59 km ²)	918 (5.8%)	2,992 (19.1%)	3,014 (19.2%)	6,924 (44.1%)
	High (> 80 pairs/2.59 km ²)	825 (5.3%)	1,262 (8.0%)	414 (2.6%)	2,501 (15.9%)
	Year Totals	1,910 (12.2%)	5,229 (33.3%)	8,565 (54.5%)	15,704 (100%)
2001	Low (< 40 pairs/2.59 km ²)	1,908 (12.1%)	1,801 (11.5%)	2,570 (16.4%)	6,279 (40.0%)
	Medium (40 - 80 pairs/2.59 km ²)	4,726 (30.1%)	1,643 (10.5%)	555 (3.5%)	6,924 (44.1%)
	High (> 80 pairs/2.59 km ²)	2,152 (13.7%)	305 (1.9%)	44 (0.3%)	2,501 (15.9%)
	Year Totals	8,786 (55.9%)	3,749 (23.9%)	3,169 (20.2%)	15,704 (100%)

^a Percent of the total number of sites within the Coteau region in each category.

During 2000, high nesting success was most common on sites that had low pair density and least common on sites with high pair density (Figure 4.10). In contrast, low nesting success was most common on sites that had medium or high pair density and least common on sites with low pair density (Figure 4.10). Despite reduced nesting success in 2001, high nesting success areas were again most common on sites that had low pair density and least common on sites with high pair density (Figure 4.11). In 2001, as in 2000, sites predicted to have high pair density were most frequently predicted to also have low nesting success and were very unlikely to be predicted as having high or moderate nesting success (Fig. 4.11).

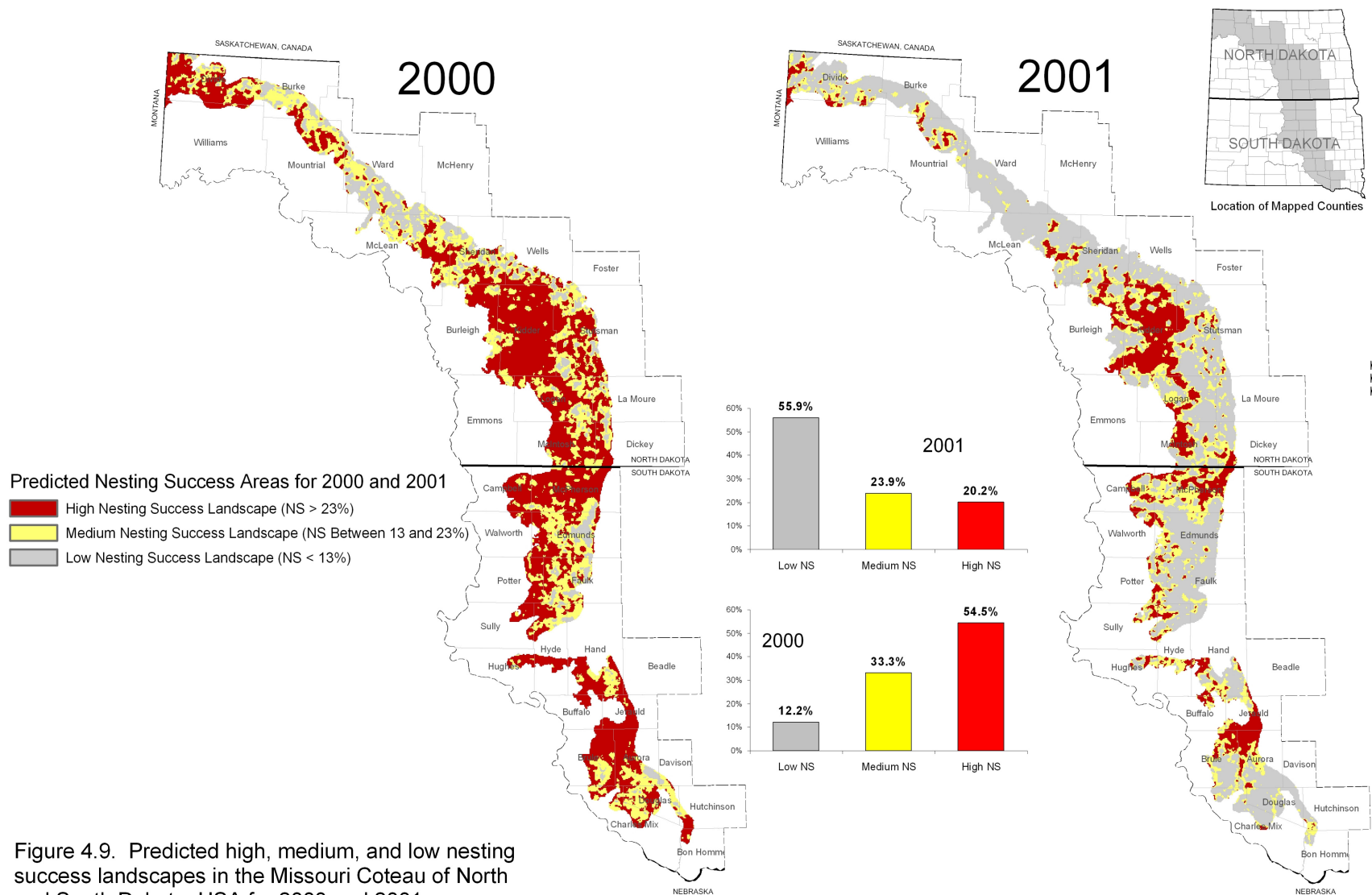


Figure 4.9. Predicted high, medium, and low nesting success landscapes in the Missouri Coteau of North and South Dakota, USA for 2000 and 2001.

Table 4.2. Daily survival rate estimates and 95% confidence limits during 2000 across a range of covariate values for Percent Grassland, Grassland Edge, and Wetland Count.

	Low Grassland Edge, Low Wetlands*			Medium Grassland Edge, Low Wetlands*			High Grassland Edge, Low Wetlands*		
Proportion Grassland	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI
0	0.984	0.921	0.997	0.9559	0.902	0.981	0.9669	0.837	0.994
0.1	0.9847	0.925	0.997	0.9578	0.908	0.981	0.9684	0.846	0.994
0.2	0.9855	0.929	0.997	0.9599	0.913	0.982	0.9699	0.855	0.994
0.3	0.9863	0.933	0.997	0.9621	0.918	0.983	0.9716	0.864	0.995
0.4	0.9872	0.937	0.997	0.9644	0.924	0.984	0.9733	0.873	0.995
0.5	0.988	0.941	0.998	0.9667	0.929	0.985	0.9751	0.883	0.995
0.6	0.9889	0.946	0.998	0.9692	0.935	0.986	0.9769	0.893	0.995
0.7	0.9898	0.95	0.998	0.9717	0.94	0.987	0.9788	0.903	0.996
0.8	0.9908	0.954	0.998	0.9742	0.945	0.988	0.9807	0.912	0.996
0.9	0.9917	0.958	0.998	0.9767	0.95	0.989	0.9826	0.922	0.996
1	0.9926	0.962	0.999	0.9792	0.954	0.991	0.9845	0.931	0.997
	Low Grassland Edge, Medium Wetlands*			Medium Grassland Edge, Medium Wetlands*			High Grassland Edge, Medium Wetlands*		
Proportion Grassland	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI
0	0.9695	0.865	0.994	0.918	0.836	0.961	0.9379	0.757	0.987
0.1	0.9709	0.871	0.994	0.9215	0.843	0.963	0.9406	0.768	0.987
0.2	0.9724	0.877	0.994	0.9253	0.85	0.964	0.9435	0.78	0.987
0.3	0.9739	0.883	0.995	0.9292	0.858	0.966	0.9465	0.792	0.988
0.4	0.9755	0.889	0.995	0.9333	0.865	0.968	0.9496	0.804	0.989
0.5	0.9771	0.896	0.995	0.9376	0.873	0.97	0.9529	0.817	0.989
0.6	0.9788	0.902	0.996	0.942	0.88	0.973	0.9563	0.831	0.99
0.7	0.9805	0.909	0.996	0.9466	0.888	0.975	0.9598	0.844	0.991
0.8	0.9823	0.916	0.996	0.9512	0.895	0.978	0.9634	0.858	0.991
0.9	0.984	0.922	0.997	0.9559	0.902	0.981	0.9669	0.871	0.992
1	0.9858	0.929	0.997	0.9606	0.908	0.984	0.9705	0.884	0.993
	Low Grassland Edge, High Wetlands*			Medium Grassland Edge, High Wetlands*			High Grassland Edge, High Wetlands*		
Proportion Grassland	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI
0	0.959	0.825	0.991	0.8918	0.784	0.949	0.9174	0.706	0.981
0.1	0.9609	0.832	0.992	0.8963	0.792	0.952	0.9209	0.718	0.982
0.2	0.9628	0.839	0.992	0.9011	0.8	0.954	0.9247	0.73	0.982
0.3	0.9648	0.846	0.993	0.9061	0.809	0.957	0.9286	0.744	0.983
0.4	0.9669	0.854	0.993	0.9115	0.817	0.959	0.9328	0.758	0.984
0.5	0.9691	0.861	0.994	0.917	0.826	0.963	0.9371	0.773	0.985
0.6	0.9714	0.869	0.994	0.9228	0.835	0.966	0.9416	0.788	0.986
0.7	0.9737	0.878	0.995	0.9288	0.844	0.969	0.9462	0.803	0.987
0.8	0.9761	0.886	0.995	0.9349	0.853	0.973	0.9508	0.819	0.988
0.9	0.9784	0.894	0.996	0.941	0.861	0.976	0.9556	0.834	0.989
1	0.9808	0.902	0.996	0.9472	0.87	0.98	0.9603	0.85	0.99

* Levels of Grassland Edge were low = 20,000 m, medium = 60,000 m, and high = 140,000 m while levels of Wetlands were low = 100, medium = 300 and high = 500.

Table 4.3. Daily survival rate estimates and 95% confidence limits during 2001 across a range of covariate values for Percent Grassland, Grassland Edge, and Wetland Count.

