

LANDSCAPE COMPOSITION, PATCH SIZE, AND DISTANCE TO EDGES: INTERACTIONS AFFECTING DUCK REPRODUCTIVE SUCCESS

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Abstract. Prairies and other North American grasslands, although highly fragmented, provide breeding habitat for a diverse array of species, including species of tremendous economic and ecological importance. Conservation and management of these species requires some understanding of how reproductive success is affected by edge effects, patch size, and characteristics of the landscape. We examined how differences in the percentage of grassland in the landscape influenced the relationships between the success of nests of upland-nesting ducks and (1) field size and (2) distance to nearest field and wetland edges. We collected data on study areas composed of 15–20% grassland and areas composed of 45–55% grassland in central North Dakota, USA during the 1996 and 1997 nesting seasons. Daily survival rates (DSRs) of duck nests were greater in study areas with 45–55% grassland than with 15–20% grassland. Within study areas, we detected a curvilinear relationship between DSR and field size: DSRs were highest in small and large fields and lowest in moderately sized fields. In study areas with 15–20% grassland, there was no relationship between probability of hatching and distance to nearest field edge, whereas in study areas with 45–55% grassland, there was a positive relationship between these two variables. Results of this study support the conclusion that both landscape composition and configuration affect reproductive success of ground-nesting birds. We are prompted to question conservation strategies that favor clustering moderately sized patches of nesting habitat within agricultural landscapes because our results show that such patches would have low nest success, most likely caused by predation. Understanding the pattern of nest success, and the predator–prey mechanisms that produce the pattern, will enable design of patch configurations that are most conducive to meeting conservation goals.

Key words: ducks; edge effects; field size; habitat fragmentation; landscape composition; nest success; North Dakota; patch size; Prairie Pothole Region.

INTRODUCTION

Prairies are among North America's most endangered ecosystems (Samson and Knopf 1996). Where conditions have favored conversion to cropland, grassland habitat has been lost and fragmented, and most of the remaining grassland is managed for economic gain as pasture or hay land (Batt 1996). Rivers, streams, and pothole wetlands augment the biological diversity of the prairie ecosystem (Samson and Knopf 1996, Knopf and Samson 1997). Despite having undergone tremen-

dous habitat losses due to drainage and conversion to agriculture, the Prairie Pothole Region (PPR) of the Northern Great Plains remains one of the most important regions of North America for migratory birds, mammals, and wetland invertebrates (McCrary et al. 1986, Johnson et al. 1994, Batt 1996, Samson and Knopf 1996, Guntenspergen et al. 2002). The PPR is an especially important area for waterfowl recruitment, producing ~50–80% of the continent's duck populations (Cowardin et al. 1983, Batt et al. 1989), and providing breeding habitat for more than half of the total number of grassland bird species breeding in North America (Knopf 1996).

Landscape effects, such as habitat fragmentation and changing land-use patterns, have important implications for planning bird species conservation. An important research priority for migratory birds is identifying "habitats and landscapes that promote high survival or reproduction" (Donovan et al. 2002). In the

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PPR, one approach is to prioritize conservation in regions such as the Missouri Coteau in North and South Dakota, protecting as much habitat as possible where remaining grassland exceeds 70% of the landscape (Stephens 2003). This approach is justified by the observation that overall abundance of birds and reproductive success is greatest in such regions (Reynolds et al. 2001, Herkert et al. 2003, Stephens 2003). Conservation, however, also depends on understanding the processes that affect vital rates within landscapes of differing composition (Wiens et al. 1993), so that wildlife ecologists can devise solutions for finer scale applications in counties or townships. These processes have produced a variety of fine-scale patterns in abundance and vital rates of ground-nesting migratory birds (Greenwood et al. 1995, Krapu et al. 1997, Pasitschniak-Arts et al. 1998, Vickery and Herkert 1999, Sovada et al. 2000, Herkert et al. 2003, Stephens et al. 2003).