	Low Grassland Edge, Low Wetlands*			Medium Grassland Edge, Low Wetlands*			High Grassland Edge, Low Wetlands*		
Proportion Grassland	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI
0	0.9682	0.853	0.994	0.9147	0.821	0.962	0.9353	0.718	0.988
0.1	0.9706	0.863	0.994	0.9208	0.834	0.964	0.94	0.738	0.989
0.2	0.9731	0.874	0.995	0.9271	0.848	0.967	0.9449	0.758	0.989
0.3	0.9755	0.885	0.995	0.9335	0.862	0.969	0.9498	0.778	0.99
0.4	0.978	0.896	0.996	0.94	0.875	0.972	0.9548	0.8	0.991
0.5	0.9805	0.907	0.996	0.9464	0.889	0.975	0.9597	0.821	0.992
0.6	0.9829	0.918	0.997	0.9528	0.902	0.978	0.9645	0.843	0.993
0.7	0.9852	0.928	0.997	0.959	0.915	0.981	0.9693	0.863	0.994
0.8	0.9874	0.938	0.998	0.965	0.926	0.984	0.9738	0.884	0.995
0.9	0.9894	0.947	0.998	0.9706	0.937	0.987	0.978	0.902	0.995
1	0.9913	0.956	0.998	0.9758	0.947	0.989	0.9819	0.92	0.996
	Low Grassland Edge, Medium Wetlands*			Medium Grassland Edge, Medium Wetlands*			High Grassland Edge, Medium Wetlands*		
Proportion Grassland	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI
0	0.9403	0.761	0.987	0.8472	0.717	0.924	0.8819	0.607	0.973
0.1	0.9447	0.776	0.988	0.8573	0.734	0.929	0.8901	0.629	0.975
0.2	0.9492	0.791	0.989	0.8679	0.751	0.935	0.8986	0.653	0.977
0.3	0.9537	0.807	0.99	0.8789	0.77	0.94	0.9072	0.678	0.978
0.4	0.9583	0.823	0.991	0.89	0.788	0.946	0.916	0.704	0.98
0.5	0.9629	0.839	0.992	0.9013	0.807	0.952	0.9249	0.731	0.982
0.6	0.9674	0.856	0.993	0.9126	0.825	0.958	0.9336	0.759	0.984
0.7	0.9717	0.872	0.994	0.9236	0.844	0.964	0.9422	0.787	0.986
0.8	0.9759	0.888	0.995	0.9344	0.862	0.97	0.9505	0.815	0.988
0.9	0.9798	0.903	0.996	0.9446	0.878	0.976	0.9583	0.841	0.99
1	0.9834	0.917	0.997	0.9541	0.894	0.981	0.9656	0.867	0.992
	Low Grassland Edge, High Wetlands*			Medium Grassland Edge, High Wetlands*			High Grassland Edge, High Wetlands*		
Proportion Grassland	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI	DSR	Lower 95% CI	Upper 95% CI
0	0.9205	0.7	0.983	0.8031	0.643	0.902	0.8461	0.543	0.962
0.1	0.9263	0.717	0.984	0.8156	0.661	0.909	0.8563	0.566	0.965
0.2	0.9321	0.734	0.986	0.8286	0.68	0.917	0.867	0.59	0.967
0.3	0.9381	0.753	0.987	0.8422	0.701	0.924	0.878	0.617	0.97
0.4	0.9442	0.771	0.988	0.8562	0.722	0.932	0.8892	0.645	0.973
0.5	0.9502	0.791	0.99	0.8705	0.743	0.94	0.9006	0.674	0.975
0.6	0.9562	0.811	0.991	0.8848	0.765	0.948	0.9119	0.705	0.978
0.7	0.962	0.831	0.992	0.899	0.787	0.955	0.923	0.736	0.981
0.8	0.9675	0.85	0.994	0.9129	0.809	0.963	0.9339	0.768	0.984
0.9	0.9727	0.869	0.995	0.9262	0.83	0.97	0.9442	0.799	0.986
1	0.9775	0.887	0.996	0.9387	0.851	0.976	0.9538	0.828	0.989

* Levels of Grassland Edge were low = 20,000 m, medium = 60,000 m, and high = 140,000 m while levels of Wetlands were low = 100, medium = 300 and high = 500.

Table 4.4. Comparisons of models that examine the influence of population performance and pair density on the distribution of sites across the Missouri Coteau region during 2000 and 2001.

Model	Number of Parameters	Year			
		2000		2001	
		AIC	Δ AIC	AIC	Δ AIC
Null	1	-203,033	11,257	-203,033	9,893
Nesting Success	3	-205,492	8,798	-205,492	7,434
Density	3	-207,601	6,689	-206,445	6,481
Nesting Success + Density	5	-210,060	4,230	-208,904	4,022
Nesting Success + Density + (Nesting Success * Density)	9	-214,290	0	-212,926	0

Figure 4.10. Proportion of sites predicted to be in different categories of population performance and pair density for mallards in the Missouri Coteau region of North and South Dakota, USA during 2000.

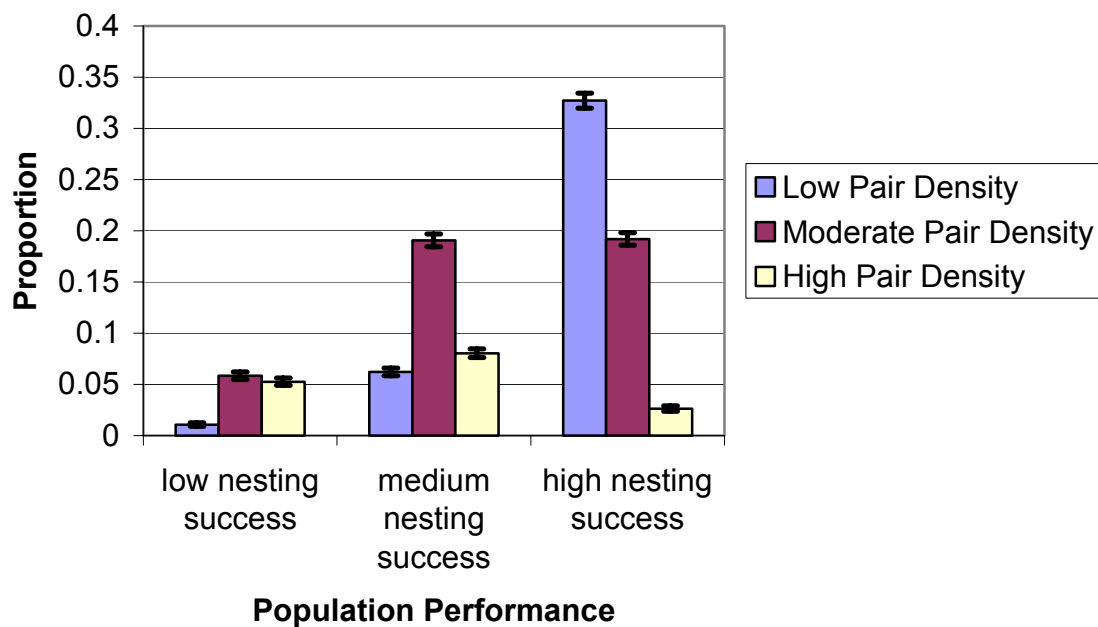
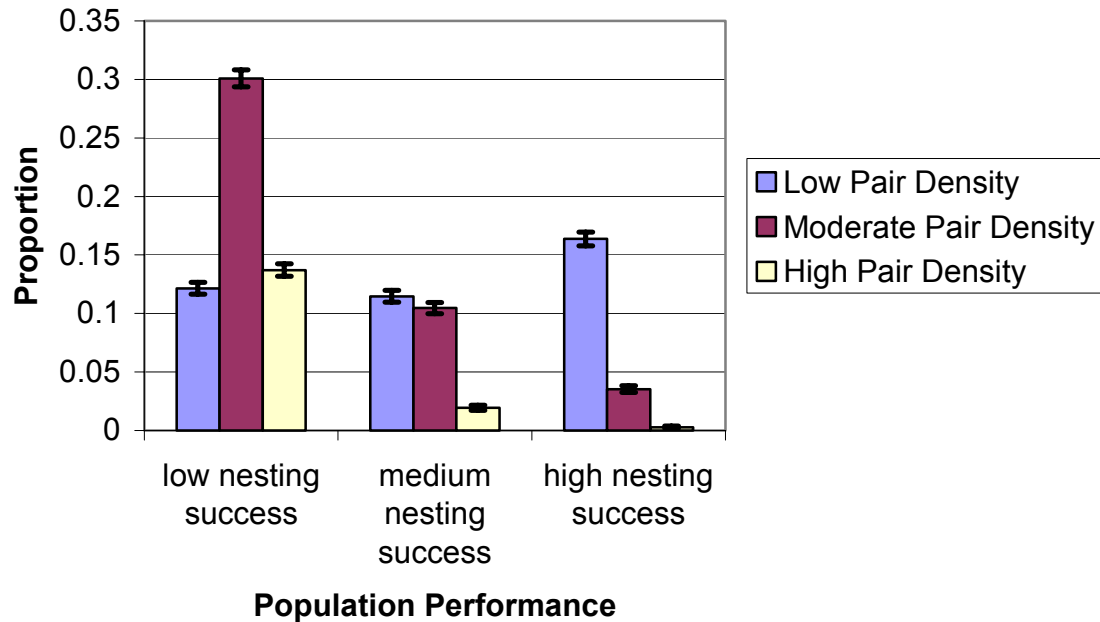


Figure 4.11. Proportion of sites predicted to be in different categories of population performance and pair density for mallards in the Missouri Coteau region of North and South Dakota during 2001.



When we assigned conservation-priority levels to sites based on predicted population performance and pair density, only 27.2% (4,271 sections) and 2.6% (408 sections) of sites in 2000 were placed in the high and highest priority classes, respectively, whereas most sites (51.8%, 8,135 sections) were assigned to the moderate conservation priority class (Table 4.5, Figure 4.12). Because of lower overall nesting success rates, many sites were downgraded to lower priority classes in 2001. Thus, in 2001, only 5.5% (864 sections) and 0.3% (47 sections) of the sites in the Coteau were placed in the high and highest conservation priority classes, respectively, and the majority of sites (67.5%, 10,600 sections) were assigned to the moderate priority class (Table 4.5, Figure 4.13).

Table 4.5. Distribution of 2.59- km² sites among conservation prioritization categories for mallards in the Missouri Coteau region, USA, 2000-2001.