Predator-prey interactions clearly have the potential to influence vital rates. Changes in mammalian predator communities, particularly the increased distribution of mesopredators such as raccoons (*Procyon lotor*) and red fox (*Vulpes vulpes*), have accompanied habitat loss and fragmentation in the PPR (Sargeant et al. 1993). Prey species presumably have adapted through habitat and nest-site selection (e.g., Clark and Shutler 1999). Hokit and Branch (2003) reviewed literature on a variety of plant and vertebrate taxa and found that there was usually, although not always, a positive association between patch size and either reproductive success or survival. They mentioned that organisms in smaller patches may be susceptible to edge or Allee effects. Associations with patch size, observed in the form of reproductive success or adult survival, may result in fitness trade-offs when patterns affecting reproduction and survival are not consistent (e.g., Spencer 2002). For example, in some systems there is a bimodal distribution of nest success across patch sizes (Clark et al. 1999), best modeled with a curvilinear relationship predicting lower nest success at intermediate patch sizes. Clark and Nudds (1991) speculated about such a pattern in duck nesting success due to functional and numerical responses of predators, and we suspected that nest success in very small patches might be higher simply because predators do not focus activity therein (Kuehl and Clark 2002). At a larger spatial scale, nest predation may be affected by landscape structure or management (e.g., Penteriani et al. 2002, Rodewald 2002, Luck 2003). The interactions among predator abundance, reproductive success, edge effects, and landscape features are complex, however, making generalizations difficult (Andr n 1995, Oehler and Litvaitis 1996, Donovan et al. 1997, Tewksbury et al. 1998, Lahti 2001, Chalfoun et al. 2002).

In the PPR, research attention has turned recently to landscape composition, grassland patch size and configuration, and edge effects, following demonstrations

of their possible importance to bird population vital rates in other systems. Although numerous studies have examined the relationships predicted from other systems, results from studies of ducks have been inconsistent (Clark and Nudds 1991). Some studies found greater nest success or productivity in large patches compared to smaller patches or strip habitats (Krasowski and Nudds 1986, Klett et al. 1988, Kantrud 1993, Ball et al. 1995, Greenwood et al. 1995), whereas others have found no relationship between nest success and patch size (reanalysis of Duebbert and Lokemoen [1976] by Clark and Nudds [1991]), or little evidence of a patch size effect after other variables, such as year and date of nest initiation, were considered (Sovada et al. 2000).

Results of studies examining the relationship between distance to edges and nest success likewise have been inconsistent. Using artificial duck nests, Pasitschniak-Arts and Messier (1995, 1996) found positive relationships between probability of hatching and distance to nearest field edge. A study of natural nests by Pasitschniak-Arts et al. (1998), however, found little evidence that the probability of a nest hatching was influenced by distance to nearest habitat ecotone, wetland edge, or road edge.

Studies of effects of landscape composition on nest success in the PPR have been few. Greenwood et al. (1995) and Reynolds et al. (2001) reported that nest success of ducks was positively correlated with the amount of grassland in the landscape. Lower nest success in landscapes with less grassland may be the result of different predator communities (Johnson et al. 1989, Sargeant et al. 1993, Sovada et al. 1995, 2001). For example, coyotes (*Canis latrans*) were associated with landscapes with large amounts of grassland in a study by Greenwood et al. (1995), whereas Sovada et al. (2000) detected greater levels of red fox activity in smaller fields. Red fox, a major nest predator, tends to be displaced by coyotes (Sargeant 1972, Sargeant et al. 1984), and nest success is greater in landscapes where coyotes are present (Sovada et al. 1995). Thus, with increased grassland loss and fragmentation, we should expect decreased nest success.

In this study we examined the interactions among landscape composition, patch size, edges, duck nests, and predators. We focused on understanding how the amount of grassland in the landscape influenced duck nest success among fields of varying size and distances to edges. Specifically, in study areas that varied in their amount of grassland, we examined the relationships between: (1) daily survival rate (DSR) and field size, and (2) probability of hatching and distance to nearest field and wetland edges. We predicted that relationships between nest success and field size, and probability of hatching and distance to nearest edges, would be most apparent in landscapes with lower amounts of grassland (McLellan et al. 1986, Fahrig 1998), as a result of changes in predator-prey relationships in different

TABLE 1. Percentage habitat composition for study areas in central North Dakota, USA, during the 1996 and 1997 breeding seasons.

Study area [†]	Planted cover [‡]	Hay land	Pastureland	Wetland [§]	Cropland	Other
Low grassland						
Litchville	12.5	0.3	2.3	11.6	66.9	6.4
Bowdon	13.8	3.2	2.7	18.5	56.4	5.4
High grassland						
Medina	22.1	4.1	19.0	13.4	34.3	7.1
Hurdsfield	22.5	1.5	27.8	21.2	23.0	4.0

[†] The low-grassland study area was located in Litchville (Svea Township in Barnes County) in 1996, and in Bowdon (Berlin Township in Wells County) in 1997. The high-grassland study area was located in Medina (Iosco Township in Stutsman County) in 1996, and Hurdsfield (Silver Lake Township in Wells County) in 1997.

[‡] Planted cover comprised Conservation Reserve Program, Water Bank Program, and Waterfowl Production Area habitat.

[§] Temporary and seasonal wetlands (Stewart and Kantrud 1971) were the most common wetland types in our study areas.

landscapes. Although this paper focuses on nest success, our study was accompanied by intensive study of predators (Phillips et al. 2003, 2004) that helped to explain the patterns that we observed.

METHODS

Study areas

This study was conducted in the PPR of central North Dakota, USA during the 1996 and 1997 waterfowl breeding seasons. Each year, we selected two 6.4×6.4 km areas of different landscape composition so that, over two years, we had two study areas of each type (Phillips et al. 2003). One landscape type, called low-grassland composition, contained 15–20% grassland. The remaining cover types were primarily wetland and cropland such as wheat, sunflower, canola, corn, and soybeans (Table 1). The other landscape type, called high-grassland composition, contained 45–55% grassland and 45–55% other habitat (Table 1). The low-grassland study areas were in areas where cultivation is common because of level topography and productive soil, whereas the high-grassland study areas were in areas with rolling stagnation moraine (Bryce et al. 1998). Fields that we collectively refer to as planted cover were primarily enrolled in the U.S. Department of Agriculture (USDA) Conservation Reserve Program (CRP), the USDA Water Bank Program (WBP), and U.S. Fish and Wildlife Service (USFWS) Waterfowl Production Areas (WPA). The high-grassland study areas contained greater amounts of planted cover compared to the low-grassland study areas and also contained larger amounts of other perennial grassland habitat, particularly hay land and pastureland (Table 1).

In 1996, we selected the 6.4×6.4 km study areas using habitat composition information from 10.4-km² plots used by the USFWS for breeding duck surveys (Cowardin et al. 1995). In 1997, we used data from Landsat Thematic Mapper images in a Geographic Information System (GIS) to identify study areas with habitat compositions similar to those in 1996. We used

aerial videography to record cover types for each landscape, digitized coverages for use in a GIS using Map and Imaging Processing Software (MicroImages, Lincoln, Nebraska, USA), and verified cover type identity by ground checks. We obtained wetland data from the National Wetlands Inventory (USFWS, St. Petersburg, Florida, USA) and digital road data from the U.S. Geological Survey.

Field and edge definitions

The Missouri Coteau and drift plain regions of North Dakota are both characterized by a diversity of wetlands (Stewart and Kantrud 1971), with distinct patches of perennial grasslands (primarily rectangular or square) surrounded by small-grain crop agriculture (Sovada et al. 2000, Phillips et al. 2003). We defined habitat patches to reflect how patches are likely to be perceived and used by nest predators (Phillips et al. 2003). Patches of perennial grassland were bordered by other habitat classes such as cropland or roads. Thus, CRP patches divided by a paved or gravel road (hard edges) were considered to be different patches. Wetlands were within a patch or served as a patch border. Fencerows and unmaintained dirt roads were considered within-patch features (soft edges) and were not used to divide patches of perennial grassland (i.e., CRP land containing a fencerow was considered a single patch). We considered perennial grasslands, pasturelands, and hay lands to be a distinct habitat from planted cover because of differences in vegetation height, density, and disturbance. Throughout the paper, we refer to each patch of planted cover where we searched for duck nests as a field.

We defined field edge as the boundary where a planted-cover field adjoins a different habitat type (e.g., cropland, wetland, hay land, or pastureland), or a paved or gravel road, creating a hard edge. Predators recognize the edges of croplands, wetlands, and gravel roads (Phillips et al. 2003). We did not consider fencerows

and unmaintained dirt roads, which are more or less vegetated, to be field edges.