Conservation Prioritization Categories	Year	
	2000	2001
Highest Priority	414 (2.6%)	44 (0.3%)
High Priority	4,276 (27.2%)	860 (5.5%)
Moderate Priority	8,129 (51.8%)	4,213 (26.8%)
Low Priority	975 (6.2%)	1,801 (11.5%)
Lowest Priority	1,910 (12.2%)	8,786 (55.9%)
Column Totals	15,704 (100.0%)	15,704 (100.0%)

Discussion

We developed an empirically based, spatially explicit model of mallard nesting success and combined it with an existing model of mallard pair density to prioritize areas for habitat conservation across broad spatial scales. Because wetland density is positively related to duck density (U.S. Fish and Wildlife Service 2003b) but appears to be negatively related to nesting success (Stephens 2003, Chapter 3), prioritizing areas for conservation is not straightforward, especially across a region as large and diverse as the Coteau. Previous research has pointed out the weaknesses of using density alone to identify conservation targets (Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991, Remeš 2003). Our results provide further evidence that density alone is an inadequate metric to use when assigning conservation priority levels to sites of interest. Our finding that density and population performance were negatively associated represents the first such evidence from small-scale field studies on ducks. By using GIS and models of key aspects of population dynamics, we were able to more realistically and therefore, more accurately prioritize areas for future conservation work. We believe that

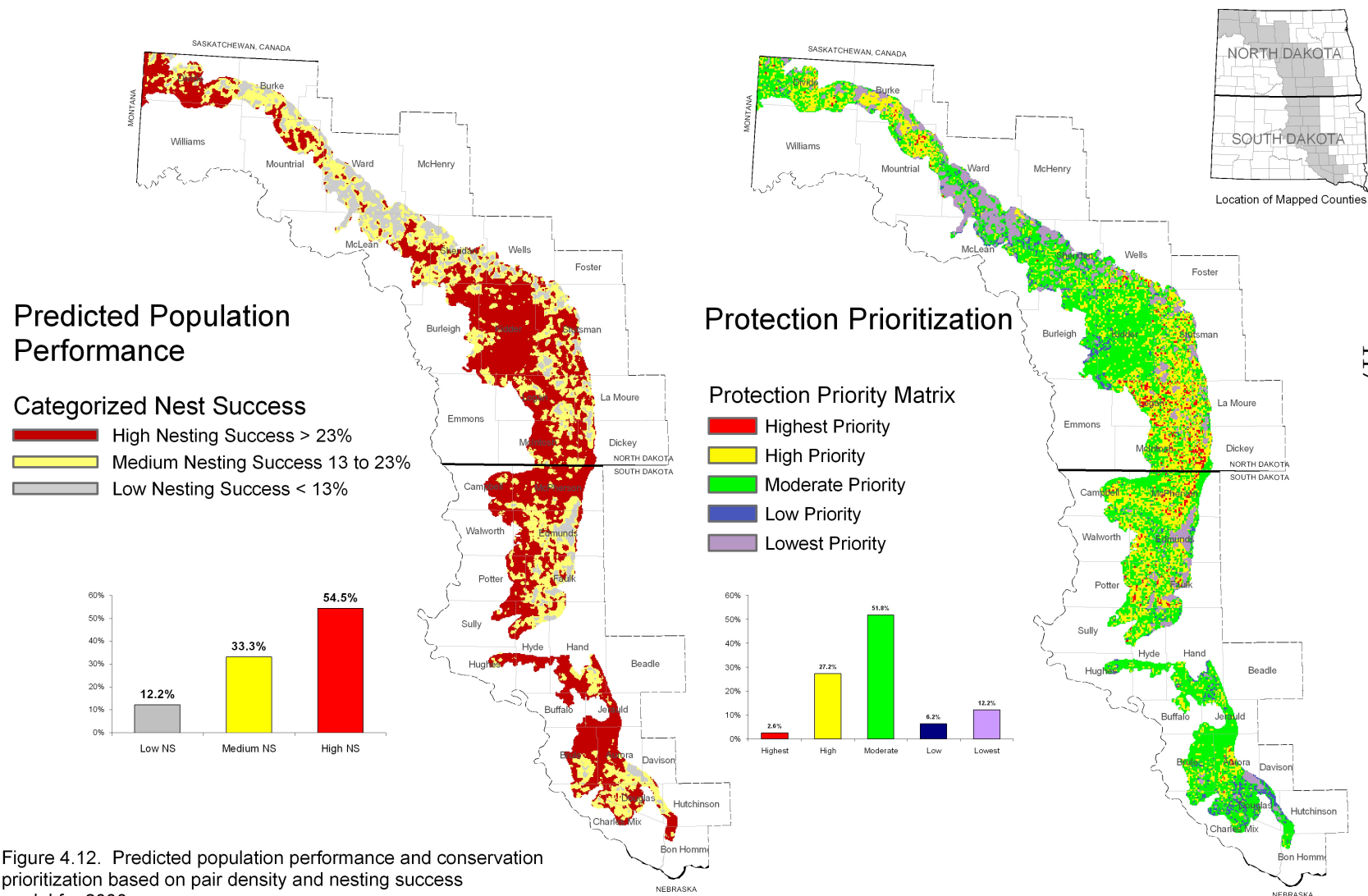


Figure 4.12. Predicted population performance and conservation prioritization based on pair density and nesting success model for 2000.

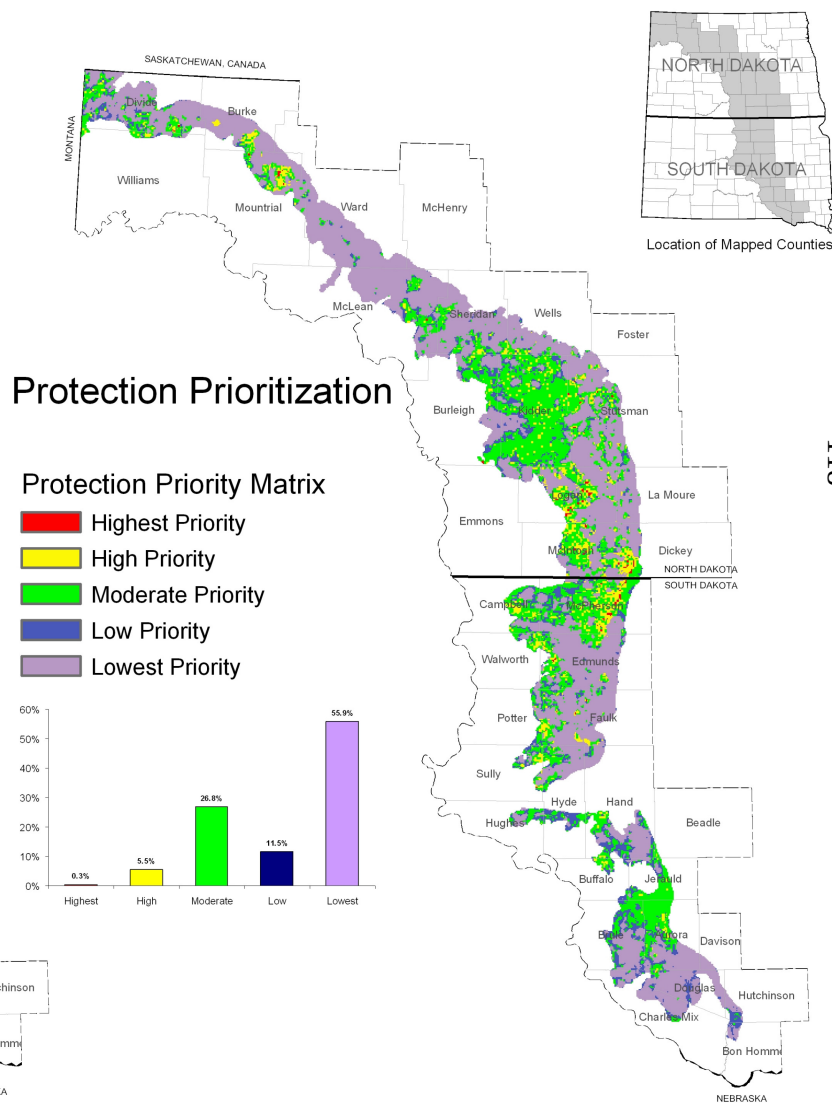
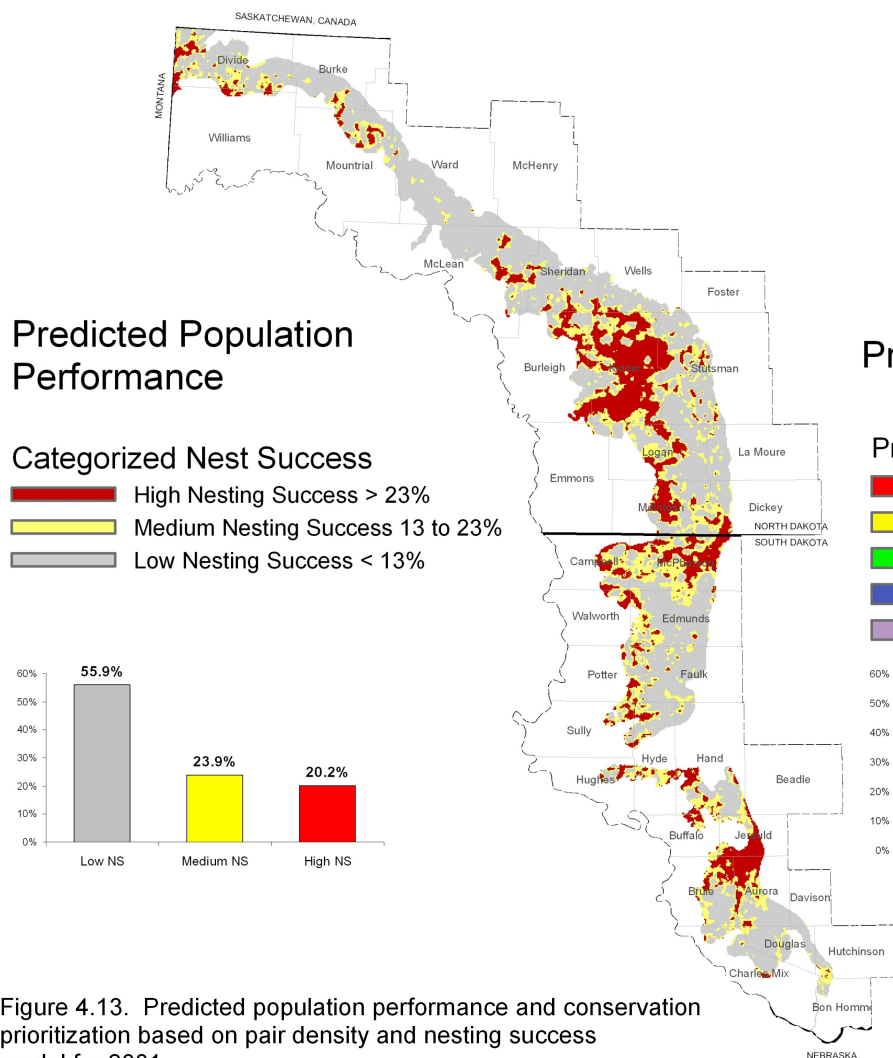


Figure 4.13. Predicted population performance and conservation prioritization based on pair density and nesting success model for 2001.

the strategy we used represents an example of how empirical information on multiple vital rates can be used in spatially explicit models to quantitatively prioritize conservation efforts for species of interest.

Our results may help explain two key features of the results of past work on population dynamics of ducks in PPR. First, many researchers have found poor nesting success across the PPR and questioned how populations are sustaining themselves (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995). This result may be because most research has been conducted in areas with the highest wetland density, i.e., on sites where our models would predict low nesting success due to the negative influence of wetlands. Although data from sites with lower wetland densities would be informative, it will be challenging to achieve adequate samples on such sites because pair densities tend to be lower on sites with few wetlands.

Second, Adaptive Harvest Management models suggest that recruitment rates of mallards breeding in the PPR are strongly density dependent (U.S. Fish and Wildlife Service 2003a). The negative influence of wetlands on nesting success that we identified provides a mechanism for density-dependent recruitment to occur spatially throughout portions of the PPR. We suggest that nest survival is lower on sites with higher wetland densities because several species of nest predators have been shown to preferentially select wetland areas for foraging (Greenwood 1999, Lariviere and Messier 2000, Phillips 2001). Thus, we speculate that on sites with more wetland basins, ducks are more likely to nest closer to wetlands and to consequently suffer greater nest mortality than they are sites with fewer wetland basins. Additionally, we speculate that landscapes with more

wetlands also support a greater abundance of predators because of higher overall productivity on the site and are thus, inherently more difficult settings in which to successfully nest. However, our measure of wetland density is the number of wetland basins; not wetlands containing water. Thus, our metric of wetland density does not change across years. As a result, our results do not help explain lower recruitment rates during years with higher overall populations. It is important to point out our empirical data were collected over only 2 years during a period of extended wet conditions across the Coteau. Thus, we suggest that the negative influence of wetlands be validated across additional years under different wetland conditions. However, we speculate that the negative influence of wetlands may be reduced or absent during initial wet years following drought and thus, the negative influence of density on recruitment may be temporarily removed. We believe that in initial wet years following drought, duck densities may initially swamp predator populations that may be reduced during drought periods. However, predator densities may numerically increase as wetter conditions persist. Alternative explanations are also possible. Higher pair densities may simply result in predators developing search images for duck nests and/or immigration of predators to areas with high duck pair densities. And although we suspect that nesting success rates will increase on sites with high wetland densities during initial years following drought, additional empirical data will be necessary to test this hypothesis. Research across a diversity of pair densities and wetland densities will facilitate a better understanding of these density-dependent issues. It is also important to point out that our population models don't contain information on duckling survival, which is also an

important component of recruitment (Hoekman et al. 2002). Although brood and duckling survival are poorly studied (Talent et al. 1983, Orthmeyer and Ball 1990, Rotella and Ratti 1992), one study suggests that wetland density is positively related to survival (Rotella and Ratti 1992). Thus, incorporation of relationships between the wetland density and duckling survival would allow trade-offs between density and recruitment to be more fully examined. However, collecting data on duckling and brood survival across multiple sites with a gradient of wetland densities will be both challenging and expensive.

The spatially explicit prioritization tools we developed allowed us to identify conservation priorities across the Coteau. However, the substantial shifts in priorities between years, as a result of large differences in year-specific nesting success, presents challenges for using such tools. Temporal variation in duck nesting success rates has been previously observed in the Coteau (Higgins et al. 1992). However, few studies have been designed to specifically address temporal variation in nesting success rates or collected long-term data on individual study sites (Higgins et al. 1992). Prioritization maps developed with long-term (i.e., 5 - 10 years) data that capture temporal variation in nesting success should prove valuable when deciding where to target conservation programs. This approach based on long-term data is especially appropriate for conservation programs such as perpetual conservation easements that are inherently long-term investments.

In the meantime, it seems appropriate to focus on the highest priority sites identified during 2001 when nesting success was quite low. If sites are working well

under overall poor conditions, then it seems reasonable to expect that they would perform well when overall conditions are favorable. Priorities could also be ranked on a continuous basis; starting with the best sites (i.e., highest pair density and nesting success) and then work down the list. Protecting the sites that were assigned to the high or highest priority classes in 2001 would not be a trivial task, however. The 911 sites in these two highest classes comprise nearly 236,000 hectares of land and thousands of landowners. Protecting just these with permanent grassland easements would cost approximately \$29,000,000.

Sources of Uncertainties

There are many uncertainties that may influence the validity and utility of our model. First, there is model uncertainty due to model-selection uncertainty, i.e., we are unsure that the approximating model selected is indeed the best model. However, AIC values suggested that our best approximating model explained variation substantially better than other competing models examined, and we estimated that this model explained approximately 90% of the spatial process variance in nesting success rates in our data set (Stephens 2002, Chapter 3). Second, our best statistical model, which resulted from a limited amount of exploratory modeling, was largely based on *a priori* thinking (exploratory analyses refined our latest ideas on the most relevant scale at which to measure landscape covariates). Third, there is uncertainty in the parameter estimates that result from our model. We quantified this uncertainty by calculating confidence limits on our nest survival estimates across the range of covariate values. Ultimately, producing maps that depict spatial uncertainty in parameter estimates across the map

space will be most useful to assure conservation practitioners are aware of the uncertainty and incorporate the measures of uncertainty into their decision making process.

Additionally, this will facilitate adapting new research to reduce the uncertainty across the range of covariate values where sampling variance is greatest. Fourth, although our modeling examined several spatial scales, our examination of scales was not exhaustive. Thus, different results may occur if nesting success is modeled as a function of covariates measured at either larger or smaller spatial scales. However, we believe our scales bracketed those likely to be influential. Finally, there is uncertainty in the estimates of the landscape characteristics derived from remotely sensed imagery that were used to apply our model spatially to the entire U.S. portion of the Coteau region. However, we validated the landscape metrics from the remotely sensed imagery with finer-resolution aerial photography collected from the study sites that we used to develop our statistical model. The results suggested that most metrics were similar, and we empirically adjusted the remotely sensed metric that was biased (see Landscape Characteristics). Thus, we believe the model applied here represents the best approximation currently available to assist in guiding conservation programs.

Recommendations for Future Research

Although we believe that the planning tools that we developed here are a useful starting point, additional work is required to validate and refine our model. Because a large proportion of the Coteau region was outside the empirical range used to develop our model, largely as a result of lower wetland densities, substantial uncertainty exists in the model predictions outside of the empirical range. Empirical data from areas with lower

wetland densities will help to broaden the inference space of our model. Thus, validation of the current model will be important across broader areas of the Coteau. Confidence limits on nest survival estimates, across the range of landscape covariates present in the Coteau, cover a substantial range of values. Thus, continued data collection and validation of model output is a critical yet often ignored step in successfully implementing adaptive resource management (Walters 1986). Additionally further work on the development of spatially explicit maps of parameter variances and confidence limits will be important. However, current GIS software cannot accommodate this effort and thus development of mathematical programs that integrate with GIS software will be required. Collection of data on relationships between duckling survival and landscape characteristics would be an important addition to our current models also.

Perhaps the most important challenge remaining is determining how to deal with the substantial annual variation in conservation priorities that results from annual variation in nesting success. Long-term research on a set of study sites will strengthen confidence in our model and improve the utility of it. Such long-term work would allow partitioning of variation in nesting success into spatial and temporal components and thus, facilitate improved ecological understanding of factors responsible for affecting each component of variation, which should improve conservation decisions. Ultimately, long-term data will allow researchers to develop demographic models that identify characteristics of landscapes that result in the highest nesting success rates over long time frames across a variety of environmental conditions. We believe that such demographic models combined with pair-density models based on long-term data will facilitate

identification of the most important areas for maintaining populations and allow those sites to be targeted by conservation programs. Finally, we also believe that development of models that predict risk of wetlands and grassland tracts being converted would be useful to further prioritize conservation activities like protection via easements. Risk models combined with the model presented here could be used to identify areas that have high pair density and high nesting success and that are at the highest risk of being converted to cropland.

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CHAPTER 5.

MANAGEMENT AND RESEARCH IMPLICATIONS

Conclusions and Management Implications

Because of the importance of nesting success rates to avian populations dynamics (Lack 1954, Ricklefs 1969, Hoekman et al. 2002), and the extensive and ubiquitous nature of habitat fragmentation (Richards 1990, Skole and Tucker 1993, Noss et al. 1995, Hansen et al. 2002), many studies have attempted to address the relationship between fragmentation and nesting success (e.g., Martin 1988; Robinson et al. 1995; Donovan et al. 1997; Marzluff et al. 2000, Herkert et al. 2003, Howerter 2003). However, an overall theory of fragmentation effects on nesting success has remained elusive, and the impacts of fragmentation of specific habitat types remains poorly understood for most species and groups. As a result, if conservation actions are to be successful in mitigating the effects of fragmentation and maintaining viable bird populations, additional research will be necessary to refine our understanding of how habitat fragmentation influences nesting success for the species and groups of interest.

In Chapter 2, we demonstrated that research conducted over multiple years, that measures fragmentation at landscape scales, is most likely to refine our knowledge on the topic. However, our review also suggests that many species and groups are poorly represented in the literature on fragmentation effects on nesting success. Further, we suggest that the appropriate landscape scale for measuring fragmentation will likely vary

depending upon the predator species present and can be dependent on the larger landscape context (Lahti 2001, Chalfoun et al. 2002). Thus, research on the species of interest in the landscape setting where management activity will be applied will prove critical to ensuring the success of conservation programs.

In Chapter 3, we describe field research conducted on upland nesting dabbling ducks in Missouri Coteau region of North Dakota that was designed to refine our understanding of how fragmentation and other habitat characteristics influence nesting success. Our best models of the factors related to duck nest survival included variables measured at multiple landscape scales. Landscape variables that we identified as having important relationships with nesting success were: (1) the amount of grassland measured at a 41.4 km² scale, (2) the amount of grassland edge measured at a 10.4 km² scale, and (3) the number of wetland basins measured at a 10.4 km² scale. This model suggests nesting success is positively related to the amount of grassland, related to grassland edge in a quadratic form and negatively related to the density of wetland basins. We also estimated that our model accounted for nearly 90 % of spatial process variation in nesting success in our data set.

In Chapter 4, we combined the statistical model developed in Chapter 3 with existing models of pair density to produce predicted mallard density and nesting success for the entire Coteau region of North and South Dakota. Previous population models have assumed that duck pair density and nesting success are independent. However, our analyses of nesting success suggest that the density of wetland basins, which is positively related to pair density, is negatively related to nest survival (Stephens 2003, Chapter 3).

Thus, inherent trade-offs may exist between the density of breeding pairs and nesting success, which is commonly used as a proxy to population growth rate. However, dependencies of pair density and nesting success are not a foregone conclusion. Pair density is modeled as a function of wetland area and nesting success as a function of wetland density, and the other landscape variables (i.e., percent grassland, grassland edge) are not strongly correlated with wetland density but exert important influences on nesting success. The results of our modeling work that combined information on predicted population performance (i.e., sink, stable and source populations) with predicted pair density across real landscapes of the Coteau suggests that pair density and predicted population performance were negatively associated with one another; source populations were most common on sites that had low pair density and least common on sites with high pair density. In contrast, sink populations were most common on sites that had medium or high pair density and least common on sites with low pair density. As a result, 29.8% and 5.8% of sites were classified as highest/high priorities during 2000 and 2001, respectively. The spatially explicit prioritization tools we developed allowed us to identify conservation priorities across the Coteau. However, the substantial shifts in priorities between years, as a result of large differences in year-specific nesting success rates, present challenges for using such tools. Collection of data across many years and corresponding varied environmental conditions will facilitate identification of the sites most important to populations over the long-term.

Our review of the evidence for fragmentation effects on avian nesting success for diverse taxa across a variety of habitat types and physiographic areas (Chapter 2)

suggests that an overarching and unifying theory of fragmentation may not exist (Haila 2002). Effects of fragmentation seem to vary across organisms, habitat types and geographic areas (Haila 2002). Thus, development of empirical models on the species of interest in the systems of interest, such as those we developed in Chapter 3, may be required. We suspect that important differences may exist in how landscape variables influence nesting success across avian taxa. For example, several grassland-nesting songbirds nest on the same sites within the Coteau region where we collected data on nesting ducks. Nest predators of songbirds include those that prey on waterfowl nests along with species of mice and voles that may buffer predation on duck nests. Thus, differing responses of different predator communities to landscape characteristics may make drawing conclusions across taxa difficult even within the same habitat types and physiographic areas. And Chalfoun et al. (2002) found that the response of nest predators was inconsistent and variable across geographic areas.