Duck nest data collection

Each year, we searched for duck nests in most of the duck-nesting habitat within the two landscape types. We searched all portions of the CRP and WBP fields for which we had permission to search. By restricting our nest searching to CRP and WBP fields, we reduced the effect of variation in vegetation on nest success. In addition, nesting ducks prefer planted cover, such as that on CRP and WBP fields, over other habitats such as pastureland and hay land (Klett et al. 1988).

We conducted searches for duck nests with a chain dragged between two all-terrain vehicles or jeeps using procedures described by Higgins et al. (1969) and Klett et al. (1986). Nest searching took place from early May to early July. When we discovered nests, we recorded standard data, and determined the age of the clutch by candling eggs (Weller 1956). Duck nests were rechecked approximately every 10 days until their fate (e.g., hatched, destroyed by predator, abandoned due to predator, abandoned due to investigator) was determined (Klett et al. 1986). We also determined the Universal Transverse Mercator (UTM) coordinates of each duck nest with a global positioning system. Using the GIS maps and UTM coordinates of ducks nests, we determined distances from a duck nest to the nearest field and wetland edges using ArcInfo (Environmental Systems Research Institute 1994).

We estimated DSRs of duck nests for each field using methods developed by Mayfield (1975) and modified by Johnson (1979), where $DSR = 1 - (\text{total number of nests where failure was attributed to predators/exposure days})$. Nests of all species were pooled within each field to increase precision of estimates. The species within the guild of upland-nesting waterfowl have somewhat different nesting chronology and microhabitat preferences. However, we found nests of all species intermingled in space and time, and in our study, 95% confidence limits of Mayfield hatch rates for the five most abundant duck species, Blue-winged Teal, Gadwall, Mallard, Northern Pintail, and Northern Shoveler, were overlapping in both 1996 and 1997, with minor exceptions (D. J. Horn, *unpublished data*). Moreover, by including explanatory variables such as date of nest initiation and distance to nearest wetland edge, which differ among species, some portion of any species effect would be taken into account. Thus, we feel that pooling was appropriate, and by pooling we were able to obtain robust estimates of DSR and standard error. Because of this pooling, though, inferences apply generally to ducks in the study region, not to individual species.

Statistical analyses

We constructed a series of general linear models to examine variation in arcsine-transformed DSR of nests

among fields within landscape types. In this analysis, the sample unit for DSR was a field within a 41-km² landscape. Explanatory variables included year, landscape type, log of field size, (log field size)², interaction between landscape type and log of field size, and interaction between landscape type and (log field size)² (Zar 1984). We used the log of field size because we examined the effects over a wide range of field sizes. We included the quadratic term, (log field size)², because we wanted to model the possibility that there might be a curvilinear relationship as suggested by both nest success and predator activity studies (Clark and Nudds 1991, Phillips et al. 2003). DSRs were weighted by the number of exposure days for each field (Klett et al. 1988). Therefore, an observation's contribution in the analysis was equal to the number of exposure days for that observation, divided by the total number of exposure days from all observations. We examined a limited set of models in a model selection framework using Akaike Information Criterion (AIC) values (Burnham and Anderson 1998). Models with $\Delta AIC < 2$ were considered equally plausible models of the data (Burnham and Anderson 1998). The model set was (1) log of field size, (2) log of field size and (log field size)², and (3) four additional models that included the best of these two initial models with various combinations of year, landscape type, and two-way interactions between landscape type and the two field size variables. We did not examine the landscape type by year interaction because it was confounded with our four study areas. Data were analyzed using PROC REG in the SAS statistical package (SAS Institute 1999).

We examined the effects of the position of individual nests within fields using logistic regression to model success or failure (i.e., probability of an individual duck nest hatching). We focused a priori on the main effects of interest, which included landscape type and distance of the nest to the nearest field or wetland edge. We included the date of nest initiation, years, and exposure days in models to account for the chronology of nesting, potential yearly variation in conditions, and the fact that nests are discovered at various stages of incubation before we could observe the success or failure outcome. We included potential interactions between landscape type and distance to nearest field and wetland edge, and between date of nest initiation and distance to nearest edge, year, and exposure days. We used the stepwise method in PROC LOGISTIC (Stokes et al. 1995, SAS Institute 1999) to reduce the number of candidate models, and we used AIC values to select among candidate models. If an interaction was detected between landscape type and distance to edge, we further modeled the relationship between probability of success and distance to edge within each landscape type. We report only the detailed results for the best four candidate models.

TABLE 2. Mean daily survival rate (DSR) of duck nests ($n = 1625$ duck nests) for study areas in central North Dakota during the 1996 and 1997 breeding seasons.

Study area	Year	No. fields sampled	No. nests/field		DSR of duck nests		
			Mean	SD	Mean [†]	95% CI	SD
Low grassland							
Litchville	1996	12	23	36	0.91	0.90–0.93	0.35
Bowdon	1997	12	33	50	0.92	0.91–0.93	0.26
High grassland							
Medina	1996	10	74	107	0.96	0.94–0.97	0.60
Hurdsfield	1997	7	32	23	0.93	0.90–0.95	0.52

[†] Mean DSR of duck nests among fields, weighted by the number of exposure days in each field.

RESULTS

We searched 41 fields ranging from 2 ha to 606 ha. In the low-grassland study areas, we searched 12 fields in both 1996 and 1997, comprising 1083 ha (range 2–192 ha, median 24 ha). In the high-grassland study areas, we searched 10 fields in 1996 and seven fields in 1997, comprising 2681 ha (range 4–606 ha, median 66 ha). Overall, we found 1810 duck nests of nine species: Blue-winged Teal (*Anas discors*; $n = 572$ nests), Gadwall (*A. strepera*; $n = 509$), Mallard (*A. platyrhynchos*; $n = 363$), Northern Pintail (*A. acuta*; $n = 174$), Northern Shoveler (*A. clypeata*; $n = 111$), American Wigeon (*A. americana*; $n = 32$), Green-winged Teal (*A. crecca*; $n = 22$), Lesser Scaup (*Aythya affinis*; $n = 17$), Redhead (*Aythya americana*; $n = 4$), and unknown ($n = 6$ nests). Of the 1810 duck nests, 1625 nests were included in analyses of DSR and patch size (Appendix), and 1423 nests were included in analyses of probability of hatching and distance to nearest edges. Many nests were found in habitats not used in the analyses, were abandoned due to investigator disturbance, or were not used in the analyses because UTM coordinates were not recorded at the nest ($n = 185$ for patch size analyses and $n = 387$ for edge analyses).

On average, nesting success was greater in fields located in the high-grassland landscape in 1996, but no difference was evident in 1997 (Table 2). The multiple linear regression models that we examined to explain

DSR in fields clearly indicated that the model with log of field size and $(\log \text{ of field size})^2$ was better than the model with log of field size (Table 3). We therefore used this curvilinear relationship in subsequent models that included landscape type and year. Two models were nearly indistinguishable with regard to explaining variation in DSR of duck nests among fields, as indicated by ΔAIC values ≤ 0.02 (Table 3). The best models both included a curvilinear effect of field size and an effect of study-area type, and explained 47–50% of observed variation in DSR (Table 3, Fig. 1). The effect of year was not of specific ecological interest to us, and we therefore focused on the most parsimonious of the two models, the one without a year effect. Estimated parameters for this model are -0.226 for log field size ($\text{SE} = 0.094$, $P = 0.022$), 0.061 for $(\log \text{ field size})^2$ ($\text{SE} = 0.024$, $P = 0.014$), and 0.048 for landscape type ($\text{SE} = 0.018$, $P = 0.011$).

Logistic regression analysis of the probability of an individual duck nest hatching ($n = 1423$ nests with known UTM coordinates) and six explanatory variables (and four interaction terms) resulted in a final model with the following variables: distance to nearest field edge; interaction between landscape type and distance to nearest field edge; year; and exposure days (Table 4). Both distance to nearest field edge and landscape type were retained in all models because the preliminary analysis indicated that the interaction between these variables was important. Including the interaction

TABLE 3. Models examined to explain variation in arcsine-transformed daily survival rate of duck nests ($n = 1625$ nests) in central North Dakota during the 1996–1997 breeding seasons.