Research Needs

Our work suggest that longer term studies that capture a variety of environmental conditions will be important for separating the effects of fragmentation from temporal fluctuations in nest survival caused by other factors. For ducks breeding in the Coteau region of the Prairie Pothole Region (PPR), we further speculate that important interactions may exist between the landscape variables that influence nesting success and environmental conditions. Our results also suggest that important trade-offs exist between key population parameters such as pair density and nesting success. Given these

complexities, continued research and evaluation will be important for refining our understanding of factors that influence long-term population growth rates for waterfowl that breed in the PPR.

Several additional topics for further research are evident from our work. It is clear that to develop a more encompassing understanding of habitat fragmentation, research on many poorly represented taxa and groups will be necessary across several habitat types. Additionally, the models of duck nesting success that we developed in the Coteau will require further validation; additional spatial replicates across broader areas of the Coteau, and continued research on some sites over longer time frames (i.e., 5-10 years) across varied environmental conditions will be necessary to improve the utility of, and confidence in our model. The empirical range of landscape variables in our models encompassed a little over half of the actual range of those variables across the entire Coteau. Thus, information collected on sites that expand that range, particularly at lower wetland densities, will prove especially useful in broadening the inference space of our model. Although our model captured most of the spatial process variation in nesting success, estimating and modeling factors related to temporal variation in nesting success will require additional research. We believe that a more thorough understanding of small mammal population dynamics may help explain temporal variation in nest-survival rates. Additionally, comparisons of small mammal populations among landscapes will also be informative to management activities. Accompanying work on the response of mammalian predators to landscape gradients will prove useful in explaining the trends we documented. Rigorous methodologies to estimate changes in predator diversity,

community composition and foraging behavior in different landscape settings should prove especially informative.

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APPENDICES

APPENDIX A:

NEST-TYPE AND SPATIAL SCALE OF HABITAT FRAGMENTATION
EXAMINED BY 86 STUDIES USED IN THIS REVIEW.

Appendix A1. Nest-type and spatial scale of habitat fragmentation examined by 86 studies used in this review.

Nest Type ¹	Scale Studied and Resulting Effect						Sources
	Edge	Effect	Patch	Effect	Landscape	Effect	
Artificial	X	Yes					Andrén and Angelstam 1988, Møller 1989, Burkey 1993, Linder and Bollinger 1995, Marini et al. 1995, Pasitschniak-Arts and Messier 1995, Fenske-Crawford and Niemi 1997, Niemuth and Boyce 1997, King et al. 1998, Wong et al. 1998, Brand and George 2000
Artificial	X	No					Boag et al. 1984, Yahner and Wright 1985, Angelstam 1986, Ratti and Reese 1988, Yahner et al. 1989, Telleria and Santos 1992, Esler and Grand 1993, Laurance et al. 1993, Picman et al. 1993, Yahner et al. 1993, Berg 1996, Russo and Young 1997
Artificial			X	Yes			Møller 1988, Haskell 1995*, Yahner and Mahan 1996, Darveau et al. 1997*, Clawson and Rotella 1998, Wilson et al. 1998
Artificial			X	No			Santos and Telleria 1992,

							DeGraaf and Angelstam 1993, DeGraaf 1995
Artificial					X	Yes	Andrén et al. 1985, Yahner and Scott 1988, Langen et al. 1991*, Andrén 1992, Gering and Blair 1999 [†]
Artificial					X	No	Seitz and Zegers 1993
Artificial	X	Yes	X	Yes			Gibbs 1991, Burger et al. 1994
Artificial	X	Yes	X	No			Storch 1991 [†] , Pasitschniak- Arts and Messier 1996
Artificial	X	No	X	No			Rudnicky and Hunter 1993, Huhta et al. 1998, Matthews et al. 1999
Artificial	X	No	X	Yes			Nour et al. 1993, Arango-Velez and Kattan 1997, Hannon and Cotterill 1998*, Keyser et al. 1998
Artificial			X	Yes	X	Yes	Wilcove 1985
Artificial	X	Yes			X	Yes	Donovan et al. 1997, Hartley and Hunter 1998
Artificial	X	No			X	Yes	Bayne and Hobson 1997, Sargent et al. 1998
Artificial	X	Yes	X	No	X	Yes	Huhta et al. 1996
Artificial	X	No	X	Yes	X	No	Small and Hunter 1988
Real	X	Yes					Bjorklund 1990, King et al. 1996, Suarez et al. 1997, Clark and Shutler 1999
Real	X	No					Vickery et al. 1992, Lutz et al.

							1994, Robinson and Wilcove
							1994, Berg 1996, Hanski et al.
							1996, D'Eon 1997, Drobney et
							al. 1998, Fleming and Giuliano
							1998, McKee et al. 1998,
							Pasitschniak-Arts et al. 1998,
							Morse and Robinson 1999
Real			X	Yes			Møller 1988, Møller 1991,
							Burhans and Thompson 1999
Real			X	No			Bryan and Best 1994, Gale et
							al. 1997, Hughes et al. 1999,
							Taylor et al. 1999
Real					X	Yes	Donovan et al. 1995,
							Greenwood et al. 1995,
							Robinson et al. 1995
Real					X	No	Porneluzi and Faaborg 1999
Real	X	Yes	X	Yes			Johnson and Temple 1990,
							Winter and Faaborg 1999
Real	X	No	X	No			Friesen et al. 1999
Real	X	No	X	Yes			Hoover and Brittingham 1998
Real	X	Yes			X	Yes	Clark et al. 1999
Real	X	No	X	Yes	X	Yes	Hoover et al. 1995
Real	X	No	X	No	X	Yes	Tewksbury et al. 1998**

[†]Storch (1991) reported higher nesting success near edges than in the interior of forests.

*Hannon and Cotterill (1988), Langen et al. (1991), Haskell (1995) and Daurveau et al. (1997) detected lower nesting success in larger patches.

[‡]Gering and Blair (1999) found lower nesting success in “natural” habitats than urbanized habitats.

** Tewksbury et al. (1998) detected lower nesting success in unfragmented landscapes than in fragmented agricultural landscapes.

APPENDIX B:

SAS CODE USED IN ANALYSES AND RANKINGS OF TOP
CANDIDATE MODELS.

Appendix B1. Example SAS code used in analysis of nest survival data from the Missouri Coteau region of North Dakota, USA, 2000-2001.

```

Proc Nlmixed tech=quanew method=gauss maxiter=1000;
ods select Specifications Dimensions IterHistory ConvergenceStatus
FitStatistics ParameterEstimates;
ods output FitStatistics= AICvalues ParameterEstimates=Beta;
parms B0=2.5649 B1=0.6817 B2=-0.00335 B3=0.2248 B4=-0.4229 B5=-0.03358
B6=-0.06625 B7=0.1146 B8=-0.639 B9=2.4019 B10=0.01464 B11=-0.1735 B12=-
0.4014 B13=0.02216 B14=0.357 B15=4.2598 v=0.01933;
                                p=1;
    do i=0 TO intleng-1;
        eta=B0+ u +B1*(exppg16) + B2*(sp1) + B3*(sp2)+B4*(sp3)+
B5*(sp4)+B6*(sp5)+B7*(sp6)+B8*(lnwetcount4)+B9*(expbuildng4) +
B10*(na+i)+ B11*(y1)+B12*(medge4)+ B13*(medge42)+B14*(exppg16*y1)+
B15*(expbuildng4*y1);
        p=p*(exp(eta)/(1+exp(eta)));
    end;

    model intfate~binomial(1,p);
    random u~normal(0,v) subject=study_area;

RUN;

```


Appendix B2. Rankings based on AIC, and estimated beta parameters for models relating landscape, habitat, and other covariates to daily survival rate for duck nests in the Missouri Coteau region of North Dakota, USA, 2000-2001.

Model Suite	Model	AIC	K	Δ AIC	w_i	Estimated parameters (95% CI)
A priori fixed effect 10.4- and 93.2- square km scale	$\ln(\text{wetcount}_{10.4}) +$ $\exp(\text{pctgrass}_{10.4}) +$ $\exp(\text{building}_{10.4}) +$ year	10,627.1	5	0	0.33	$B_0 = -5.605$ (-7.634 , -3.576) $B_1 = 0.672$ (0.556 , 0.789) $B_2 = -0.519$ (-0.635 , -0.403) $B_3 = 6.039$ (4.288 , 7.789) $B_4 = -0.213$ (-0.253 , -0.174)
	$\ln(\text{wetcount}_{10.4}) +$ $\exp(\text{pctgrass}_{10.4}) +$ building _{10.4} + year	10,628.2	5	1.1	0.19	$B_0 = 0.434$ (0.076 , 0.791) $B_1 = 0.668$ (0.552 , 0.785) $B_2 = -0.522$ (-0.634 , -0.406) $B_3 = 6.329$ (4.474 , 8.184) $B_4 = -0.213$ (-0.253 , -0.173)
A prior random and fixed effects 10.4- and 93.2 square km scale	$\exp(\text{pctgrass}_{10.4}) +$ Species + edge _{10.4} + year	10,509.3	11	0	0.98	$B_0 = 2.145$ (1.376 , 2.915) $B_1 = 0.604$ (0.185 , 1.024) $B_2 = -0.030$ (-0.541 , 0.481) $B_3 = 0.202$ (0.045 , 0.358) $B_4 = -0.335$ (-1.180 , 0.511) $B_5 = -0.021$ (-0.181 , 0.139) $B_6 = -0.085$ (-0.237 , 0.068) $B_7 = 0.092$ (-0.107 , 0.290) $B_8 = -0.228$ (-0.272 , -0.184) $B_9 = -0.061$ (-0.148 , 0.026) $v = 0.089$ (0.020 , 0.158)