Model	R^2	AIC	ΔAIC
Log field size + $(\log \text{ field size})^2$ + landscape type + year	0.50	-4.99	0
Log field size + $(\log \text{ field size})^2$ + landscape type	0.47	-4.97	0.02
Log field size + $(\log \text{ field size})^2$ + landscape type + $(\log \text{ field size} \times \text{landscape type})$	0.52	-4.62	0.37
+ $([\log \text{ field size}]^2 \times \text{landscape type})$			
Log field size + $(\log \text{ field size})^2$ + landscape type + $(\log \text{ field size} \times \text{landscape type})$	0.54	-4.44	0.55
+ $([\log \text{ field size}]^2 \times \text{landscape type})$ + year			
Log field size + $(\log \text{ field size})^2$ + year	0.42	-0.86	4.13
Log field size + $(\log \text{ field size})^2$	0.37	0.30	5.29
Log field size	0.19	9.34	14.33

Notes: The simplest model included only the effect of field size. More complex models incorporated a quadratic effect of field size, year, landscape type (low- or high-grassland), and the interaction between field size and landscape type.

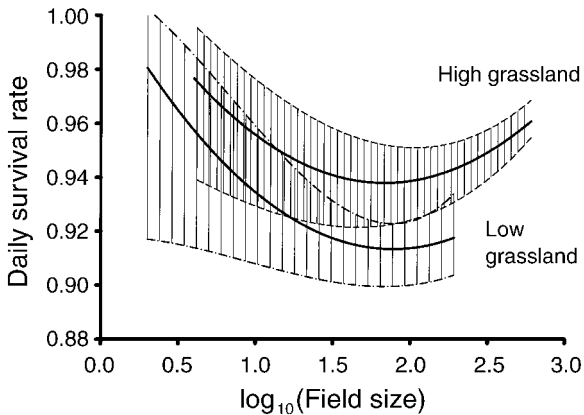


FIG. 1. Curvilinear relationships (and 95% confidence limits) between daily survival rate of duck nests ($n = 1625$ nests) and the log of field size (measured in hectares) in landscape types with high- and low-grassland composition in central North Dakota, USA, in 1996–1997.

in the final modeling step lowered the AIC value by 4, indicating that the interaction between landscape type and distance to nearest field edge was an important determinant of the probability of hatching. We found that the following factors had no effect on the probability of hatching: nest initiation date; distance to nearest wetland edge; and interactions involving nest initiation date and distance to nearest wetland edge. In study areas with high-grassland composition, we found a positive relationship between the probability of hatching and distance to nearest field edge ($P < 0.001$; Table 5, Fig. 2), whereas in study areas with low-grassland composition, we did not detect a relationship ($P = 0.580$; Table 5, Fig. 2).

The positive relationship between probability of hatching and distance to nearest field edge in high-grassland study areas was strongly influenced by nests at extreme distances from field edges. For example, of 80 nests found >400 m from the nearest field edge in high-grassland study areas, 57 (71%) hatched. Of 783 nests found <400 m from the nearest field edge, only 299 (38%) hatched. Because the greatest distance to a field edge for a nest in the low-grassland study areas was 379 m, we also examined the relationship between probability of hatching and distance to nearest field edge for nests <380 m from a field edge in the high-grassland areas; no relationship was found ($P = 0.706$).

DISCUSSION

Our findings led us to three conclusions: (1) nest success was greater in large fields than in medium-sized fields; (2) this higher nest success in high-grassland study areas may have been due to the greater probability of nests hatching when farther from field edges; and (3) the amount of perennial grassland in the landscape influenced the relationship between fate of the duck nest and distance to field edge. The relationship between nest success and field size was curvilinear: nest success was highest in small and large fields; but was lower in moderate-sized fields. In study areas with 15–20% grassland, daily survival rates of duck nests were lower, and no relationship was detected between probability of hatching and distance to nearest field edge. However, in landscapes with 45–55% grassland, daily survival rates were higher, and we detected a positive relationship between probability of hatching and distance to nearest field edge. Thus, the difference in landscape composition (15–20% grassland vs. 45–55% grassland) in this study affected edge effects, further demonstrating that landscape composition influences results of habitat fragmentation studies (Andr n 1994, Donovan et al. 1997, Howerter 2003). Given the documented importance of predation as the primary cause of nest failure in waterfowl (Sargeant and Raveling 1992, Sovada et al. 2001) and many other bird species (Newton 1998), considering the effects of predator activity on nest success is important to understanding these patterns.