Exploratory random and fixed effects 10.4- and 93.2 square km scale	$\ln(\text{wetcount}_{10.4}) +$ $\exp(\text{pctgrass}_{10.4}) +$ $\exp(\text{building}_{10.4}) +$ $\text{year} + \text{Species} +$ $\text{edge}_{10.4} + \text{edge}_{10.4}^2$ $+ \text{nest age} +$ $\exp(\text{pctgrass}_{10.4}) * \text{year}$ $+ \exp(\text{building}_{10.4}) * \text{year}$	10,460.3	17	0	0.66	$B_0 = -0.941 (-7.160, 5.278)$ $B_1 = -0.820 (-1.242, -0.399)$ $B_2 = 0.434 (0.049, 0.820)$ $B_3 = 3.028 (-2.003, 8.058)$ $B_4 = -4.068 (-6.268, -1.869)$ $B_5 = -0.064 (-0.568, 0.441)$ $B_6 = 0.208 (0.050, 0.366)$ $B_7 = -0.311 (-1.166, 0.543)$ $B_8 = -0.042 (-0.203, 0.119)$ $B_9 = -0.073 (-0.227, 0.081)$ $B_{10} = 0.104 (-0.096, 0.304)$ $B_{11} = -0.480 (-0.827, -0.132)$ $B_{12} = 0.029 (0.009, 0.049)$ $B_{13} = 0.015 (0.009, 0.021)$ $B_{14} = 0.166 (0.038, 0.294)$ $B_{15} = 3.362 (1.445, 5.278)$ $v = 0.032 (0.004, 0.060)$
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	$\ln(\text{wetcount}_{10.4}) +$ $\exp(\text{pctgrass}_{10.4}) +$ $\exp(\text{building}_{10.4}) +$ $\text{year} + \text{Species2} +$ $\text{edge}_{10.4} + \text{edge}_{10.4}^2 +$ $\text{nest age} +$ $\exp(\text{pctgrass}_{10.4}) * \text{year}$ $+$ $\exp(\text{building}_{10.4}) * \text{year}$	10,461.6	12	1.3	0.34	$B_0 = -0.540 (-6.759, 5.679)$ $B_1 = -0.825 (-1.246, -0.404)$ $B_2 = 0.434 (0.049, 0.819)$ $B_3 = 2.871 (-2.157, 7.899)$ $B_4 = -4.064 (-6.258, -1.870)$ $B_5 = 0.113 (0.063, 0.162)$ $B_6 = -0.511 (-0.859, -0.165)$ $B_7 = 0.030 (0.011, 0.050)$ $B_8 = 0.015 (0.009, 0.021)$ $B_9 = 0.168 (0.041, 0.296)$ $B_{10} = 3.354 (1.443, 5.265)$ $v = 0.032 (0.003, 0.060)$
A priori fixed effect 23.3-square km scale	$\exp(\text{pctgrass}_{23.3}) +$ $\text{edge}_{23.3} + \text{edge}_{23.3}^2$ $+ \text{patchden}_{23.3} +$ $\text{patchden}_{23.3}^2 +$ $\ln(\text{building}_{23.3})$ $+ \text{nest age} + \text{year}$	10,561.1	9	0	0.57	$B_0 = 2.961 (2.126, 3.796)$ $B_1 = 1.197 (0.973, 1.421)$ $B_2 = -0.277 (-0.362, -0.191)$ $B_3 = 0.005 (0.003, 0.007)$ $B_4 = 0.088 (-0.107, 0.282)$ $B_5 = 0.001 (-0.030, 0.032)$ $B_6 = 0.136 (0.080, 0.192)$ $B_7 = 0.017 (0.012, 0.022)$ $B_8 = -0.212 (-0.253, -0.172)$

	exp(pctgrass23.3) + edge23.3 + edge23.3 ² + patchden23.3 + patchden23.3 ² + ln(building23.3) + ln(juliandate) + nest age + year	10,562.8	10	1.7	0.24	B ₀ =2.859 (1.948, 3.770) B ₁ =1.199 (0.975, 1.423) B ₂ =-0.275 (-0.361, -0.189) B ₃ =0.005 (0.003, 0.007) B ₄ =0.086 (-0.108, 0.281) B ₅ =0.001 (-0.029, 0.032) B ₆ =0.134 (0.078, 0.190) B ₇ =0.016 (0.011, 0.022) B ₈ =-0.215 (-0.256, -0.173) B ₈ =0.027 (-0.068, 0.121)
A priori fixed and random effects 23.3- square km scale	exp(pctgrass23.3) + Species + edge23.3 + nest age + year	10,473.2	12	0	0.70	B ₀ =1.856 (1.171, 2.542) B ₁ =0.788 (0.435, 1.140) B ₂ =-0.012 (-0.518, 0.493) B ₃ =0.204 (0.049, 0.360) B ₄ =-0.366 (-1.202, 0.471) B ₅ =-0.029 (-0.188, 0.130) B ₆ =-0.076 (-0.229, 0.076) B ₇ =0.103 (-0.095, 0.301) B ₈ =-0.046 (-0.082, -0.011) B ₉ =0.015 (0.009, 0.021) B ₁₀ =-0.215 (-0.259, -0.171) v=0.052 (0.009, 0.095)

	pctgrass23.3 + species + edge23.3 + nest age + year	10,474.9	12	1.7	0.27	$B_0=2.571$ (1.937, 3.205) $B_1=1.409$ (0.708, 2.109) $B_2=-0.083$ (-0.584, 0.417) $B_3=0.190$ (0.031, 0.348) $B_4=-0.221$ (-1.084, 0.641) $B_5=-0.043$ (-0.205, 0.119) $B_6=-0.091$ (-0.246, 0.064) $B_7=0.088$ (-0.112, 0.289) $B_8=-0.049$ (-0.087, -0.012) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.215$ (-0.259, -0.171) $v=0.057$ (0.011, 0.103)
Exploratory fixed and random effects 23.3 -square km scale	exp(pctgrass23.3) + edge23.3 + edge23.3 ² + Species + ln(wetlandcount23.3) + nest age + year	10,472.8	14	0	0.27	$B_0=3.415$ (1.160, 5.670) $B_1=0.628$ (0.257, 1.000) $B_2=-0.255$ (-0.502, -0.008) $B_3=0.006$ (-0.0003, 0.013) $B_4=-0.071$ (-0.576, 0.433) $B_5=0.184$ (0.025, 0.343) $B_6=-0.211$ (-1.080, 0.658) $B_7=-0.045$ (-0.207, 0.118) $B_8=-0.094$ (-0.249, 0.062) $B_9=0.079$ (-0.122, 0.280) $B_{10}=-0.589$ (-1.166, -0.012) $B_{11}=0.015$ (0.009, 0.21) $B_{12}=-0.215$ (-0.260, -0.171) $v=0.039$ (0.006, 0.073)

	pctgrass23.3 + edge23.3 + Species + nest age + year	10,473.2	12	0.4	0.22	$B_0=1.860$ (1.174, 2.545) $B_1=0.787$ (0.434, 1.139) $B_2=-0.046$ (-0.082, -0.011) $B_3=-0.011$ (-0.517, 0.495) $B_4=0.205$ (0.049, 0.360) $B_5=-0.369$ (-1.204, 0.467) $B_6=-0.028$ (-0.187, 0.130) $B_7=-0.076$ (-0.228, 0.076) $B_8=0.103$ (-0.095, 0.301) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.215$ (-0.259, -0.171) $v=0.052$ (0.009, 0.095)
	exp(pctgrass23.3) + edge23.3 + Species2 + nest age + year + exp(pctgrass23.3) *year	10,474.1	8	1.3	0.14	$B_0=1.990$ (1.307, 2.672) $B_1=0.775$ (0.420, 1.131) $B_2=-0.047$ (-0.083, -0.011) $B_3=0.110$ (0.060, 0.160) $B_4=0.015$ (0.009, 0.021) $B_5=-0.347$ (-0.538, -0.155) $B_6=0.070$ (-0.029, 0.169) $v=0.054$ (0.010, 0.098)

	exp(pctgrass23.3) + edge23.3 + edge23.3 ² + Species2 + nest age + year	10,474.4	7	1.6	0.12	B ₀ =1.972 (1.293, 2.650) B ₁ =0.786 (0.432, 1.140) B ₂ =-0.047 (-0.083, -0.011) B ₃ =0.110 (0.059, 0.159) B ₄ =0.015 (0.009, 0.021) B ₅ =-0.214 (-0.258, -0.170) v=0.053 (0.010, 0.097)
A priori fixed effects 41.4-square km scale	exp(pctgrass41.4) + Species + edge41.4 + nest age + year	10,547.9	11	0	0.99	B ₀ =1.920 (1.682, 2.157) B ₁ =0.904 (0.771, 1.038) B ₂ =-0.071 (-0.548, 0.405) B ₃ =0.142 (-0.003, 0.288) B ₄ =0.020 (-0.786, 0.825) B ₅ =-0.080 (-0.230, 0.070) B ₆ =-0.154 (-0.297, -0.011) B ₇ =0.011 (-0.173, 0.195) B ₈ =-0.033 (-0.041, -0.026) B ₉ =0.017 (0.012, 0.022) B ₁₀ =-0.200 (-0.241, -0.160)

A priori fixed and random effects 41.4 - square km scale	exp(pctgrass41.4) + Species + edge41.4 + nest age + year	10,469.4	12	0	0.68	$B_0=1.751$ (1.117, 2.385) $B_1=0.946$ (0.597, 1.295) $B_2=-0.065$ (-0.564, 0.433) $B_3=0.202$ (0.045, 0.358) $B_4=-0.302$ (-1.148, 0.544) $B_5=-0.031$ (-0.190, 0.129) $B_6=-0.079$ (-0.232, -0.074) $B_7=0.101$ (-0.098, 0.300) $B_8=-0.032$ (-0.051, -0.012) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.215$ (-0.259, -0.171) $v=0.041$ (0.006, 0.075)
	pctgrass41.4 + Species + edge41.4 + nest age + year	10,471.1	12	1.7	0.29	$B_0=2.539$ (1.952, 3.126) $B_1=1.693$ (0.999, 2.387) $B_2=-0.108$ (-0.603, 0.388) $B_3=0.192$ (0.033, 0.350) $B_4=-0.207$ (-1.070, 0.656) $B_5=-0.041$ (-0.203, 0.121) $B_6=-0.089$ (-0.244, -0.066) $B_7=0.090$ (-0.111, 0.290) $B_8=-0.033$ (-0.054, -0.012) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.215$ (-0.259, -0.171) $v=0.045$ (0.008, 0.082)

Exploratory fixed and random effects 41.4 -square km scale	exp(pctgrass41.4) + Species + edge41.4 + nest age + year + exp(pctgrass41.4) *year	10,461.2 13 0 0.51			B ₀ =1.773 (1.130, 2.417) B ₁ =0.917 (0.562, 1.271) B ₂ =-0.033 (-0.534, 0.468) B ₃ =0.206 (0.050, 0.362) B ₄ =-0.339 (-1.181, 0.503) B ₅ =-0.025 (-0.184, 0.135) B ₆ =-0.083 (-0.236, 0.070) B ₇ =0.099 (-0.099, 0.298) B ₈ =0.031 (-0.051, -0.011) B ₉ =0.015 (0.009, 0.021) B ₁₀ =-0.512 (-0.716, -0.309) B ₁₁ =0.160 (0.053, 0.265) v=0.042 (0.007, 0.078)
	exp(pctgrass41.4) + Species2 + edge41.4 + nest age + year + exp(pctgrass41.4) *year	10,462.6 8 1.4 0.25			B ₀ =1.881 (1.244, 2.518) B ₁ =0.906 (0.549, 1.263) B ₂ =0.111 (0.061, 0.161) B ₃ =-0.031 (-0.051, -0.011) B ₄ =0.015 (0.009, 0.021) B ₅ =-0.509 (-0.713, -0.306) B ₆ =0.158 (0.052, 0.264) v=0.043 (0.007, 0.079)

	exp(pctgrass41.4) + Species2 + edge41.4 + nest age + year + exp(pctgrass41.4) *year	10,462.9	14	1.7	0.22	B ₀ =1.807 (1.163, 2.451) B ₁ =0.884 (0.529, 1.239) B ₂ =-0.073 (-0.570, 0.423) B ₃ =0.199 (0.042, 0.357) B ₄ =-0.268 (-1.121, 0.584) B ₅ =-0.032 (-0.192, 0.129) B ₆ =-0.089 (-0.243, 0.065) B ₇ =0.096 (-0.104, 0.295) B ₈ =-0.030 (-0.050, -0.010) B ₉ =0.003 (-0.005, 0.011) B ₁₀ =0.015 (0.009, 0.021) B ₁₁ =-0.534 (-0.750, -0.318) B ₁₂ =0.127 (-0.019, 0.274) v=0.042 (0.007, 0.078)
A priori fixed effect 64.7 -square km scale	exp(pctgrass64.7) + Species + edge64.7 + nest age + year	10,565.6	11	0	0.61	B ₀ =1.705 (1.442, 1.967) B ₁ =1.025 (0.868, 1.181) B ₂ =-0.075 (-0.550, 0.400) B ₃ =0.148 (0.004, 0.293) B ₄ =0.044 (-0.753, 0.841) B ₅ =-0.093 (-0.242, 0.056) B ₆ =-0.162 (-0.305, -0.020) B ₇ =0.005 (-0.179, 0.188) B ₈ =-0.022 (-0.027, -0.017) B ₉ =0.017 (0.012, 0.022) B ₁₀ =-0.196 (-0.236, -0.156)

	pctgrass64.7 + Species + edge64.7 + nest age + year	10,566.7	11	1.1	0.35	$B_0=2.508$ (2.273, 2.743) $B_1=1.863$ (1.577, 2.148) $B_2=-0.058$ (-0.532, 0.416) $B_3=0.157$ (0.014, 0.301) $B_4=-0.006$ (-0.793, 0.780) $B_5=-0.088$ (-0.236, 0.060) $B_6=-0.155$ (-0.296, -0.013) $B_7=0.012$ (-0.171, 0.194) $B_8=-0.022$ (-0.027, -0.017) $B_9=0.017$ (0.012, 0.023) $B_{10}=-0.195$ (-0.236, -0.155)
A priori fixed and random effects 64.7 - square km scale	exp(pctgrass64.7) + Species + edge64.7 + nest age + year	10,471.7	12	0	0.42	$B_0=1.586$ (0.835, 2.337) $B_1=1.016$ (0.579, 1.453) $B_2=-0.010$ (-0.516, 0.497) $B_3=0.203$ (0.047, 0.359) $B_4=-0.358$ (-1.194, 0.479) $B_5=-0.032$ (-0.191, 0.127) $B_6=-0.079$ (-0.231, 0.073) $B_7=0.100$ (-0.098, 0.298) $B_8=-0.020$ (-0.034, -0.006) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.214$ (-0.258, -0.170) $v=0.048$ (0.009, 0.088)

	pctgrass64.7 + Species + edge64.7 + nest age + year	10,471.9	12	0.2	0.38	$B_0=2.455$ (1.836, 3.075) $B_1=1.874$ (1.074, 2.674) $B_2=-0.067$ (-0.569, 0.434) $B_3=0.191$ (0.033, 0.350) $B_4=-0.242$ (-1.100, 0.615) $B_5=-0.042$ (-0.203, 0.119) $B_6=-0.090$ (-0.245, 0.064) $B_7=0.088$ (-0.112, 0.288) $B_8=-0.022$ (-0.036, -0.008) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.214$ (-0.259, -0.171) $v=0.048$ (0.009, 0.087)
	ln(pctgrass64.7) + Species + edge64.7 + nest age + year	10,473.7	12	2.0	0.15	$B_0=4.064$ (3.138, 4.990) $B_1=0.946$ (0.513, 1.380) $B_2=-0.054$ (-0.555, 0.447) $B_3=0.198$ (0.041, 0.356) $B_4=-0.281$ (-1.131, 0.568) $B_5=-0.038$ (-0.198, 0.123) $B_6=-0.083$ (-0.237, 0.071) $B_7=0.093$ (-0.106, 0.292) $B_8=-0.021$ (-0.036, -0.006) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.214$ (-0.258, -0.170) $v=0.054$ (0.011, 0.097)

Exploratory fixed and random effects 64.7 -square km scale	exp(pctgrass64.7) + Species + edge64.7 + nest age + year + exp(pctgrass64.7) *year	10,471.5	13	0	0.27	B ₀ =1.659 (0.991, 2.406) B ₁ =0.999 (0.565, 1.433) B ₂ =-0.096 (-0.593, 0.400) B ₃ =0.195 (0.036, 0.353) B ₄ =-0.219 (-1.079, 0.640) B ₅ =-0.040 (-0.201, 0.122) B ₆ =-0.091 (-0.246, -0.063) B ₇ =0.088 (-0.112, 0.289) B ₈ =-0.020 (-0.034, -0.007) B ₉ =0.015 (0.009, 0.021) B ₁₀ =-0.382 (-0.622, -0.142) B ₁₁ =0.091 (-0.037, 0.218) v=0.048 (0.009, 0.086)
	exp(pctgrass64.7) + Species + edge64.7 + nest age + year + exp(pctgrass64.7) *year + edge64.7*year	10,472.4	14	0.9	0.17	B ₀ =1.609 (0.853, 2.364) B ₁ =1.046 (0.607, 1.485) B ₂ =-0.005 (-0.516, 0.507) B ₃ =0.184 (0.026, 0.342) B ₄ =-0.256 (-1.114, 0.601) B ₅ =-0.050 (-0.211, 0.111) B ₆ =-0.103 (-0.258, 0.052) B ₇ =0.079 (-0.121, 0.279) B ₈ =-0.021 (-0.035, -0.007) B ₉ =0.015 (0.009, 0.021) B ₁₀ =-0.427 (-0.675, -0.180) B ₁₁ =0.044 (-0.128, 0.216) B ₁₂ =0.003 (-0.003, 0.008) v=0.049 (0.008, 0.089)

	exp(pctgrass64.7) + Species2 + edge64.7 + nest age + year + exp(pctgrass64.7) *year	10,472.7	8	1.2	0.15	B ₀ =1.703 (0.954, 2.451) B ₁ =1.025 (0.584, 1.466) B ₂ =0.110 (0.061, 0.161) B ₃ =-0.021 (-0.035, -0.007) B ₄ =0.015 (0.009, 0.021) B ₅ =-0.385 (-0.625, -0.144) B ₆ =-0.092 (-0.035, 0.220) v=0.050 (0.009, 0.090)
	exp(pctgrass64.7) + Species2 + edge64.7 + nest age + year	10,473.0	7	1.5	0.13	B ₀ =1.687 (0.941, 2.433) B ₁ =1.035 (0.596, 1.474) B ₂ =0.110 (0.060, 0.159) B ₃ =-0.021 (-0.035, -0.007) B ₄ =0.015 (0.009, 0.021) B ₅ =-0.214 (-0.258, -0.170) v=0.049 (0.009, 0.089)

	exp(pctgrass64.7) + Species + edge64.7 + ln(wetcount64.7) + nest age + year	10,473.4	13	1.9	0.10	$B_0=1.573$ (0.811, 2.334) $B_1=0.895$ (0.396, 1.394) $B_2=-0.121$ (-0.617, 0.375) $B_3=0.186$ (0.027, 0.346) $B_4=-0.169$ (-1.039, 0.701) $B_5=-0.047$ (-0.209, 0.115) $B_6=-0.094$ (-0.250, 0.062) $B_7=0.087$ (-0.115, 0.288) $B_8=-0.013$ (-0.035, 0.008) $B_9=-0.274$ (-0.909, 0.360) $B_{10}=0.015$ (0.009, 0.021) $B_{11}=-0.215$ (-0.259, -0.171) $v=0.046$ (0.008, 0.085)
	exp(pctgrass64.7) + Species + edge64.7 + ln(wetcount64.7) + nest age + year	10,473.4	13	1.9	0.10	$B_0=1.848$ (0.488, 3.207) $B_1=1.006$ (0.483, 1.528) $B_2=-0.109$ (-0.606, 0.388) $B_3=0.187$ (0.027, 0.346) $B_4=-0.173$ (-1.043, 0.696) $B_5=-0.047$ (-0.209, 0.115) $B_6=-0.095$ (-0.251, 0.060) $B_7=0.081$ (-0.120, 0.282) $B_8=-0.020$ (-0.035, -0.005) $B_9=-0.075$ (-0.349, 0.199) $B_{10}=0.015$ (0.009, 0.021) $B_{11}=-0.215$ (-0.259, -0.171) $v=0.046$ (0.008, 0.085)

A priori fixed effect 93.2-square km scale	pctgrass93.2 + Species + edge93.2 + nest age + year	10,599.6	11	0	0.32	B ₀ =2.482 (2.242, 2.723) B ₁ =1.798 (1.495, 2.102) B ₂ =0.019 (-0.463, 0.502) B ₃ =0.170 (0.029, 0.311) B ₄ =-0.124 (-0.886, 0.639) B ₅ =-0.082 (-0.227, 0.064) B ₆ =-0.147 (-0.286, -0.008) B ₇ =0.015 (-0.165, 0.195) B ₈ =-1.522 (-1.892, -1.153) B ₉ =0.018 (0.013, 0.023) B ₁₀ =-0.191 (-0.231, -0.150)
	ln(pctgrass93.2) + Species + edge93.2 + nest age + year	10,600.6	11	1	0.19	B ₀ =4.031 (3.676, 4.387) B ₁ =0.853 (0.711, 0.996) B ₂ =0.057 (-0.422, 0.536) B ₃ =0.193 (0.054, 0.333) B ₄ =-0.232 (-0.975, 0.512) B ₅ =-0.075 (-0.218, 0.069) B ₆ =-0.129 (-0.266, 0.008) B ₇ =0.033 (-0.145, 0.212) B ₈ =-1.534 (-1.904, -1.164) B ₉ =0.018 (0.013, 0.024) B ₁₀ =-0.190 (-0.230, -0.150)