The curvilinear nature of the relationship between nest success and field size is possibly due to differences in predator activity levels in patches of different sizes. Small fields may not be visited by mammalian predators, or may be searched infrequently during the breeding season. Consequently, nest success in small fields may be high, but variable. Nest success is high in large fields possibly because: (1) predators cannot effectively search the entire field, and (2) the predator community in landscapes with large fields is different from that in smaller fields. Medium-sized fields would be less successful because they are more thoroughly searched by predators. Working simultaneously on our study areas, Phillips et al. (2003, 2004) radio-collared and monitored movements of red fox and striped skunk (*Mephitis mephitis*), major nest predators on our study

TABLE 4. Models examined to explain variation in duck nest fate ($n = 1423$ nests with known UTM coordinates) in central North Dakota during the 1996–1997 breeding seasons.

Model	R^2	AIC	Δ AIC
Landscape type + distance to field edge + exposure days + year + (landscape type \times distance to field edge)	0.29	1305	0
Landscape type + distance to field edge + exposure days + year	0.29	1309	5
Landscape type + distance to field edge + exposure days	0.28	1334	25
Landscape type + distance to field edge	0.07	1689	384

Notes: A logistic regression model was used with two fates: successful or unsuccessful. Both main effects involved in the interaction were forced to be included in the model.

TABLE 5. Logistic regression models of the probability of an individual duck nest hatching ($n = 1423$ nests with known UTM coordinates) and distance to nearest field edge (measured in meters), year, and number of exposure days, for study areas with low- or high-grassland composition, in central North Dakota during the 1996 and 1997 breeding seasons.

Model and variable	Parameter estimate	SE	<i>P</i>
Low-grassland study areas ($R^2 = 0.31$)			
Intercept	1355.1	603.0	0.025
Distance to field edge	-0.0011	0.0020	0.580
Year	-0.6809	0.302	0.024
Exposure days	0.2459	0.0228	<0.001
High-grassland study areas ($R^2 = 0.23$)			
Intercept	2085.6	410.1	<0.001
Distance to field edge	-0.002	0.000522	<0.001
Year	-1.0459	0.2055	<0.001
Exposure days	0.1264	0.0109	<0.001

Note: Two models are presented because there was an interaction between landscape type and distance to field edge.

areas. The analyses of habitat selection and movement patterns of mammalian predators, recorded simultaneously with duck nest success in our study areas, revealed that these predators spent a disproportionately large amount of activity in medium-sized fields (Phillips et al. 2003).

Consistent with the curvilinear relationships and the literature on forest systems (e.g., Donovan et al. 1997), we found that distance to field edge was predictive of nest success in high-grassland landscapes, but not in low-grassland landscapes. As a mechanism for this relationship, we predicted and observed that predator activity levels would be different in the two types of study area. Specifically, we expected different predator activity levels within the edges and cores of planted-cover fields in the low- and high-grassland study areas (Phillips et al. 2003, 2004). Phillips et al. (2003) found that red foxes used the planted-cover core less frequently in the high-grassland study areas than in the low-grassland study areas (core area was defined as planted cover >50 m from the field edge). Large amounts of pastureland and planted cover in high-grassland study areas provided additional foraging opportunities for foxes, but also provided more cover for ducks, thereby resulting in greater nest success far from field edges. Thus, the interaction that we detected between probability of hatching, study-area type, and distance to nearest field edge, is due in part to differences in predator movement patterns within contrasting study-area types.

Increased probability of hatching among nests far (i.e., hundreds of meters) from edges also may have been affected by differences in the predator community. Duck nest success is greater in areas occupied by coyotes than it is in areas occupied by red foxes (Sovada et al. 1995). Coyotes often occupy landscapes with large amounts of grassland away from human activity (Greenwood et al. 1995), but where coyotes and red foxes occur together, foxes are typically found around the periphery of coyote home ranges (Sargeant

et al. 1987). Thus, lower nest success occurs along the periphery of large fields, where red fox are most likely to be active. Previous studies of duck nest success related to distance from edges have found inconsistent effects (Pasitschniak-Arts and Messier 1995, 1996, Pasitschniak-Arts et al. 1998), probably, in part, because they were unable to account for differences in predator activity.

In addition to field edges, we expected to find lower nest success close to wetland edges. Recent studies conducted in the Prairie Pothole Region (current study, Pasitschniak-Arts et al. 1998) have not detected an effect of wetland edges, whereas previous studies had suggested that nests destroyed by predators were more likely to be closer to water (Keith 1961). The study of predators by Phillips et al. (2003, 2004) suggested that success should be low near wetlands because activity levels of striped skunks and red foxes were high within 50 m of wetland edges. In the current study, distances between wetland edges and nests were relatively short, and few nests in the sample were far from wetland

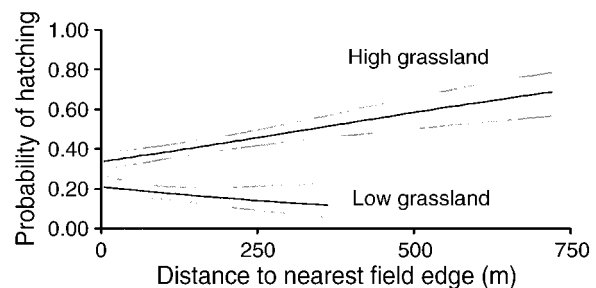


FIG. 2. Relationships between probability of an individual duck nest hatching ($n = 1423$ nests with known UTM coordinates) and distance to nearest field edge in landscape types with high- and low-grassland composition in central North Dakota in 1996–1997. Plotted incidence functions include the 95% confidence limits of expected values of the mean for each distance to nearest field edge. The relationships may be a result of different red fox activity levels in cores of high- and low-grassland composition landscapes.

edges, making it difficult to detect an effect on the probability of hatching. Only 54 nests were >300 m from wetland edges; for comparison, the effects that we detected related to field edges were negligible at distances <380 m. Thus, before distance to wetland edge can be discounted as a factor influencing the probability of hatching, additional studies should examine the relationship between predator behavior and the fate of nests in relation to the spatial arrangement of wetlands.

Often the inconsistency of observations of distance-to-edge relationships is related to the sampling constraints imposed by the landscape. For example, Pasitschniak-Arts et al. (1998) primarily sampled fields that were small enough (i.e., 20–64 ha, with maximum distance of a nest to a habitat edge being 150 m) to be effectively searched by mammalian predators. We did not sample fields larger than 192 ha, nor did we find nests >379 m from the nearest field edge in low-grassland study areas. It would be valuable to determine, in low-grassland study areas, if mean nest success is high in very large fields (i.e., >600 ha) due to increases in nest success very far from field edges. However, because landscape composition and configuration tend to be related, very large fields are rare in low-grassland landscapes.

The landscape surrounding a patch is an important determinant influencing bird communities (Wiens 1989). Regional abundance of perennial grassland influences duck nest success (Greenwood et al. 1995, Reynolds et al. 2001) as well as predator community composition (Sargeant et al. 1993, Sovada et al. 1995). In general, grassland bird conservation has emphasized preserving landscapes with large tracts of remaining grassland, or restoring extensive grassland, to enhance the success of ground-nesting birds. Results from this study and others (Reynolds et al. 2001, Herkert et al. 2003) demonstrate the importance of protecting large habitat patches within landscapes having a high composition of that habitat. This strategy rests on the fact that, in landscapes composed of >50% grassland configured in large fields, not only does the predator community differ, but also predator foraging behavior is diluted, thus increasing the probability of hatching of individual nests.

In part, grassland conservation efforts have been limited by a lack of understanding of the mechanisms that link landscape pattern, nesting success of grassland birds, and predation. This study of duck nest success, coupled with the complementary studies on predators by Phillips et al. (2003, 2004), provides conservationists with some understanding of the importance of processes related to landscape configuration that influence the complex relationships between nesting birds and predation. The prediction that nest survival rates in small patches are often as great as in very large patches certainly does not mean that conservation strategies can ignore patch size, because there are relatively few nests

in small patches. However, it does enhance our understanding of the importance of landscape configuration in determining predator–prey dynamics. For example, this study suggests that we should question conservation strategies that favor clustering medium-sized patches within agricultural landscapes, both because of patch size and edge relationships. Our results show that such patches would have low nest success, largely due to predation. It remains to be seen if the patterns of reproductive success observed in this study have more general relevance. Our results are not taxon-specific and are likely to reflect the interactions of many large ground-nesting grassland birds and their predators.

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APPENDIX

A table showing characteristics of fields in study areas in central North Dakota during the 1996 and 1997 breeding seasons is available in ESA's Electronic Data Archive: *Ecological Archives* A015-037-A1.