	$\ln(\text{pctgrass}_{93.2}) +$ $\text{edge}_{93.2} + \text{edge}_{93.2}^2$ $+ \text{patchden}_{93.2} +$ $\text{patchden}_{93.2}^2 +$ $\ln(\text{building}_{93.2}) +$ $\text{nest age} + \text{year}$	10,600.9	9	1.3	0.17	$B_0=7.945 (6.474, 9.416)$ $B_1=1.419 (1.036, 1.802)$ $B_2=-10.805 (-14.523, -7.087)$ $B_3=6.079 (3.757, 8.397)$ $B_4=0.081 (-0.243, 0.405)$ $B_5=-0.007 (-0.059, 0.046)$ $B_6=0.310 (0.193, 0.427)$ $B_7=0.018 (0.012, 0.023)$ $B_8=-0.198 (-0.238, -0.158)$
	$\ln(\text{pctgrass}_{93.2}) +$ $\text{Habclass} +$ $\ln(\text{edge}_{93.2}) + \text{nest}$ $\text{age} + \text{year}$	10,601.0	13	1.4	0.16	$B_0=2.533 (2.288, 2.779)$ $B_1=0.961 (0.807, 1.115)$ $B_2=0.134 (-0.083, 0.352)$ $B_3=0.149 (-0.156, 0.455)$ $B_4=0.096 (-0.176, 0.367)$ $B_5=-1.231 (-2.721, 0.259)$ $B_6=0.033 (-0.327, 0.393)$ $B_7=0.496 (-0.129, 1.120)$ $B_8=-0.095 (-0.311, 0.120)$ $B_9=0.315 (0.042, 0.588)$ $B_{10}=-1.227 (-1.494, -0.960)$ $B_{11}=0.018 (0.013, 0.023)$ $B_{12}=-0.196 (-0.237, -0.156)$

	$\ln(\text{pctgrass}_{93.2}) +$ $\text{edge}_{93.2} + \text{edge}_{93.2}^2$ $+ \text{patchden}_{93.2} +$ $\text{patchden}_{93.2}^2 +$ $\ln(\text{building}_{93.2}) +$ $\ln(\text{juliandate}) + \text{nest}$ $\text{age} + \text{year}$	10,601.6	10	2.0	0.12	$B_0=7.808 (6.320, 9.297)$ $B_1=1.419 (1.037, 1.802)$ $B_2=-10.894 (-14.613, -7.175)$ $B_3=6.145 (3.823, 8.467)$ $B_4=0.064 (-0.262, 0.390)$ $B_5=-0.004 (-0.056, 0.048)$ $B_6=0.306 (0.189, 0.423)$ $B_7=0.054 (-0.040, 0.148)$ $B_8=0.016 (0.011, 0.022)$ $B_9=-0.202 (-0.243, -0.161)$
A priori fixed and random effects 93.2-square km scale	$\text{pctgrass}_{93.2} + \text{Species}$ $+ \text{edge}_{93.2} + \text{nest age}$ $+ \text{year}$	10,475.7	12	0	0.27	$B_0=2.445 (1.737, 3.152)$ $B_1=1.823 (0.869, 2.776)$ $B_2=-0.004 (-0.511, 0.502)$ $B_3=0.205 (0.049, 0.360)$ $B_4=-0.374 (-1.208, 0.460)$ $B_5=-0.029 (-0.188, 0.129)$ $B_6=-0.076 (-0.228, 0.076)$ $B_7=0.102 (-0.095, 0.300)$ $B_8=-1.516 (-2.693, -0.339)$ $B_9=0.015 (0.009, 0.021)$ $B_{10}=-0.214 (-0.258, -0.170)$ $v=0.062 (0.012, 0.112)$

	ln(pctgrass93.2) + Species + edge93.2 + nest age + year	10,475.8	12	0.1	0.24	$B_0=4.067$ (3.044, 5.090) $B_1=0.895$ (0.422, 1.368) $B_2=-0.002$ (-0.508, 0.504) $B_3=0.206$ (0.051, 0.361) $B_4=-0.380$ (-1.213, 0.453) $B_5=-0.029$ (-0.187, 0.130) $B_6=-0.075$ (-0.227, 0.076) $B_7=0.103$ (-0.094, 0.301) $B_8=-1.539$ (-2.739, -0.340) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.214$ (-0.258, -0.170) $v=0.063$ (0.013, 0.113)
	exp(pctgrass93.2) + Species + edge93.2 + nest age + year	10,476.4	12	0.7	0.18	$B_0=1.704$ (0.806, 2.602) $B_1=0.971$ (0.434, 1.508) $B_2=-0.005$ (-0.512, 0.502) $B_3=0.204$ (0.048, 0.360) $B_4=-0.371$ (-1.206, 0.464) $B_5=-0.030$ (-0.189, 0.129) $B_6=-0.077$ (-0.229, 0.075) $B_7=0.102$ (-0.096, 0.300) $B_8=-1.457$ (-2.649, -0.266) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.214$ (-0.258, -0.170) $v=0.065$ (0.013, 0.117)

	ln(pctgrass93.2) + species + patchden93.2 +nest age + year	10,477.3	12	1.6	0.12	$B_0=3.140$ (2.722, 3.558) $B_1=0.312$ (-0.134, 0.758) $B_2=-0.006$ (-0.513, 0.501) $B_3=0.204$ (0.048, 0.360) $B_4=-0.380$ (-1.213, 0.454) $B_5=-0.029$ (-0.187, 0.130) $B_6=-0.076$ (-0.228, 0.076) $B_7=0.108$ (-0.090, 0.305) $B_8=-0.196$ (-0.372, -0.020) $B_9=0.015$ (0.009, 0.021) $B_{10}=-0.215$ (-0.259, -0.171) $v=0.069$ (0.015, 0.123)
Exploratory fixed and random effects 93.2-square km scale	exp(pctgrass93.2) + species + edge93.2 +edge93.2 *year + nest age + year	10,475.7	13	0	0.28	$B_0=1.711$ (0.809, 2.612) $B_1=0.980$ (0.441, 1.520) $B_2=0.008$ (-0.499, 0.514) $B_3=0.203$ (0.048, 0.359) $B_4=-0.372$ (-1.203, 0.460) $B_5=-0.032$ (-0.191, 0.126) $B_6=-0.081$ (-0.233, 0.071) $B_7=0.101$ (-0.096, 0.299) $B_8=-1.487$ (-2.684, -0.289) $B_9=0.269$ (-0.040, 0.578) $B_{10}=0.015$ (0.009, 0.021) $B_{11}=-0.396$ (-0.609, -0.183) $v=0.066$ (0.014, 0.118)

	exp(pctgrass93.2) + species + edge93.2 +edge93.2 *year + exp(pctgrass93.2) *year + nest age + year	10,476.3	14	1.2	0.16	$B_0=1.695$ (0.791, 2.599) $B_1=0.994$ (0.452, 1.535) $B_2=0.011$ (-0.495, 0.517) $B_3=0.202$ (0.047, 0.357) $B_4=-0.373$ (-1.203, 0.457) $B_5=-0.034$ (-0.193, 0.124) $B_6=-0.081$ (-0.233, 0.071) $B_7=0.104$ (-0.094, 0.301) $B_8=-1.500$ (-2.701, -0.299) $B_9=0.377$ (-0.033, 0.787) $B_{10}=-0.075$ (-0.263, 0.112) $B_{11}=0.015$ (0.009, 0.021) $B_{12}=-0.333$ (-0.598, -0.067) $v=0.066$ (0.014, 0.119)
	pctgrass93.2 + Species2 + edge93.2 + nest age + year	10,476.9	7	1.8	0.11	$B_0=2.534$ (1.837, 3.236) $B_1=1.841$ (0.884, 2.798) $B_2=0.110$ (0.060, 0.159) $B_3=-1.530$ (-2.712, -0.348) $B_4=0.015$ (0.009, 0.021) $B_5=-0.214$ (-0.258, -0.170) $v=0.063$ (0.013, 0.113)

	ln(pctgrass93.2) + Species2 + edge93.2 + nest age + year	10,476.9	7	1.8	0.11	B ₀ =4.204 (3.187, 5.220) B ₁ =0.910 (0.436, 1.384) B ₂ =0.110 (0.060, 0.160) B ₃ =-1.588 (-2.789, -0.386) B ₄ =0.015 (0.009, 0.021) B ₅ =-0.214 (-0.258, -0.170) v=0.063 (0.013, 0.113)
Exploratory fixed and random effects Multi-scale	exp(pctgrass41.4) + species + ln(wetcount10.4) + exp(building10.4) + nest age + year + edge10.4 + edge10.4 ² + exp(pctgrass41.4)*year + exp(building10.4)*year	10,428.0	17	0	0.45	B ₀ =2.565 (2.377, 2.753) B ₁ =0.682 (0.330, 1.033) B ₂ =-0.0033 (-0.512, 0.506) B ₃ =0.225 (-0.069, 0.381) B ₄ =-0.4229 (-1.264, 0.418) B ₅ =-0.034 (-0.1929, 0.126) B ₆ =-0.066 (-0.2189, 0.086) B ₇ =0.115 (-0.084, 0.313) B ₈ =-0.639 (-1.013, -0.265) B ₉ =2.402 (-1.286, 6.090) B ₁₀ =0.015 (0.009, 0.020) B ₁₁ =-0.1735 (0.220, -0.127) B ₁₂ =-0.401 (-0.694, -0.109) B ₁₃ =0.022 (0.005, 0.039) B ₁₄ =0.357 (0.226, 0.488) B ₁₅ =4.260 (2.607, 5.9124) v=0.019 (0.000, 0.039)

	exp(pctgrass41.4) + species + ln(wetcount10.4) + exp(building10.4) + year + nest age + edge10.4 + edge10.4 ² + exp(pctgrass41.4)*year + exp(building41.4)*year + edge41.4	10,428.3	18	0.3	0.39	B ₀ =0.330 (-4.169, 4.828) B ₁ =0.784 (0.390, 1.178) B ₂ =-0.049 (-0.553, 0.456) B ₃ =0.219 (0.061, 0.377) B ₄ =-0.333 (-1.189, 0.524) B ₅ =-0.043 (-0.203, 0.118) B ₆ =-0.077 (-0.231, 0.078) B ₇ =0.103 (-0.098, 0.302) B ₈ =-0.496 (-0.917, -0.075) B ₉ =2.055 (-1.496, 5.606) B ₁₀ =0.015 (0.009, 0.020) B ₁₁ =-5.316 (-7.211, -3.420) B ₁₂ =-0.419 (-0.699, -0.140) B ₁₃ =0.024 (0.008, 0.040) B ₁₄ =0.356 (0.225, 0.488) B ₁₅ =4.218 (2.565, 5.871) B ₁₆ =-0.016 (-0.040, 0.008) v=0.016 (0.000, 0.035)
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	exp(pctgrass41.4) + species2 + ln(wetcount10.4) + exp(building10.4) + year + nest age + edge10.4 + edge10.4 ² + exp(pctgrass41.4)*year + exp(building10.4)*year	10,430.0	12	2.0	0.16	B ₀ =0.771 (-4.036, 5.578) B ₁ =0.645 (0.288, 1.002) B ₂ =0.117 (0.067, 0.167) B ₃ =-0.649 (-1.024, -0.273) B ₄ =1.422 (-2.342, 5.186) B ₅ =-5.469 (-7.360, -3.577) B ₆ =0.015 (0.009, 0.020) B ₇ =-0.443 (-0.738, -0.148) B ₈ =0.024 (0.007, 0.042) B ₉ =0.361 (0.230, 0.492) B ₁₀ =4.355 (2.706, 6.004) v=0.020 (0.000, 0.040)
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